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THÈSE PRÉSENTÉE

POUR OBTENIR LE GRADE DE

**DOCTEUR DE
L'UNIVERSITÉ DE BORDEAUX**

ÉCOLE DOCTORALE SCIENCE ET ENVIRONNEMENTS
SPÉCIALITÉ ÉCOLOGIE ÉVOLUTIVE, FONCTIONNELLE ET DES COMMUNAUTÉS

Par Nicolas LAVESQUE

**Révision des vers spaghetti (Annélides, Terebellidae *sensu lato*)
des côtes françaises**

**Revision of spaghetti worms (Annelida, Terebellidae *sensu lato*)
from the French coasts**

Sous la direction de : Xavier de MONTAUDOUIN et Pat HUTCHINGS

Soutenue le 09 novembre 2021

Membres du jury :

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Mr GILLET Patrick, Professeur Université Catholique de l'Ouest, Angers	Rapporteur
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Révision des vers spaghetti (Annélides, Terebellidae *sensu lato*) des côtes françaises

Résumé :

Cette thèse a pour objectif de réviser la taxonomie des espèces françaises d'annélides polychètes appartenant aux cinq familles des Terebellidae *sensu lato* (Polycirridae, Telothelepodidae, Terebellidae *sensu stricto*, Thelepodidae et Trichobranchidae). Ces vers spaghetti sont caractérisés par la présence de nombreux tentacules buccaux non rétractables servant à leur nutrition et leur assurant un régime dépositivore.

Les individus étudiés dans le cadre de cette thèse ont été prélevés lors de différents projets de recherche et d'observation menés par les équipes hébergées dans les stations marines françaises, mais également lors d'échantillonnages spécifiques. Des matériels types, archivés au Museum National d'Histoire Naturelle, ont également été empruntés. Cette étude est au centre du « Spaghetti Project », projet collaboratif impliquant les taxonomistes benthiques des différentes stations marines françaises (RESOMAR, RESeau des Stations et Observatoires MARins).

Les eaux côtières françaises sont des zones étudiées depuis plusieurs siècles par les premiers taxinomistes et les écologistes benthiques. Cependant, l'étude de nombreux spécimens de vers spaghetti à l'aide de nouveaux outils, comme la microscopie électronique à balayage ou l'analyses moléculaire, a révélé l'existence de 31 espèces nouvelles pour la science.

Ces espèces ont probablement « toujours » été présentes le long des côtes mais mal identifiées pendant des décennies. Plusieurs raisons peuvent expliquer ces lacunes. La première est que ces vers sont extrêmement complexes à identifier car les caractères morphologiques nécessitent des observations pointues et des outils modernes. Deuxièmement, la plupart des espèces européennes ont été décrites aux 18^{ème} et 19^{ème} siècles. Les standards taxonomiques de l'époque étaient très différents, avec des descriptions très brèves et des illustrations (quand elles étaient présentes) de qualité médiocre. De plus, les matériels types étaient rarement déposés dans une collection d'un muséum, et quand ils l'étaient ont malheureusement souvent été endommagés ou perdus, empêchant des comparaisons avec des spécimens nouvellement collectés. Enfin, il y a eu jusque dans les années 1980, une idée largement répandue selon laquelle les espèces de polychètes à large distribution étaient très communes. L'étude de ces espèces soi-disant cosmopolites a révélé l'existence de nombreuses espèces cryptiques dans le monde entier en général, et en France en particulier.

Mots clés :

Annélides Polychètes, taxinomie, nouvelles espèces, morphologie, analyses moléculaires, espèces cosmopolites, espèces cryptiques.

Revision of spaghetti worms (*Annelida, Terebellidae sensu lato*) of the French coasts

Abstract:

The objective of this thesis is to revise the taxonomy of the French species of polychaetes belonging to the five families of Terebellidae sensu lato (Polycirridae, Telothelepoidae, Terebellidae, Thelepodidae and Trichobranchidae). These spaghetti worms are characterised by the presence of multiple non-retractable buccal tentacles used for feeding (deposit feeders).

The specimens studied in this thesis were collected during different research and observation programs or specific samplings carried out by scientists in the different French laboratories. Type materials from the Museum National d'Histoire Naturelle were also loaned.

This study is at the heart of the “Spaghetti Project”, project involving benthic taxonomists from French marine stations (RESOMAR network).

French coastal waters are well-known areas, studied for several centuries by early taxonomists and benthic ecologists. However, studying numerous spaghetti worms with new tools, like scanning electron microscope and molecular analysis, has revealed the existence of 31 species new for science.

These species have probably “always” been present along the French coasts but misidentified for decades. Several reasons can explain this situation. First, these worms are relatively challenging to identify because of diagnostic characters requiring detailed examination and modern tools. Secondly, most of the European species were described in the 18 and 19th centuries. Taxonomic standards at that time were very different with very brief descriptions and illustrations (when present) of poor quality. Moreover, type material was rarely deposited in a museum collection, and when deposited subsequently often lost or damaged, preventing any comparison with specimens newly collected. Finally, until 1980s, there was a wide perception that widespread species were very common among polychaetes. Studying these so-called “cosmopolitan” species in detail reveals the existence of numerous cryptic species in different parts of the world, in France in particular.

Keywords:

Polychaeta, taxonomy, new species, morphology, molecular analysis, cosmopolitan species, cryptic species

“When seen alive in a glass of sea water (terebellids) are some of the most elegant creatures inhabiting the great deep.” (Parfitt, 1867)

“Mal nommer les choses, c’est ajouter du malheur au monde” Albert Camus

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La deuxième n'était absolument pas prévue. Mais quelle rencontre ! Ce jour-là, lors d'un atelier taxonomie à Caen, j'ai à la fois rencontré Pat Hutchings, la plus grande spécialiste mondiale des annélides polychètes (aka the Queen of Worms), mais aussi un incroyable mentor et une vraie amie. Je me rends compte tous les jours de la chance que j'ai de travailler avec toi. Nos échanges quotidiens par mail n'arrivent pas à faire passer le manque de nos sessions derrière la loupe binoculaire et nos « private coffees » à l'Australian Museum. Merci pour nous avoir accueillis en Australie, toi et Peter, comme des membres de votre famille. Merci pour le pique-nique de Noël, le feu d'artifice sur le Harbour Bridge aux premières loges avec bouteille de champagne, merci pour le week-end en voilier dans le Ku Ring Gai Park et j'en passe et des meilleurs. And don't forget, we are always playing a game (Hutchings, pers. comm.)

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Station Marine

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Un dernier mot

La dernière session de remerciements va évidemment à ma famille. Mes parents tout d'abord, qui m'ont toujours soutenu dans cette voie professionnelle hasardeuse. Je pense que mes travaux sur les « sables benthiques » et ces descriptions de nouvelles espèces vous ont rendus fiers, alors mission remplie !

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Synthèse

Quelle drôle d'idée ! Quelle drôle d'idée que d'étudier et de se passionner pour les annélides polychètes ? Pourquoi passer des heures à observer ces animaux d'apparence simple ? Comme l'aurait répondu Kristian Fauchald, le plus grand spécialiste des polychètes, la réponse évidente est : « just for fun ! ». En effet, derrière leur construction basique se cache une diversité de formes fascinantes, qui pourrait passionner n'importe quel biologiste. L'autre (vraie) réponse est que malgré des décennies d'études, et alors que la biodiversité de ce groupe zoologique était soi-disant bien connue, il reste encore énormément d'espèces à découvrir le long des côtes françaises avec malheureusement peu (pas) de spécialistes en France. La nature ayant horreur du vide, il semblait donc naturel de combler cette « niche scientifique » laissée vacante depuis les années 1980 et de se spécialiser dans la taxinomie de ces vers marins. Depuis la description des premières espèces d'annélides polychètes par Linnaeus en 1758 (Linnaeus 1758), plus de 12000 espèces valides appartenant à 1320 genres et 87 familles ont été décrites dans le monde (Read & Fauchald, 2021). En 2019, 138 espèces ont été décrites (Magalhães *et al.* 2021) et des modélisations récentes estiment qu'environ 5200 espèces seront encore décrites d'ici la fin du siècle (Pamungkas *et al.* 2019).

I- Un peu d'histoire française

En France, l'étude des annélides polychètes par les naturalistes et les premiers explorateurs est une histoire qui remonte aux balbutiements de cette discipline. C'est d'ailleurs le Français Jean-Baptiste Pierre Antoine de Monet de Lamarck (1744-1829) qui revendique la paternité du Phylum des Annélides (décrit à l'époque comme Classe). En effet, c'est lors de son grand discours annuel au musée de Paris en 1802 que Lamarck s'est adressé aux citoyens de la République Française pour présenter et définir les Annélides (Lamarck 1802 ; Read 2019). Ce naturaliste a été un des créateurs de la biologie en tant que science et un des précurseurs de la théorie de l'évolution en proposant l'adaptation des êtres vivants à leurs milieux. Pour en revenir aux annélides, c'est lui qui a également créé en 1818 les deux grandes sous-classes de polychètes : les sédentaires vivant en général dans des tubes et les errantes capables de se déplacer (Lamarck 1818). Aux 18^{ème} et 19^{ème} siècles, la polychaetologie était florissante en France avec différents « encyclopédistes » qui se sont succédés au Muséum National d'Histoire Naturelle de Paris. Parmi les plus influents, Lamarck a décrit une centaine d'espèces dans son « Histoire Naturelle des animaux sans vertèbres » (Lamarck 1818), même si seulement 37 de ces espèces sont reconnues valides aujourd'hui. L'aventureux Jules-César Savigny (1777 - 1851) a lui suivi les troupes de Napoléon lors des campagnes égyptiennes et décrit 14 espèces de cette région (Savigny 1822 ; Read 2019). Le baron Arthur d'Anthoine de Saint-Joseph (1829-1911) attiré par les marées d'amplitudes exceptionnelles de Dinard a passé neuf étés à échantillonner les annélides des plages et îles de cette région, lui permettant de décrire 32 espèces (e.g. Saint-Joseph 1888 ; 1894). Nous pouvons également citer le binôme Jean Victor Audouin, (1797-1841, entomologiste) et Henri Milne Edwards (1800-1885, d'origine anglaise) qui ont décrit 14 espèces en France (Audouin & Milne Edwards 1834) (Solis-Weiss *et al.* 2004). Le plus prolifique d'entre tous fut probablement Jean-François de Quatrefages de Bréau (1767-1858) qui décrit 129 espèces, la plupart dans son « Histoire naturelle des Annelés marins et d'eau douce » (de Quatrefages 1866). Ce médecin, féru de sciences, obtiendra quatre thèses de

doctorat : une en balistique (sur la « Théorie des coups de canons »), une sur le « Mouvement des aérolithes considérés comme des masses disséminées dans l'espace par l'impulsion des volcans lunaires », une autre en médecine (sur « l'extroversion de la vessie ») et finalement une en sciences naturelles (sur « les caractères zoologiques des rongeurs et sur leur dentition en particulier »). Passionné d'anthropologie, c'est également lui, en collaboration avec Ernest Hamy, qui définit la « race » de Cro-Magnon en 1874 (Quatrefages & Hamy 1874).

Lors du 20^{ème} siècle, quelques taxonomistes se sont également distingués en décrivant de nombreuses espèces en France mais aussi et surtout à travers le monde. Charles Gravier a en effet décrit plus de 100 nouvelles espèces mais aucune des côtes de France métropolitaine. La plupart de son matériel type provenait de la Mer Rouge (e.g. Gravier 1900) ou de différentes expéditions telle que l'expédition Antarctique Française du *Pourquoi-Pas*, dirigée par le commandant Charcot de 1908 à 1910 (Gravier 1911 ; Solis-Weiss *et al.* 2004). La référence absolue reste l'abbé Pierre Fauvel (1866-1958), professeur de zoologie à l'Université catholique d'Angers. Sa faune de France consacrée aux polychètes errantes (Fauvel 1923) et sédentaires (Fauvel 1927) des côtes françaises est utilisée depuis plus d'un siècle dans les laboratoires et bureaux d'études du monde entier (Lavesque *et al.* 2021). Durant sa carrière, Fauvel a décrit 141 espèces de polychètes, mais de façon surprenante seulement quatre en France. Ses études ont surtout été réalisées en Inde (e.g. Fauvel 1932) et en Afrique (e.g. Fauvel 1918). Pour la petite histoire, Fauvel était également un passionné de cyclisme et écrivait des chroniques sous un pseudonyme (Hollow-Rim) dans la revue *Le Cycliste* (Solis-Weiss *et al.* 2004). Plus récemment, une poignée de taxonomistes a décrit des espèces de polychètes. Au sein de l'école angevine, nous pouvons citer François Rullier (1907-1981) qui succéda à Fauvel et qui fut lui aussi Doyen de la faculté de Sciences (Gillet 2016). Il décrit 48 espèces, dont certaines provenant des campagnes océanographiques de la *Calypso* du commandant Cousteau, mais aucune de France. A Angers toujours, Louis Amoureux (1919-2001) participa notamment aux campagnes de l'*Albatros* en Italie et de la *Thalassa* en Espagne et en France, et décrit 25 espèces mais seulement trois en France. Plus récemment, nous retrouvons Lucien Laubier (1936-2008) qui fut professeur de biologie marine et d'océanographie à l'Université de Marseille et à l'Institut Océanographique de Paris (58 espèces, dont 24 en France). Michel Bhaud (1940-2012), chercheur à Banyuls-sur-Mer, a beaucoup étudié le recrutement et le comportement des annélides polychètes, des térebelliens en particulier (Lavesque *et al.* 2021). Il a également publié 14 espèces nouvelles pour la science, aucune de France, tout comme Patrick Gillet, professeur à l'Université Catholique d'Angers qui a décrit sept espèces mais aucune en France métropolitaine. Enfin, Daniel Desbruyères (retraité du Département études des écosystèmes profonds, Ifremer Brest) et Stéphane Hourdez (chercheur CNRS au laboratoire LECOB, Banyuls-sur-Mer) sont spécialistes des annélides polychètes vivant au niveau des sources hydrothermales marines. Ils ont décrit 38 et 19 espèces respectivement de ces milieux profonds. Pour conclure sur cet aspect historique, cette spécialité a fortement décliné depuis 1980, en lien avec le départ à la retraite des taxonomistes seniors et leur non remplacement dans les laboratoires universitaires, CNRS ou MNHN. Cette absence de spécialistes se traduit par le faible nombre d'espèces décrites en France, avec seulement huit descriptions depuis 1980 (Amoureux & Dauvin, 1981 ; Cantone & Bellan, 1996 ; Dauvin & Lee, 1983 ; Fauchald *et al.* 2012 ; Jourde *et al.* ; 2015 ; Olivier *et al.* 2012a, b),

II- Les vers spaghetti

Comme nous venons de le voir, l'étude des polychètes a longtemps été réservée aux naturalistes. Depuis quelques années, les études d'écologie benthique ont cependant montré qu'ils jouaient un rôle essentiel dans la plupart des écosystèmes marins, en particulier dans les fonds meubles, qu'ils dominent à la fois en terme de diversité mais également d'abondance (Capa & Hutchings 2021 ; Magalhães *et al.* 2021). Ces annélides sont présents de la zone intertidale aux fond abyssaux, des zones polaires aux zones équatoriales et jouent un rôle essentiel dans la plupart des réseaux trophiques marins grâce à des stratégies alimentaires très variées (Capa & Hutchings 2021). Certaines de ces espèces ont une réelle importance économique (comme appâts pour la pêche ou nourriture pour les poissons d'élevage) (Lavesque *et al.* 2017 ; Gillet 2016 ; Read 2019) ; d'autres peuvent avoir des intérêts thérapeutiques (transport d'oxygène par des hémoglobines dérivées du sang d'arénicole ; Batool *et al.* 2021), d'autres encore peuvent servir de bio-indicateurs (Gillet 2016; Capa & Hutchings 2021).

Parmi les polychètes, les vers spaghetti appartenant aux Terebellidae Johnston, 1846 *sensu lato* (*s.l.*), occupent une place importante par leur nombre d'espèces extrêmement important (environ 730 espèces et 67 genres) (Read & Fauchald 2021) et leur présence dans la plupart des écosystèmes marins (Hutchings *et al.* 2021a, b). Les Trichobranchidae, après avoir longtemps été considérés comme une sous-famille des Terebellidae (Fauvel 1927 ; Garraffoni & Lana 2004), sont maintenant reconnus comme une famille valide (Glasby *et al.* 2004 ; Lavesque *et al.* 2019). Le statut des autres Terebellidae est lui beaucoup plus complexe. Ils regroupent quatre familles précédemment considérées comme des sous-familles mais dont Nogueira *et al.* (2013) ont montré qu'elles avaient évolué indépendamment : les Polycirridae Malmgren, 1866, les Terebellidae Johnston, 1846 *sensu stricto* (*s.s.*), les Thelepodidae Hesse, 1917, ainsi que la famille des Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 récemment décrite (Nogueira *et al.* 2013; Hutchings *et al.* 2021a). Même si un consensus est loin d'être atteint au sein de la communauté scientifique (Stiller *et al.* 2020), le Spaghetti Project et ce mémoire de thèse suivent la division des vers spaghettis en cinq familles comme proposés par les taxonomistes spécialistes de ce groupe (Nogueira *et al.* 2013 ; Hutchings *et al.* 2021a, b).

Les vers spaghettis sont caractérisés par la présence de nombreux tentacules buccaux utilisés pour une nutrition sélective de la matière organique. Ces tentacules, originaires du prostomium (partie antérieure de la tête), sont en général lisses, non rétractables dans la bouche et traversés d'une gouttière sur toute leur longueur. Ces gouttières munies de cils microscopiques permettent d'acheminer les particules alimentaires, du sédiment vers la bouche. Ce comportement alimentaire consistant à remobiliser de grandes quantités de sédiments modifie les propriétés physiques et chimiques des écosystèmes benthiques (Maire *et al.* 2007 ; Ziegler *et al.* 2020). En particulier, les vers spaghetti ont un impact important sur les taux de matière organique à l'interface eau-sédiment (Jumars & Nowell 1984). La plupart des espèces sont sédentaires et vivent dans des tubes robustes, dans le sédiment ou le plus souvent attachés à des substrats rocheux ou des coquilles (Hutchings *et al.* 2021b). Certaines espèces sont retrouvées en agrégations denses et peuvent même former des structures biogéniques comme les banquettes à *Lanice conchilega* et sont alors considérées comme des ingénieurs de l'écosystème (Rabaut *et al.* 2009). La plupart des espèces ont au contraire des distributions isolées (Hutchings *et al.* 2021b).

La taille des vers spaghetti varie de quelques millimètres à plusieurs dizaines de centimètres (Lavesque *et al.* 2017b). Ces animaux sont dioïques, sans différences

morphologiques entre les mâles et les femelles, excepté pendant la période de reproduction durant laquelle les gamètes matures peuvent colorer le corps des femelles de teintes rosâtres ou verdâtres alors que les mâles restent typiquement couleur crème (Hutchings *et al.* 2021b). Jusqu'à présent, aucune multiplication asexuée n'a été observée chez ces individus mais ils sont capables de régénérer leurs parties postérieures, leurs branchies ou bien encore leurs tentacules buccaux. Les gamètes sont libérés dans la cavité cœlomique où se déroulent la vitellogenèse ou la spermatogénèse. Les gamètes sont ensuite relâchés dans l'eau de façon synchrone, pendant des périodes de quelques jours à plusieurs mois (Hutchings *et al.* 2021b). Les vers spaghetti possèdent différentes stratégies de reproduction comme l'émission de larves lecitrophiques, l'incubation d'œufs à l'intérieur du tube, ou le développement d'embryons dans des cocons gélatineux (Hutchings *et al.* 2021a). Peu d'études ont été menées sur les stades larvaires des térébelliens mais celles-ci montrent des variations importantes, avec l'existence de larves benthiques, pélagiques pour quelques heures, ou de juvéniles qui peuvent s'installer à différents stades de maturation (de un à plusieurs segments développés) (Hutchings *et al.* 2021a). Il peut également y avoir un développement direct dans un cocon avant qu'un juvénile ne soit relâché directement dans l'eau (McHugh & Tunnicliffe 1993).

III- le Spaghetti Project

Ce projet a été lancé après avoir réalisé que la taxinomie des vers spaghetti en France, mais également en Europe, était très mal documentée. En effet, le manque de littérature adéquate et l'absence de clés d'identification facilement utilisables et à jour a conduit à des identifications erronées pendant des décennies. En 2016, un workshop national avait été organisé à Arcachon avec Mario Londoño-Mesa (Université d'Antioquia, Medellin, Colombie) et un atelier taxonomique du Réseau des Stations et Observatoires Marins (RESOMAR) à Caen avec Pat Hutchings (Australian Museum de Sydney). Après l'observation de plusieurs individus en compagnie de ces deux experts mondialement reconnus, nous avons réalisé que de nombreuses espèces méritaient d'être analysées en détail. Ce projet collaboratif impliquant tous les benthologues du RESOMAR visait à réviser toutes les espèces de Terebellidae (*s.l.*) des côtes françaises en se basant à la fois sur des individus en collection dans les laboratoires et au MNHN de Paris mais également sur du matériel frais échantillonné pour l'occasion. Au total, plus de 400 spécimens ont pu être observés, plus de 100 séquences moléculaires obtenues et 31 nouvelles espèces décrites.

Le Spaghetti Project et cette thèse s'articulent autour de six articles scientifiques principaux et trois articles en annexe.

Introduction

Hutchings P., Carrerette O., Nogueira J.M.N.N., Hourdez S., Lavesque N. (2021) The Terebelliformia - recent developments, future directions. *Diversity* 13, 60.

Cet article a été publié dans une série spéciale consacrée à la systématique et la biodiversité des principales familles d'annélides. Cet article présente l'historique de la taxinomie des annélides appartenant aux Terebelliformia, leur morphologie, leurs relations phylogénétiques, leurs rôles dans les écosystèmes, et leur distribution à l'échelle mondiale et l'évolution des méthodes

utilisées pour les décrire. Cette étude a également permis d'identifier les zones d'ombre qui subsistaient dans leur étude, les défis pour le futur, et enfin comment ces données de biodiversité pouvaient être utilisées par les gestionnaires de l'environnement.

Chapitre 1 - Révision des Trichobranchidae

Lavesque N., Hutchings P., Daffe G., Nygren A., Londoño-Mesa M.H. (2019). A revision of the French Trichobranchidae (Polychaeta), with descriptions of nine new species. *Zootaxa* 4664(2): 151-190.

Cet article, le premier dédié à la taxinomie, a permis d'observer et de redécrire deux espèces connues des eaux européennes (*Octobranchus lingulatus* (Grube, 1863) et *Trichobranchus glacialis* Malmgren, 1866) et de décrire neuf nouvelles espèces pour la science : *Terebellides bonifi* **n. sp.**, *Terebellides ceneresi* **n. sp.**, *Terebellides europaea* **n. sp.**, *Terebellides gentili* **n. sp.**, *Terebellides gralli* **n. sp.**, *Terebellides lilasae* **n. sp.**, *Terebellides resomari* **n. sp.**, *Terebellides parapari* **n. sp.** et *Trichobranchus demontaudouini* **n. sp.**

Chapitre 2 - Révision des Telothelepodidae and Thelepodidae

Lavesque N., Londoño-Mesa M.H., Daffe G., Hutchings P. (2020a). A revision of the French Telothelepodidae and Thelepodidae (Annelida, Terebelliformia), with descriptions of three species and first European record of a non-indigenous species. *Zootaxa* 4810 (2) 305-327.

Cet article a permis d'observer et de redécrire une seule espèce connue des eaux européennes (*Parathelepus collaris* (Southern, 1914)), de détecter pour la première fois en Europe une espèce originaire d'Asie (*Thelepus japonicus* Marenzeller, 1884) et de décrire trois nouvelles espèces pour la science : *Streblosoma cabiochi* **n. sp.**, *Streblosoma lindsayae* **n. sp.** et *Thelepus corsicanus* **n. sp.**

Chapitre 3 - Révision des Polycirridae

Lavesque N., Hutchings P., Daffe G., Londoño-Mesa M.H. (2020b) Revision of the French Polycirridae (Annelida, Terebelliformia), with descriptions of eight species. *Zootaxa* 4869 (2): 151-186.

Cet article a permis de redécrire une seule espèce connue des eaux européennes (*Polycirrus denticulatus* Saint-Joseph, 1894), et de décrire huit nouvelles espèces pour la science : *Amaeana gremarei* **n. sp.**, *Polycirrus catalanensis* **n. sp.**, *Polycirrus glasbyi* **n. sp.**, *Polycirrus gujanensis* **n. sp.**, *Polycirrus idex* **n. sp.**, *Polycirrus nogueirai* **n. sp.**, *Polycirrus pennarbedae* **n. sp.** et *Polycirrus readi* **n. sp.**

Chapitre 4 - Révision des Terebellidae sensu stricto

Lavesque N., Daffe G., Londoño-Mesa M.H., Hutchings P. (2021a) Revision of the French Terebellidae sensu stricto (Annelida, Terebelliformia), with descriptions of nine species. *Zootaxa*, 5038 (1): 1-63.

Dans ce dernier article taxinomique, huit espèces connues des eaux européennes ont pu être observées (*Amphitrite edwardsi* (Quatrefages, 1866), *Amphitrite figulus* (Dalyell, 1853), *Amphitritides gracilis* (Grube, 1860), *Lanice conchilega* (Pallas, 1766), *Loimia ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017, *Pista colini* Labrune, Lavesque, Bonifácio & Hutchings, 2019, *Pista mediterranea* Gaillande, 1970 et *Terebella lapidaria* Linnaeus, 1767). Neuf nouvelles espèces pour la science ont également été décrites : *Eupolymnia gili* n. sp., *Eupolymnia lacazei* n. sp., *Eupolymnia meissnerae* n. sp., *Lanice kellyslateri* n. sp., *Paramphitrite dragovabeci* n. sp., *Pista labrunae* n. sp., *Pista miossecci* n. sp., *Pista sauriaui* n. sp. et *Terebella banksyi* n. sp.

Discussion et perspectives

Lavesque N., Hutchings P., Londoño-Mesa M., Nogueira J.M.M., Daffé G., Nygren A., Blanchet H., Bonifácio P., Broudin C., Dauvin J.C., Droual G., Gouillieux B., Grall J., Guyonnet B., Houbin C., Humbert S., Janson A.L., Jourde J., Labrune C., Lamarque B., Latry L., Le Garrec V., Pelaprat C., Pézy P., Sauriau P.G., de Montaudouin X (2021b). The Spaghetti Project: the final guide of identification of European Terebellidae (sensu lato) (Annelida, Terebelliformia). *European Journal of Taxonomy*, 782: 108-156.

Cet article qui implique tous les participants du Spaghetti Project permet de conclure le projet en fournissant des clés d'identifications pour toutes les espèces de térebéliens en Europe, clés qui pourront être à la fois utilisées par les taxinomistes mais également par les gestionnaires et bureaux d'études. Cet article permet également de discuter des principaux résultats obtenus pendant ce projet. En particulier il permet d'expliquer pourquoi autant de nouvelles espèces ont pu être décrites dans des zones côtières si bien connues des scientifiques depuis plusieurs centaines d'années. Il essaye également de montrer à quel point il est important de savoir différencier des espèces en apparence similaires et ce que cela implique en termes de biodiversité, d'écologie, de management et de risques environnementaux. Enfin, il ouvre sur des perspectives, en ciblant les zones encore peu connues en France mais également en imaginant ce qui pourrait être réalisé à l'échelle européenne.

Annexes

Lavesque N., Bonifácio P., Londoño-Mesa M.H., Le Garrec V., Grall J. (2017). *Loimia ramzega* sp. nov., a new giant species of Terebellidae (Polychaeta) from French waters (Brittany, English Channel). *Journal of the Marine Biological Association of the United Kingdom* 97(5) 935-942.

Labrune C., **Lavesque N.**, Bonifácio P., Hutchings P. (2019). A new species of *Pista* Malmgren, 1866 (Annelida, Terebellidae) from the Western Mediterranean Sea. *Zookeys* 838: 71-83.

Nygren A., Parapar J., Pons J., Meißner K., Bakken T., Kongsrud J.A., Oug E., Gaeva D., Sikorski A., Johansen R.A., Hutchings P., **Lavesque N.**, Capa M. (2018). A megacryptic species complex hidden among one of the most common annelids in the North East Atlantic. *Plos One*.

En amont de ce projet, j'avais décrit en 2017 une espèce de Terebellidae des côtes bretonnes (Lavesque *et al.* 2017) et participé à la description d'une autre espèce de Terebellidae du Golfe du Lion (Labrune *et al.* 2019). Ces deux articles m'ont permis de me rendre compte de la biodiversité cachée des vers spaghetti le long des côtes françaises et d'imaginer ce Spaghetti Project. Ma participation à une étude européenne (Nygren *et al.* 2018) sur une autre espèce de Terebellidae (*Terebellides stroemii* Sars, 1835), uniquement basée sur de la biologie moléculaire m'a permis de prendre conscience de l'importance de cet outil en taxinomie moderne. En effet, après avoir analysé des centaines de spécimens appartenant à cette soi-disant espèce cosmopolite, nous nous sommes rendus compte que nous avions finalement 25 espèces différentes.

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INTRODUCTION





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Eupolymnia lacazei Lavesque, Daffe, Londoño-Mesa & Hutchings 2021

Review

The Terebelliformia-Recent Developments and Future Directions

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Abstract: Terebelliformia comprises a large group of sedentary polychaetes which live from the intertidal to the deep sea. The majority live in tubes and are selective deposit feeders. This study synthesises the current knowledge of this group, including their distribution, in the different biogeographic regions. We highlight the new methodologies being used to describe them and the resolution of species complexes occurring in the group. The main aim of this review is to highlight the knowledge gaps and to stimulate research in those directions, which will allow for knowledge of their distribution and abundances to be used by ecologists and managers.



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Keywords: Annelida; polychaetes; biodiversity assessment; geographical distribution; methods; knowledge gaps

1. Introduction

This review of the diversity of the Terebelliformia deals with the taxa previously considered as subfamilies of the Terebellidae Johnston, 1846, namely Polycirridae Malmgren, 1866, Terebellidae Johnston, 1846 (previously referred to as the Amphitritinae) and Thelepodidae Hesse, 1917, together with the closely related family Trichobranchidae Malmgren, 1866, and the recently described family Telothelepodidae Nogueira, Fitzhugh and Hutchings, 2013. For a detailed discussion of the elevation of the subfamilies of the Terebellidae sensu lato (s.l.) to family level, see Nogueira et al. [1] and Hutchings et al. [2]. As well, we include Alvinellidae Desbruyères and Laubier, 1986, Pectinariidae Johnston, 1865 and Ampharetidae Malmgren, 1866, which are all included within the Terebelliformia.

Terebelliformia are common worldwide, including the polar regions, and may be abundant in some areas [3–5]. While some genera are highly speciose, others are represented by few species or only by a single one (for details of genera and numbers of species, see [2] for terebellids, see [6] for pectinariids, see [7] for alvinellids and [8] for ampharetids).

Members of this diverse group are characterised by the presence of multiple grooved buccal tentacles used for selective deposit feeding. Although it is still debatable whether those structures are homologous among all the families of Terebelliformia, we assume they are [1,9] and, therefore, all are of prostomial origin. Due to the extensible characteristic of these structures, they can be easily recognized around their tubes or galleries, rendering these animals the name “spaghetti worms” (Figures 1–3). Typically, the tentacles are smooth, but some polycirrids have papillose tentacles and ampharetids may also have

also discuss the major gaps in our knowledge of Terebellomorpha and their phylogeny, including some taxonomic issues, and point to directions to solve them, as well as highlighting other issues which need to be addressed.

The aims of this paper are (1) to present the taxonomic history of these worms, (2) their morphology, (3) the recent studies on their phylogenetic relationships, (4) their roles in the ecosystem and their distribution around the world, (5) the evolution of the methods used to describe them, (6) the knowledge gaps and challenges for the future, with focus on species complexes and taxonomic issues and finally, (7) how such data can be used in marine park management as well as comments regarding the importance of using correct names. (Figure 1e–g).

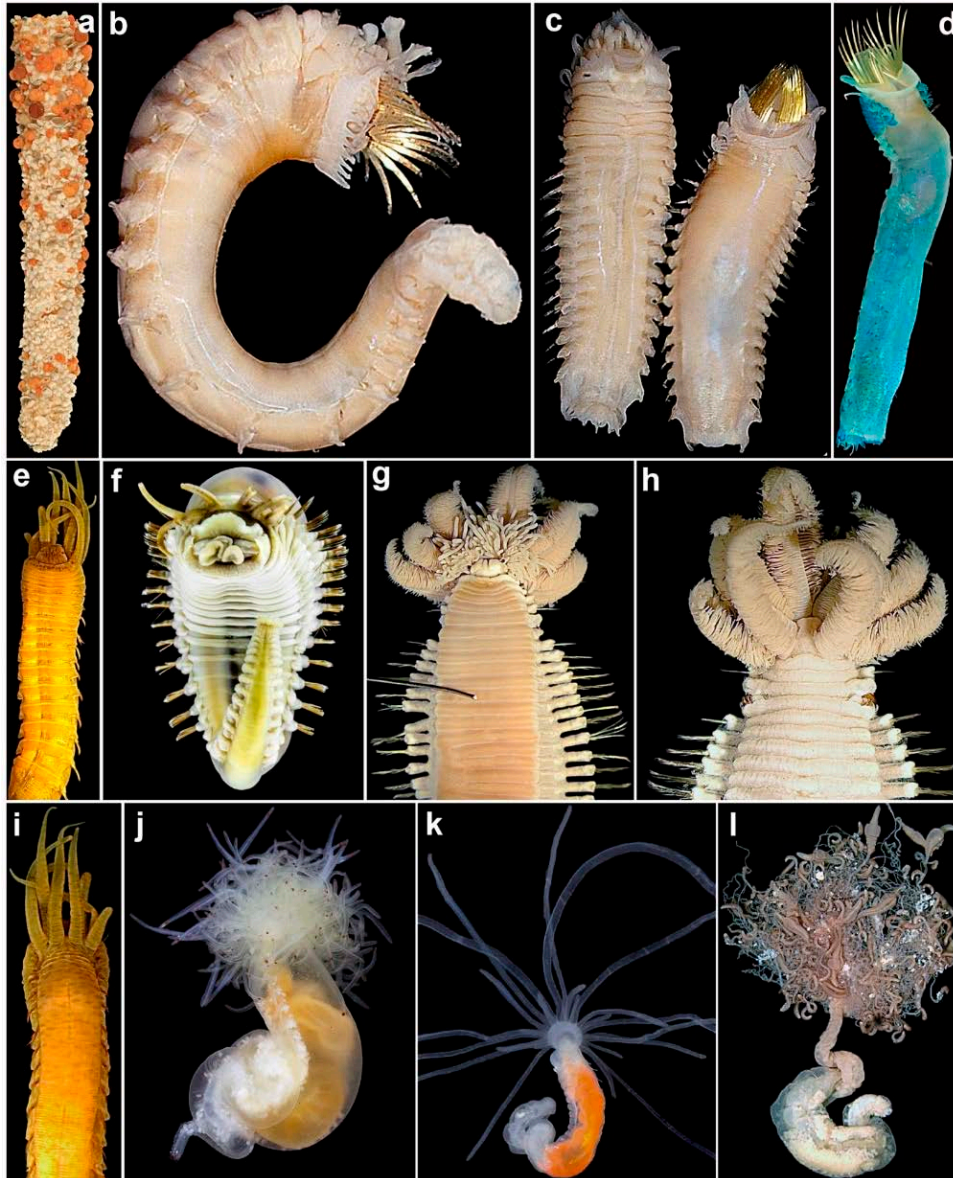


Figure 1. Diversity of Terebellidae (PE), Pectopliantidae (PE), Ampharetidae (AM), Alvinellidae (AL) and Bobyriidae (PO). (a) *Petta investigatoris* (PE) in tube; (b) *Petta investigatoris* (PE): worm, ventral (left) and dorsal (right) views; (c) *Dania* (PE) worm; (d) *Petta investigatoris* (PE): entire worm, dorsal view stained in methyl green; (e,i) *Amphicteis dalmatica* (paratype AM W.11667) (AM): anterior end, ventral and dorsal views, respectively; (f) *Amythas membranifera* (AM): entire worm, ventral view; (g,h) *Alvinella pompejana* (AM W.29585) (AL): anterior end, ventral and dorsal views, respectively; (j) *Polycirrus oculus* (paratype AM W.44612) (PO): entire live worm, dorso-lateral view; (k) *Polycirrus rubrointestinalis* (PO): entire worm live, dorsal view; (l) *Hauchiella tentaculata* (holotype NTM W.023154) (PO): entire live worm, dorsal ventral view. Photos: (d)—E. Wong; (f)—Gabriel Monteiro; (j–l)—A. Semenov.

left lateral view; (e) *Petta pusilla* (PE): entire worm, dorsal view stained in methyl green; (e,i) *Amphicteis dalmatica* (paratype AM W.11667) (AM): anterior end, ventral and dorsal views, respectively; (f) *Amythas membranifera* (AM): entire worm, ventral view; (g,h) *Alvinella pompejana* (AM W.29585) (AL): anterior end, ventral and dorsal views, respectively; (j) *Polycirrus oculus* (paratype AM W.44612) (PO): entire live worm, dorso-lateral view; (k) *Polycirrus rubrointestinalis* (PO): entire worm live, dorso-lateral view; (l) *Hauchiella tentaculata* (holotype NTM W.023154) (PO): entire live worm, dorsal ventral view. Photos: (d)–E. Wong; (f)–Gabriel Monteiro; (j–l)–A. Semenov.



Figure 2. Diversity of Terebelliformia: Telothelapodidae (TE), Theleporididae (TH) and Trichobranchidae (TR); (a,b) *Telothelapoda ampensis* (topotype NHMUK ANEA 1957.12.30.1) (TE): anterior end, dorsal and ventral views, respectively; (c,d) *Rhinotherlepus mexicanus* (holotype LACM-AHF Poly 1449) (TE): anterior end, dorsal and ventral views, respectively; (e,f) *Thelepus paiderotos* (AM W.44600 and AM W.44283, respectively) (TH): entire live worms in right lateral and ventro-lateral views, respectively; (g) *Streblosoma curvus* (paratype AM W.44287) (TH): entire live worm (incomplete), dorsal view; (h,i) *Terebellides akares* (paratype AM W.45450) (TR): ventral and left dorso-lateral views, respectively, of live animals; (j) *Trichobranchus hirsutus* (AM W.45444) (TR): complete live worm, left lateral view. Photos: (e–j)—A. Semenov.

nothelepus mexicanus (holotype LACM-AHF Poly 1449) (TE): anterior end, dorsal and ventral views, respectively; (e,f) *Thelepus pailerotos* (AM W.44600 and AM W.44283, respectively) (TH): entire live worms in right lateral and ventro-lateral views, respectively; (g) *Streblosoma curvus* (paratype AM W.44287) (TH): entire live worm (incomplete), dorsal view; (h,i) *Terebellides akares* (paratype AM W.45450) (TR): ventral and left dorso-lateral views, respectively, of live animals; (j) *Trichobranthus hirsutus* (AM W.45444) (TR): complete live worm, left lateral view. Photos: (e–j)—A. Semenov.

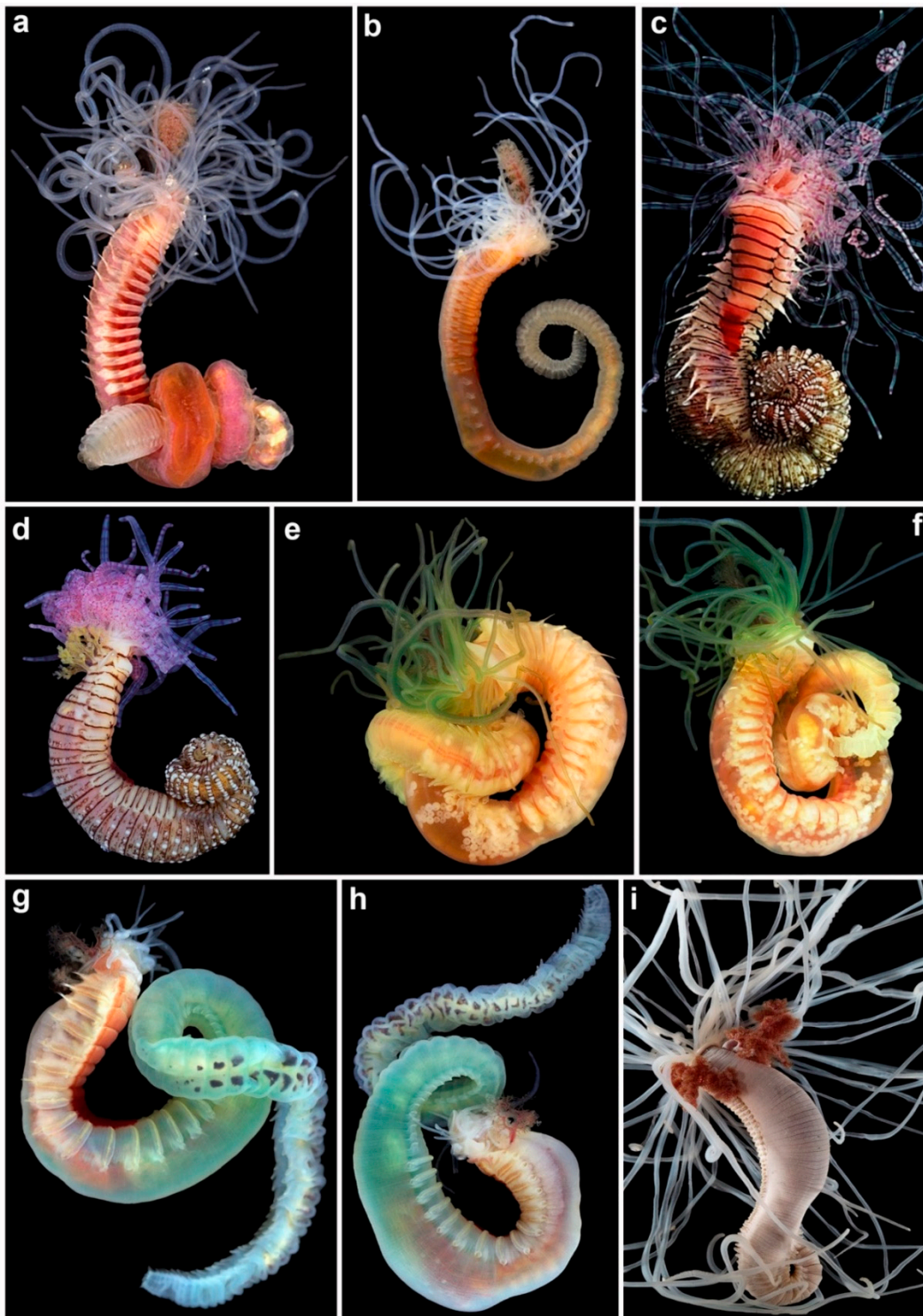


Figure 3: (a,b) Diversity of Terebelliformia: Terebellidae s.l. (TER) *Pistella franciscana*: complete live worm, right lateral views; (c,d) *Loimia tuberculata* (holotype AM W.44280): complete live worm, ventral and right lateral views, respectively; (e,f) *Pista chloroplokamia* (holotype AM W.44613): entire live worm, female, left and right lateral views; (g,h) *Loimia pseudotriloba* (holotype AM W.47810): entire live worm, right and left lateral views; (i) *Retterebella lirrj* (paratype AM W.44545): (holotype AM W.47810): entire live worm, right and left lateral views; (j) *Retterebella lirrj* (paratype AM W.44545): entire live worm, dorso-lateral view. All animals removed from their tubes. Photos: (a–i)—A. Semenov.

In this paper, we discuss the current status of our knowledge of Terebelliformia, considering all the modern techniques available, which allows for much deeper analyses and observations, including at the molecular level, to document the diversity of the

group. We also discuss the major gaps in our knowledge of Terebelliformia and their phylogeny, including some taxonomic issues, and point to directions to solve them, as well as highlighting other issues which need to be addressed.

The aims of this paper are (1) to present the taxonomic history of these worms, (2) their morphology, (3) the recent studies on their phylogenetic relationships, (4) their roles in the ecosystem and their distribution around the world, (5) the evolution of the methods used to describe them, (6) the knowledge gaps and challenges for the future, with focus on species complexes and taxonomic issues and, finally, (7) how such data can be used in marine park management as well as comments regarding the importance of using correct names.

2. Materials and Methods

This study provides a literature review of the Terebelliformia, including a list of valid species and their distribution according to biogeographical regions and their depth ranges (see Supplementary Material). This is based on the literature as well the World Register of Marine Species (WoRMS, <http://www.marinespecies.org>) to assess the number of currently valid taxa and analyses of species richness.

The citation of authors and date, and type localities policy: the original author(s) and date of a name of all taxa here included are cited the first time they appear in the text. However, due to the large number of taxa cited in this paper, we have not included all these citations in the references. Instead, they can be found in WoRMS as well as details of type localities and synonymies. We also discuss various genera for which diagnostic characters still need to be evaluated. Biodiversity information is referred to the realms proposed by Spalding et al. [10].

3. Terebelliforms

3.1. Taxonomic History of the Terebelliformia

The discovery of Terebelliformia began in 1766 (Figure 4), with the description of three species from the Dutch Sea, by Pallas: *Lanice conchilega* (Pallas, 1766) (Terebellidae), *Pectinaria belgica* (Pallas, 1766) and *P. capensis* (Pallas, 1766) (Pectinariidae). Since then, more than 1100 species of Terebelliformia have been described by 162 different first authors (Supplementary Material). During this period, four peaks were identified (Figure 4). The initial phase lasted for almost 100 years, from 1766 to 1859, and it was not the most productive, as only 46 species were described. The first peak occurred from 1860 to 1889 when 185 species were described by few taxonomists (Figure 4), as noted by Pamungkas et al. [11]. This productive period can be explained by the publication of important monographs by Europe-based polychaetologists: Grube (47 species) (e.g., [12,13]), Kinberg (12 species) [14], Malmgren (19 species) [15], McIntosh (36 species) [16] and Schmarda (13 species) [17]. Malmgren [15] launched the foundations for the modern taxonomy of Terebelliformia, describing most families of the group and a large number of genera.

By that time, most, if not all, of the researchers were European scientists, working on European material, but frequently no types were deposited in museums or zoological collections, and those species were later often reported from far-away locations. This has led to great taxonomic confusion, which in some cases threatens the stability of important genera (see below). Redescriptions and designation of neotypes from the type localities of some of these early described genera are urgently needed, such as *Amphitrite* O.F. Müller 1771, *Nicolea* Malmgren 1866, *Pista* Malmgren 1866 and *Terebella* Linnaeus 1767, for example.

The second phase of discovery occurred from 1900 to 1919, with 142 new species identified (Figure 4). This period corresponds, once again, to few active taxonomists, such as Augener (12 species) [18], Caullery (8 species) [19], Chamberlin (18 species) [20], Hesse (25 species) [21], Gravier (9 species) (e.g., [22]) and Moore (17 species) (e.g., [23]). It was not until 1970–1989 that the third phase took place, with the description of 165 species, by 34 different first authors. This peak corresponds mainly to the description of new species from Australia by Hutchings and collaborators (59 species) (e.g., [24–30]), but also to the

description of the new family Alvinellidae by Desbruyères and Laubier (12 species, all from deep-sea environments and hydrothermal vents) [31]).

Finally, the years 2000–2019 were the most prolific, with 258 species described by 38 different first authors (Figure 4). Among them, Hutchings, Nogueira and Carrerette were the most productive taxonomists (Table 1), with descriptions of 85 species of Terebellidae s.l., mostly from Brazil and Australia (e.g., [32–40]); Ampharetidae were also well studied during this period, with 32 species described [41–43].

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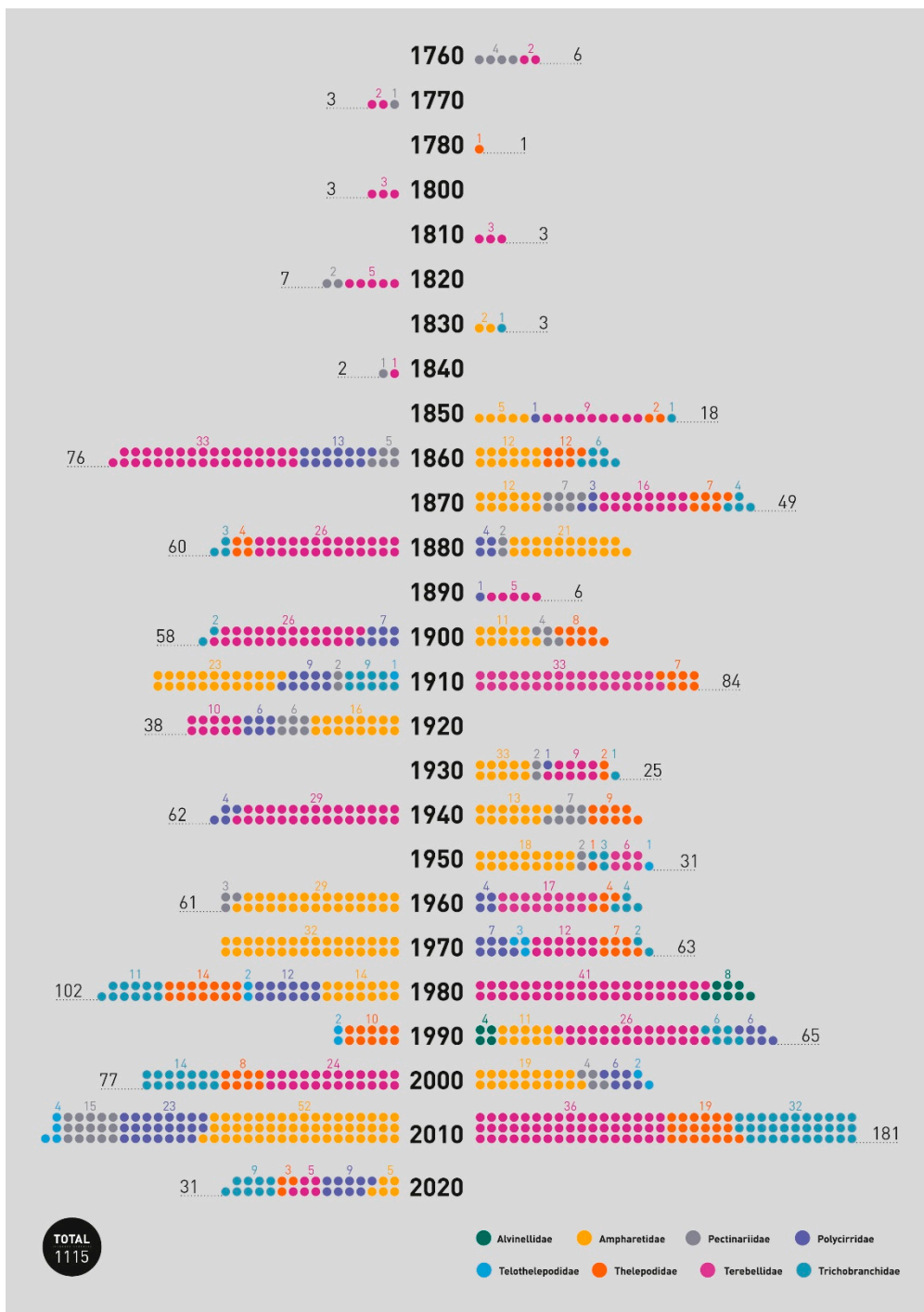


Figure 4. Number of Terebelliformia species described per period of ten years.

Table 1. The top 30 most prolific authors along with their numbers of Terebelliformia species described, first and last discoveries, and other polychaetes species described. Names in bold refer to active taxonomists.

Taxonomist	Terebelliformia Species Described	First Record	Last Record	Non Terebelliformia Species Described
P.A. Hutchings	217	1974	2020	152
J.M.N. Nogueira	74	2010	2020	54
A.E. Grube	58	1855	1878	409
M. Caullery	57	1915	1944	40
O. Carrerette	55	2013	2020	2
C.J. Glasby	49	1986	2014	43
O. Hartman	45	1941	1978	435
W.C. McIntosh	43	1869	1924	247
M.H. Londoño-Mesa	38	2003	2020	0
M. Reuscher	33	2009	2017	2
D. Fiege	31	2009	2016	39
G. Hartmann-Schröder	29	1962	1992	476
I.A. Jirkov	29	1985	2020	11
J.P. Moore	28	1904	1923	196
C. Hessle	27	1917	1917	5
M. Imajima	26	1964	2015	221
K. Fauchald	25	1971	1991	228
J. Parapar	24	1997	2020	45
N. Lavesque	23	2017	2020	3
R.V. Chamberlin	21	1919	1920	107
A.J. Malmgren	21	1865	1867	46
J. Moreira	20	2011	2020	36
J.H. Day	20	1934	1973	171
A.E. Verrill	18	1873	1901	102
P. Fauvel	17	1908	1959	125
H. Augener	15	1906	1926	197
T. Holthe	15	1985	2002	1
M. Schüller	15	2008	2013	8
D. Desbruyères	14	1977	1996	24
J.G.H. Kinberg	14	1866	1867	188

3.2. Morphology of Terebelliforms

Pectinariids are unique among terebelliforms, and among all polychaetes, by having rigid ice-cream cone-shaped tubes [6] (Figure 1a), which disintegrate once the animal dies. These animals are also unique among terebelliforms in having the prostomium and peristomium fused as a cephalic veil, of mixed prostomial and peristomial origin, together with a pair of rows of paleae at the anterior end, and the posterior end modified into a sucker-like scaphe (Figures 1b–d and 5b,i,j,m) [6].

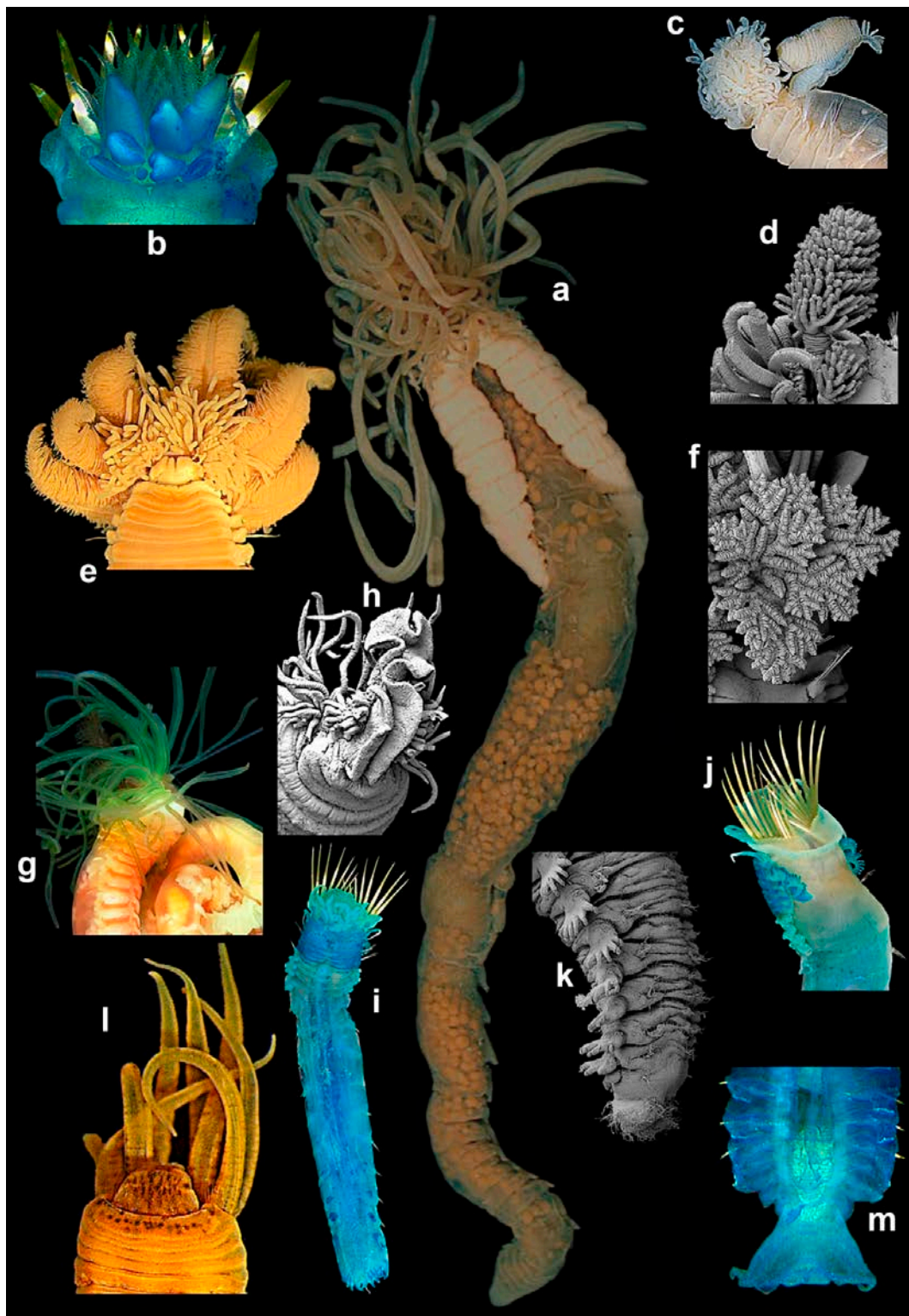


Figure 5. Diagnostic characters of terebelliforms: (a) *Nicolea lazowasemi* (holotype YPM 40593) (TER): entire worm, a gravid female, dorsal view; (b,m) *Pectinaria antipoda* (stained in methyl green) (PE): anterior and posterior ends, ventral views, respectively; (c) *Terebellides akares* (NTM W.023143) (TR): left lateral view; (d) *Pistella franciscana* (paratype AM W.44593) (PER): detail of branch; (e) *Terebellides akares* (NTM W.023143) (TR): left lateral view; (f) *Pistella franciscana* (paratype AM W.44593) (TER): detail of branch; (g) *Pista chlorobranchia* (SEM) (AM W.29585) (AL): anterior end, ventral view; (h) *Alvinia pompejana* (AM W.29585) (AL): anterior end, ventral view; (i) *Alvinia pompejana* (AM W.29585) (AL): anterior end, ventral view; (j) *Pista chlorobranchia* (SEM) (AM W.29585) (AL): anterior end, ventral view; (k) *Trichobranchia thuyae* (AM W.47510) (TR): posterior end examined under SEM; (l) *Amphicteis dalmatica* (AM): anterior end, ventral view; (m) *Pectinaria antipoda* (AM W.47510) (TR): posterior end examined under SEM.

Alvinellids and ampharetids are more closely related because members of both families have buccal tentacles fully retractable into the mouth and branchiae originating from segments II–V, but arising as free filaments from segments II–III in ampharetids (following Reuscher et al. [44]) [1,8,9,43] and associated to segments III–IV in alvinellids (Figures 1e–i and 5e,l) [7].

In ampharetids, the body regions are well marked, with notopodia restricted to the anterior part of the body (together with neuropodia, frequently called the “thorax”; see below), and posterior abdominal region with neuropodia only (Figure 6l). The shape of the prostomium can vary with the degree of the extension of the tentacles [44,45] but is typically spatulate and swollen, tri-lobed, frequently with paired glandular ridges; these latter structures are also interpreted as nuchal organs [8,43]. Eyespots may be present in ampharetids, and the peristomium is represented by a ring without appendages or chaetae. The first chaetiger is segment II, often with differentiated notochaetae (also referred to as “paleae”), directed upwards (Figures 1e, 5l and 6c), which may be modified or even absent [8,41]. Other thoracic segments usually bear limbate capillary notochaetae (Figure 6d), but some groups present modifications to the anterior segments, including the presence of hook-like chaetae (Melinninae), different sizes and thicknesses of chaetae and notopodia. Notopodia are absent in the abdominal region, although notopodial rudiments may be present (Figure 6p) [9,42,44]. Neuropodia in ampharetids are sessile tori on thoracic segments, forming pinnules after the end of notopodia (Figure 6m); both regions typically bear short uncini, which usually vary in shape and number of teeth between anterior and posterior regions.

In alvinellids, the first chaetae (notopodial only) appear on segment III in *Paralvinella* Desbruyères and Laubier, 1982 and VI in *Alvinella* Desbruyères and Laubier, 1980 (Figure 1g). Neuropodia (uncini) are sessile and start as early as segment VI (chaetiger 4 in *Paralvinella*) but sometimes much later on the body for some species (ca. chaetiger 40). They occur until the end of the body and their morphology does not change markedly in anterior and posterior regions. As a result, body regions are not marked [1,9]. Chaetiger 7 (*Paralvinella*) or 4 and 5 (*Alvinella*) have strong hooks (Figure 1h). Both prostomium and peristomium are devoid of appendages and bear no eyes. All members have four pairs of branchiae, emerging as strong stems bearing lamellae (*Alvinella*) (Figure 1g,h and Figure 5e) or cylindrical extensions (*Paralvinella*). In addition to the typically grooved tentacles, males of alvinellids also possess a pair of short, thick modified tentacles, possibly involved in pseudocopulation.

Terebellidae s.l. is a group of five families previously considered as subfamilies of a single family, Terebellidae (= Terebellidae s.l.), which Nogueira et al. [1] showed to have originated independently in the evolution of Terebelliformia, raising each of those to family level, and describing a new one, the Telothelepodidae. Animals belonging to these families all have prostomium at the dorsal side of the upper lip, with buccal tentacles originating from the distal part of prostomium, therefore out of the mouth and not retractable into it (Figure 1j,l, Figures 2a–j and 3a–i). In addition, all these animals have up to three pairs of branchiae, usually from segment II, although several forms are abranchiate, including the entire family Polycirridae (Figures 1j–l and 6a); notopodia bearing distally winged (=“smooth”) (Figure 6d,f,g,i) or serrated capillaries (Figure 6e,h), frequently restricted to the anterior region of the body; neuropodia, extending until near pygidium, bearing uncini (Figure 6j–o,q) [2]. Members of these families, however, are distinguished from each other, mostly by the morphology of the upper lip, the branchiae, the ventral glandular areas of anterior segments, and neuropodia, and by the morphology and arrangement of the uncini of anterior neuropodia, if in single or double rows [2].

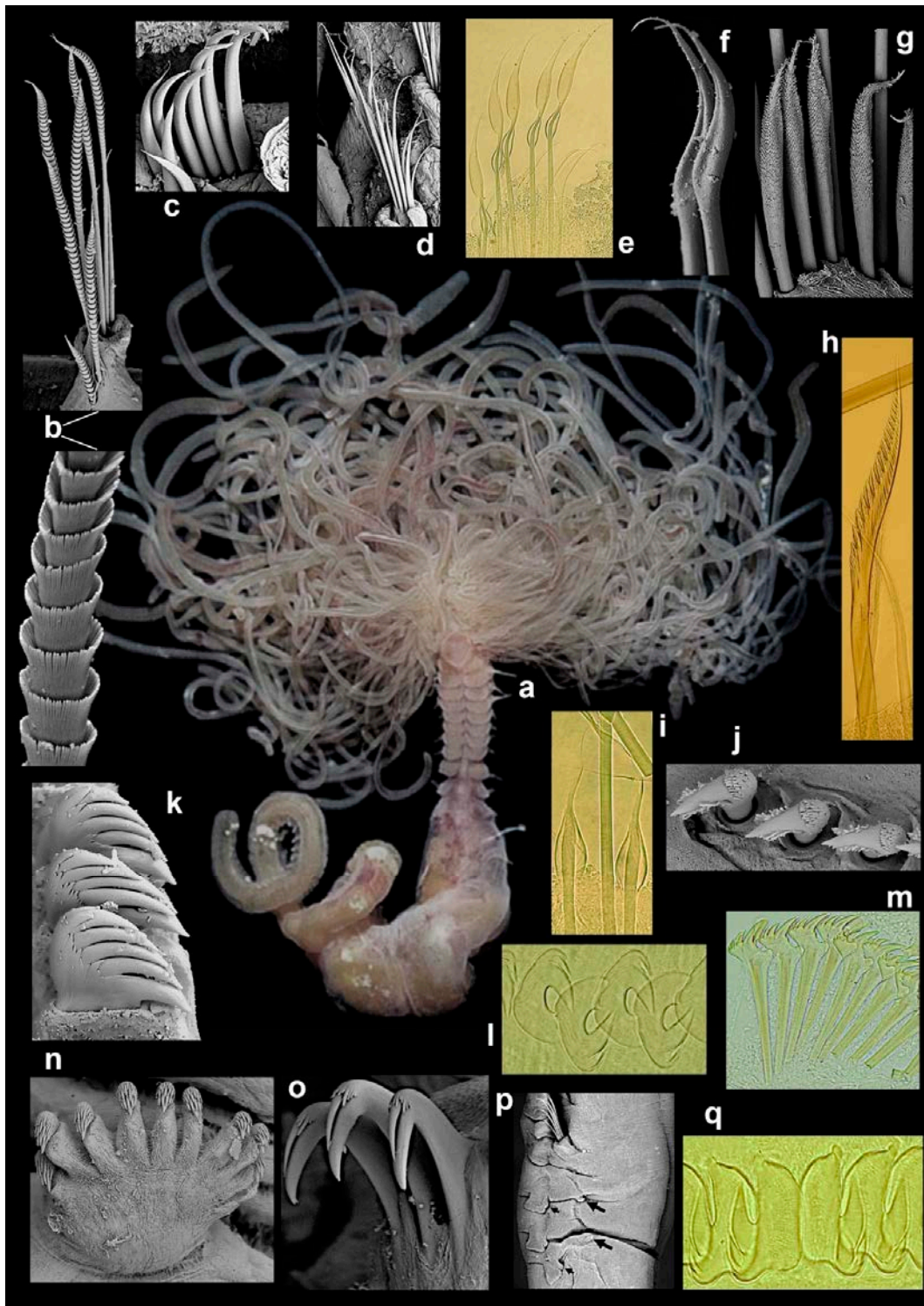


Figure 6. Diagnostic characters of terebelliforms: (a) *Polycirrus changbunker* (ZUEC 21354) (PO): entire worm, ventral view; (b,o) *Polycirrus papillatus* (PO): notochaetae, of two magnifications, and abdominal uncini, respectively (SEM); (c,d) *Amphicteis dalmatica* (AM): paleae and notochaetae of anterior segment, respectively; (e) *Spinosphaera barega* (TER): posterior thoracic notochaetae; (f) *Pista anneae* (TER): notochaetae, segment X; (g) *Pistella franciscana* (TER): notochaetae, segment VIII; (h) *Thormella pompejana* (AL): notochaetae, anterior segment; (i) *Levinseni ebrancata* (TER): notochaetae of anterior row, anterior segment; (j) *Amphicteis binusutus* (TB): uncini, segment VII (SEM); (k) *Uroclitella* (TER): abdominal uncini (SEM); (l) *Uroclitella* (TER): notopodium, segment XXI; (m) *Amphicteis dalmatica* (AM): last thoracic and first abdominal segments; large arrows point to abdominal rudimental notopodia, short arrows point to neuropodial dorsal papillae; (n) *Thelopus paiderotos* (TH): uncini, segment VII; large arrows point to abdominal rudimental notopodia, short arrows point to neuropodial dorsal papillae; (o) *Thelopus paiderotos* (TH): uncini, segment VII.

Polycirrids, in addition to being all abranchiate, have a circular upper lip, and the buccal tentacles are of two types, with the long ones often distally modified (Figures 1j–l and 6a). The body may be highly papillated and the anterior glandular areas of anterior segments are typically well developed, with paired mid-ventral shields, separated from each other within pairs by the mid-ventral longitudinal groove, extending from ~segment II or III to the pygidium (Figures 1l and 6a) [1,2,46]. In addition, there is a tendency for a reduction in parapodia in these animals, as members of some genera lack either notopodia (*Biremis* Poloni, Rowe and Teal, 1973), neuropodia (*Enoplobranchus* Verrill, 1879 and *Lysilla* Malmgren, 1866), or lacking all chaetae (*Hauchiella* Levinsen, 1893) (Figure 1l) [2,9].

Members of both Telothelepodidae and Thelepodidae have branchiae as multiple unbranched filaments, originating independently from the body wall on either side of the pairs, 2–3 pairs in thelepodids, on segments II–III or II–IV, always 3 pairs among telothelepodids, on segments II–IV (Figure 2a–c,e–g and Figure 5h). Members of these families are distinguished from each other because telothelepodids have a narrow and proportionally an elongate upper lip, frequently convoluted, very poorly developed ventral glandular areas on anterior segments and distinctly poorly developed neuropodia throughout the body, as low ridges on the anterior body (Figure 2a–d), where notochoetae are also present, and almost sessile pinnules after notopodia terminate. In contrast, members of Thelepodidae have a hood-like, almost circular upper lip and very well developed ventral glandular surfaces of anterior segments, although discrete ventral shields are not observed among these animals; fleshy, well developed neuropodia throughout, the posterior body neuropodial pinnules are frequently well raised from the body (Figure 2e–f) [1,2,9,32,39,40].

Trichobranchids are a group of three genera only, *Octobranchus* Marion and Bobretzki, 1875, *Terebellides* Sars, 1835 and *Trichobranchus* Malmgren, 1866, sharing the character of having neurochaetae on anterior segments as long-handled acicular uncini (Figure 6j), instead of avicular uncini, as in members of all other families, and also poorly developed ventral glandular areas on anterior segments and neuropodia almost sessile on the region with both noto- and neuropodia, and as developed neuropodial pinnules after notopodia terminate (Figures 2h–j and 6n). These animals have a circular, usually flaring upper lip, peristomial lobes are common and the anterior body segments present lobes as low collars of even length around the body, or only ventrally (Figures 2h–j and 5c). An eversible ventral process is present in *Trichobranchus*, in segment 1 [36]. Body regions are well marked in these animals, with notopodia extending only until ~segment XIX or XX, but beginning on segments III–VI, depending on the genus [1,2,9,32]. In *Terebellides*, branchiae are fused into a single structure with two paired lobes that bear lamellae and arise on segments II–IV (Figure 2h,i and Figure 5c) [46]. In contrast, in *Trichobranchus*, branchiae arise from segments II–IV but remain as three pairs of distinct organs (Figure 2j). In *Octobranchus*, there are four pairs present, on segments II–V, which may be digitiform or arranged as a foliaceous structure. Finally, terebellids sensu stricto (s.s.) are unique among Terebellidae s.l. in having neuropodial uncini arranged in double rows on at least some anterior segments (Figure 6l), while animals of all the other families of this group always have uncini in single rows. Terebellids s.s. also have well developed glandular ventral areas of anterior segments, with discrete, unpaired, rectangular to trapezoidal mid-ventral shields, and branchiae, whenever present, originate from a main stalk or at least a single point on the body wall on either side of pairs, and the branchial filaments may be unbranched or branching in a variety of ways (Figures 3a–i and 6a,c,d,f,g) [1,2,9,32,46].

3.3. Phylogenetic Relationships within the Group

A detailed discussion on the hypotheses for the position of Terebelliformia within Annelida through time was provided by [2,47,48]. The latest phylogenetic studies, mostly based on molecular data, suggest terebelliforms are a sister taxon to Arenicolidae Johnston, 1835, and the clade is sister to Clitellata, sometimes with Capitellida, Echiurida and Opheliida, also included in the group [49–51]. This contrasts with the traditional morphological hypotheses, which proposed a sister–taxon relationship between Terebelliformia

and Cirratuliformia, grouped together in the taxon Terebellida, which is closely related to Sabellida and Spionida [52,53].

Many of these molecular phylogenies are based on a small number of taxa, and a small number of sequenced genes. Weigert et al. [51], for example, only included two species of alvinellids and one pectinariid, while Zrzavy et al. [50] used one alvinellid, three ampharetids, one pectinariid and two terebellids s.s. This limited number of taxa does not cover the range of morphologies present in the group and often differs from morphological phylogenetic studies. Future studies need a better representation of molecular data from all the families of Terebelliformia, especially of the type species of the genera to continue to resolve the phylogeny of this diverse group of polychaetes.

The most comprehensive phylogenetic study on the phylogenetic relationships within Terebelliformia was performed by Nogueira et al. [1], but was based exclusively on morphological data. The aim of that work was to study the relationships within the Terebellidae s.l., but representatives of the other families of Terebelliformia were also included, as well as three non-terebelliform species, one cirratulid, one spionid and one sabellariid. The authors examined 118 characters in members of 82 species of terebelliforms, including the type species of nearly all genera of Terebellidae s.l., plus the three outgroups, and noticed that all the groups previously considered as subfamilies of Terebellidae had originated independently along the Terebelliformia lineage. As a result, all these groups were raised to the familial level, together with a new family, Telothelepodidae, described therein [1]. According to Nogueira et al. [1], Trichobranchidae is monophyletic, but deeply nested within the Terebellidae s.l., sister to a clade in which Terebellidae s.s. is sister to Alvinellidae/Ampharetidae/Pectinariidae together. All those families originated along the Terebelliformia lineage as follows: Polycirridae (Telothelepodidae (Thelepodidae (Trichobranchidae (Terebellidae s.s. (Alvinellidae (monophyletic Pectinariidae and paraphyletic Ampharetidae)))))). However, the authors stressed that the study was totally focused on Terebellidae s.l., using characters and terminals especially selected for terebellids, but not representative of the diversity of alvinellids, ampharetids and pectinariids; therefore, the relationships between these latter three families had not been properly evaluated [1].

Prior to the study by [1], sister taxa relationships have been suggested between (1) Trichobranchidae and Alvinellidae, the group sister to Pectinariidae, and Ampharetidae and Terebellidae s.l. [54,55]; (2) Alvinellidae and Ampharetidae, and Pectinariidae and Terebellidae s.l., with a plesiomorphic Trichobranchidae, sister to all other terebelliforms [55]; (3) monophyletic Alvinellidae, all other families polyphyletic, except for Trichobranchidae, with a single species included in the study; Pectinariidae is also monophyletic, but out of Terebelliformia [56]. The relationships within Terebellidae s.l. had never been investigated before Nogueira et al. [1], except by Garraffoni and Lana [57,58], who found Trichobranchidae nested within Terebellidae s.l. In their analysis of Terebellidae s.l., Garraffoni and Lana [58] found polycirrids nested within telothelepodids + thelepodids, rendering paraphyletic the traditional Thelepodinae (including species of both thelepodids and telothelepodids, which were regarded as a single family until 2013), and Trichobranchidae sister to Terebellidae.

More recently, a phylogenetic study combining both morphological and molecular data by Stiller et al. [59] suggested a different arrangement for the internal groups of Terebelliformia. The authors first studied transcriptomes of one outgroup plus 20 terebelliform representatives, which included 1 Pectinariidae, 5 Ampharetidae (4 Ampharetinae and 1 Melinninae), 6 Alvinellidae, 2 Trichobranchidae and 6 Terebellidae s.l. (1 Polycirridae, 4 Terebellidae and 1 Thelepodidae), totalling 12,674 orthologous genes, to generate the “backbone” to a more general analysis, with 132 species of terebelliforms (13 Alvinellidae, 49 Ampharetidae (29 Ampharetinae, 5 Amaginae, 8 Amphicteinae and 7 Melinninae), 7 Pectinariidae, 47 Terebellidae s.l. (10 Polycirridae, 27 Terebellidae s.s., 1 Telothelepodidae and 9 Thelepodidae), and 16 Trichobranchidae), combining five genes (three nuclear and two mitochondrial, and not including any of those used for the first analysis) and 90 morphological characters. As a result of the combined analyses, the authors moved the newly

erected families of Terebellidae by Nogueira et al. [1] back into the Terebellidae s.l., most of them as subfamilies and found a sister taxon relationship between Terebellidae and Melinninae, raising the latter to familial level, and also between the remaining Ampharetidae and Alvinellidae. In regard to the Terebellidae s.l., the authors found Polycirridae nested within Terebellidae s.s., and synonymised Telothelepodidae with Thelepodidae, keeping the subfamily status of Thelepodinae and Terebellinae, and suggesting the subdivision of the latter into four tribes, Lanicini, Polycirridi, Procleini and Terebellini. However, although the sampling for the combined analysis is very comprehensive, the one used for the first analysis, which was used as a “backbone” to direct the second study, only included 20 species, of which pectinariids, melinnins, polycirrids and thelepodids were all represented by a single species each, and no telothelepodids were included. In addition, Fitzhugh [60–62] thoroughly discussed the philosophical issues in comparing phylogenetic hypotheses generated by different datasets of characters, as made by Stiller et al. [59] to combine the “backbone” with the main analysis. Fitzhugh also argued against the combination of morphological and molecular data, as well as against molecular phylogenies per se, also due to philosophical issues [62]. We consider that these major changes still need to be re-evaluated, given that only one species of Melinninae was included and the limited sampling of species of Telothelepodidae and Thelepodidae and the validity of plotting morphological characters onto genetic trees. For those reasons, we prefer to follow herein the classification proposed by Nogueira et al. [1], which was subsequently confirmed in the phylogenetic analyses of Polycirridae [46], and Telothelepodidae [47]. However, this may change as additional species are added to the dataset after sequencing.

Another phylogenetic study on the relationships within Terebellidae s.s. was performed by Jirkov and Leontovich [63], which focused on the animals with large lateral lobes only, which they suggest form a monophyletic clade in the family, although the reasons for this were not given. The authors included 93 taxa with large lateral lobes and a single “outgroup” species without lobes, *Terebella lapidaria* Linnaeus, 1767, the type species of the family. They also considered the presence of short-handled or long-handled anterior uncini as a specific character, rather than generic, as had traditionally been considered. As a result, the authors considered only the following genera with large lateral lobes as valid: *Axionice* Malmgren, 1866, *Lanicides* Hessle, 1917, *Lanicola* Hartmann-Schröder, 1986, *Pista* Malmgren, 1866 and *Scionella* Moore, 1963, and synonymised under *Axionice* the genera *Betapista* Banse, 1980, *Eupistella* Chamberlin, 1919, *Euscione* Chamberlin, 1919, *Lanice* Malmgren, 1866, *Loimia* Malmgren, 1866, and *Paraxionice* Fauchald, 1972. The authors also changed the traditional diagnoses of *Axionice* and *Pista* (see below), but these changes have not been adopted by other workers.

In summary, the phylogenetic relationships within the group are still being debated as well as the boundaries of some genera. Hutchings et al. [2] provide a synthesis of the phylogeny of the group prior to the studies by Nogueira et al. [1].

3.4. Biological and Ecological Notes on Terebelliforms

3.4.1. Role of Terebelliforms in the Ecosystem

The majority of terebelliforms are tubiculous, living in robust tubes made of sand and sediment grains, which may be within the sediment or more commonly attached to rocks, algae or shells (Figure 7a–f). A few, such as some polycirrids and some alvinellids, lack tubes, instead covered in a mucous sheath. Pectinariids produce very characteristic cone-shaped tubes, using very well calibrated sediment grains (Figure 1a). The alvinellids build tubes on the walls of the vent chimneys, in basaltic cracks with venting (Figure 7f), or live in mucus sheaths at the base of vestimentiferan tubes. In all cases, once the animal dies, the tubes, which are constantly being maintained, tend to break apart, as the mucus binding the shell fragments and sediment particles degenerates.



Figure 7. Some typical habitats of terrelliforms: (a) wave-dominated coastline, Cape Leewin, WA, Australia. Photo: Pat Hutchings; (b) mangrove area in front of *Rhizophora* roots at Lizard Island. Photo: Gary Cranitch; (c) base of *Posidonia australis* beds. Photo: Clay Bryce; (d) soft mud, here collected by Van Veen grab. Photo: Pat Hutchings; (e) fine sand sampled by dredge. Photo: Jurgen Freund; (f) deep-sea hydrothermal vents, tubes of alvinellids. Chimney wall surface at Tu'i Malila, Lau Basin. Copyright: Chubacarc cruise/Ifremer.

In general, these animals appear to have reduced mobility; however, members of the polycirrid *Biremis blandi* Polloni, Rowe and Teal, 1973 have been seen swimming in mid-water, at depths of 411–597 m, in the Florida Strait and Bahamas [64]. Other species have been observed to swim for a short time when removed from their tubes, presumably an avoidance reaction (Hutchings, pers. obs.; Nogueira, pers. obs.). On the other hand, species such as *Amphisamytha galapagensis* Zottoli, 1983 can apparently live free of the tubes when the material for their construction is scarce in the environment [65]. They then use fibrous structures such as byssal threads from mussels or setae on crabs to host them.

Some species occur in dense aggregations; for example, the ampharetid *Melinna palmata* Grube, 1870 occurs in aggregations up to 9000 ind./m² in Arcachon Bay, France [4]. The alvinellid *Alvinella* spp. can also form high-density aggregations on hydrothermal vent chimney walls where it affects the chemical conditions [66] or *Lanice conchilega* (Pallas, 1766), which is also considered as an ecosystem engineer for forming reef-like structures in intertidal sandy substrates, by the aggregation of their tubes [67]. Other terebelliforms, in contrast, form small aggregations or are found as single, solitary individuals.

All the terebelliforms are selective surface deposit feeders [68] gathering food particles with the buccal tentacles, and then conveying these to the mouth, through the ciliated longitudinal tentacular groove. This trophic mode largely modifies marine benthic environments by reworking large amounts of sediments [69] and directly affects their physical and chemical properties [70,71]. Particularly, terebelliforms have a great impact on the amount of organic matter at the water–sediment interface, modifying local hydrodynamics and sediment cohesion [72]. Finally, terebelliforms can influence the structures of benthic communities through tube-building [70].

The Alvinellidae, in addition, have been reported to supplement their deposit feeding diet by collecting particles suspended in the water, by filtering water through their branchiae, as well as feeding on the bacterial residents of the worm tubes [73]. Evidence of such supplementation, however, is lacking and gut contents only revealed mineral particles and bacterial cells gathered from the environment [74]. Although both species of *Alvinella* bear epibiotic bacteria, these do not appear to contribute to the nutrition of the worm hosts. Both species, however, produce structures that allow for the settlement of these bacteria and the association must be beneficial to the host [74].

Most Terebelliformia are dioecious with no morphological differences between males and females, except at the time of spawning when the mature gametes colour the body, where females may be pinkish or greenish, and males are typically cream coloured. In alvinellids, however, reproduction appears continuous; males bear a pair of modified buccal tentacles and females have genital pores [31]. In some taxa, the genital papillae may vary between sexes, as well as the distribution of glandular areas (Figure 6a) [36].

To date, no evidence of asexual reproduction has been observed, although all are capable of regenerating posterior ends, branchiae and buccal tentacles. Gametes are proliferated from the germinal epithelium, often associated with the nephridia, and released into the coelomic cavity, where vitellogenesis and spermatogenesis occur. Synchronised spawning occurs through the nephridia, and spawning varies from only one or two days to discrete periods over several months.

In alvinellids, the presence of sperm ducts, spermathecae and oviducts have been reported, lending support to continuous gamete production, episodic release, pseudocopulation, and internal fertilization [75]. Compared to other studied Terebelliformia, alvinellid sperm cells are highly modified entaquesperm, devoid of acrosome and sometimes of flagella, providing further support for internal fertilization in this family [76].

Among the other terebelliforms, mass spawning occurs in some taxa, while others produce a lecithotrophic larva, with varying planktonic larval phase durations (PLDs), and at least one species has a direct development within a cocoon, with larvae released at the 15 chaetiger stage [74]. Although few species have been studied, most of them produce large yolky eggs, and the embryo probably does not feed in the plankton [8,74], except in pectinariids, which may have a planktotrophic larva, capable of feeding through

a capture system involving the generation of a current and the production of mucus [77]. In *Alvinella pompejana* Desbruyères and Laubier, 1980, the conditions the adults experience in their environment are actually harmful to the developing larvae and they need to encounter milder conditions to survive and develop properly [75]. Erpochaete larvae of *Paralvinella grasslei* Desbruyères and Laubier, 1982 as young as 13 segments (with a single pair of branchiae) have been captured near adults of this species, suggesting a very early recruitment following a planktonic phase [7].

Few species of ampharetids have been studied with regard to their reproduction (e.g., [65,78–85]). Some shallow water species reproduce annually, and all produce large yolky eggs, which spend only a few days in the plankton. *Melinna palmata*, for example, may spend 6 days living in the plankton before settling and building a tube at the 3-chaetiger stage [8]. *Hobsonia florida* (Hartman, 1951) has been reported as having larval development in the maternal tube and a 2-chaetiger stage leaves the tube, settles on the nearby sediment and builds its own tube [8]. Studies conducted with deep-sea species, from both hydrothermal vents and organic falls, suggest continuous reproduction and rapid maturation, possibly as a reflection of the ephemeral conditions of these chemosynthetic habitats [65,84,86].

So, in summary, among terebelliforms, we have a variety of reproductive strategies (see references in [2,7,8]).

3.4.2. Distribution and Biogeography

Historically, species were described from Europe with most of the type species of the 137 genera sampled from these waters, except for the Alvinellidae, which is restricted to deep-sea hydrothermal vents, and was erected in 1986 (although the first species was described in 1980, as an aberrant Ampharetidae *Alvinella pompejana*).

In the 1980s, the centre of gravity moved to the southern hemisphere with taxonomists based in Australia (Glasby, Hutchings), South America (Carrerette, Londoño-Mesa, Nogueira) and those involved in Pacific expeditions (Fiege, Imajima, Reuscher) (Table 1). In these regions, polychaete workers had to review earlier expeditions, which were mainly housed by European institutions, where the material was deposited, and over time some has been lost or damaged. In some cases, material from an expedition was deposited in several institutions and locating this material can be challenging. All the scientists working on the material collected during these expeditions were based in Europe and they tended to identify much of this material as European species even though they had been collected thousands of kilometres away in very different habitats and temperature regimes. This led to the idea that many polychaete species were cosmopolitan and certainly later European workers such as Fauvel [86] reinforced this view and recorded the widespread distributions of many species. Later this was reinforced by the catalogues of polychaetes produced by Hartman [87] and by Day [88]. An example of this is provided by Hutchings and Glasby [89] who analysed the species list of terebellids s.l. produced by Day and Hutchings [90] in their checklist of the polychaetes recorded from Australia and New Zealand, which was based entirely on the literature and listed 32 species in 17 genera. Hutchings and Glasby [89] showed that only 14 of these occurred in Australia, the rest having been misidentified as European species. They further analysed the diversity of Australian terebellids, as they were known in 1991, which was represented by 78 species in 27 genera, and of these 67 (85.89%) species were Australian endemics, and of the remaining 11, nine were restricted to the Indo-Pacific and only two were found in the northern hemisphere. Since that analysis in 1991, the remaining two species recorded from the northern hemisphere have been described as Australian endemics as well [91]. Since that study, many more species have been described from Australia. Similar patterns are also evident in other polychaete families, so this is certainly not solely a characteristic of terebellids but widespread across all polychaete families found in Australia.

More recently, it has been recognised that most species actually have discrete distributions, unless proven otherwise [92], and while many genera are widely distributed,

it is at the species level that discrete distributions occur. However, in many parts of the world, taxonomists and ecologists still identify their material using the well-illustrated monographs of Faune de France ([86,93], and Southern Africa [88], despite their samples being collected many thousands of kilometres away from France or Southern Africa. This has tended to reinforce the concept that polychaete species are cosmopolitan in their distribution. While this has been shown not to be true—for example, *Terebellides stroemii* Sars, 1835 is now known to represent a highly speciose group—as the nominal species is restricted to a very small area in Western Norway [5,94]. In many cases, this is also because no regional keys exist in many parts of the world, and so a student has little option but to use keys from other regions. Once those names become enshrined in the local fauna, then subsequent workers just repeat them, explaining why species such as *T. stroemii* have been so widely reported.

Our current knowledge on the diversity of Terebelliformia shows great variation from some regions of the world to others. While places such as Europe and North America have been investigated for centuries, others are still virtually unknown, as is most of the African coast and the Eastern Indo-Pacific. This is largely due to the presence of more researchers based in Europe and North America than in other regions of the world, and also for the availability of financial resources available for biological research in these regions.

However, it should be stressed that even regions where the fauna has been studied, it is now being re-examined with molecular tools, as numerous complexes of species have been found, resulting in a much greater number of species than previously considered. For example, French coastal waters are well-known areas, studied for several centuries by early taxonomists and benthic ecologists. However, studying numerous terebelliforms (spaghetti worms), within the collaborative Spaghetti Project, using modern tools, such as the scanning electron microscope and molecular analysis, has revealed the existence of more than 20 species new for science [95–99]. We assume that this marked discrepancy in our knowledge of the diversity of polychaetes in many parts of the world is common for most if not all polychaete families.

To facilitate a review of the distribution of terebelliforms, we chose to look at various biogeographic schemes which have been suggested over the years ([100,101] and we are following Spalding et al. [10]. In an effort to strategically plan exploitation and marine conservation measures, Spalding et al. [10] suggested a classification for the marine biogeographic regions, the Marine Ecoregions of the World (MEOW), dividing coastal and shelf areas into 12 Realms, 62 Provinces and 232 Ecoregions (Figure 8). As said above, our analysis of the geographic distribution of terebelliforms follows that biogeographic classification. We have compiled a list of all terebelliforms described and, just using their type locality, allocated them to each of these regions and they are plotted in Figure 8. Obviously, these numbers are influenced by the number of taxonomists working in each area, which has varied over time, and the resources available.

As expected, the most diverse realm is the Central Indo-Pacific, with 233 species of terebelliforms described from the region (Table 2, Figure 8). This realm, corresponding to the area from the South China Sea, through the Pacific side of Indochina Peninsula, Philippines, Indonesia, Papua, Melanesia and Micronesia islands, Northwestern, Northern and Northeastern Australia, including the northern Great Barrier Reef (Figure 8), is considered as the world biodiversity hotspot for many groups of marine animals and is referred to as the Coral Triangle [102]. The following most diverse realms match the observations discussed above, as the regions with more polychaete taxonomists and economic resources are also the most diverse, Temperate Northern Atlantic (210 species), Temperate Northern Pacific (175 species), Tropical Atlantic (95 species), Southern Ocean (82 species), Temperate Australasia (76 species) and Temperate South America (67 species) (Table 2 and Figure 8).

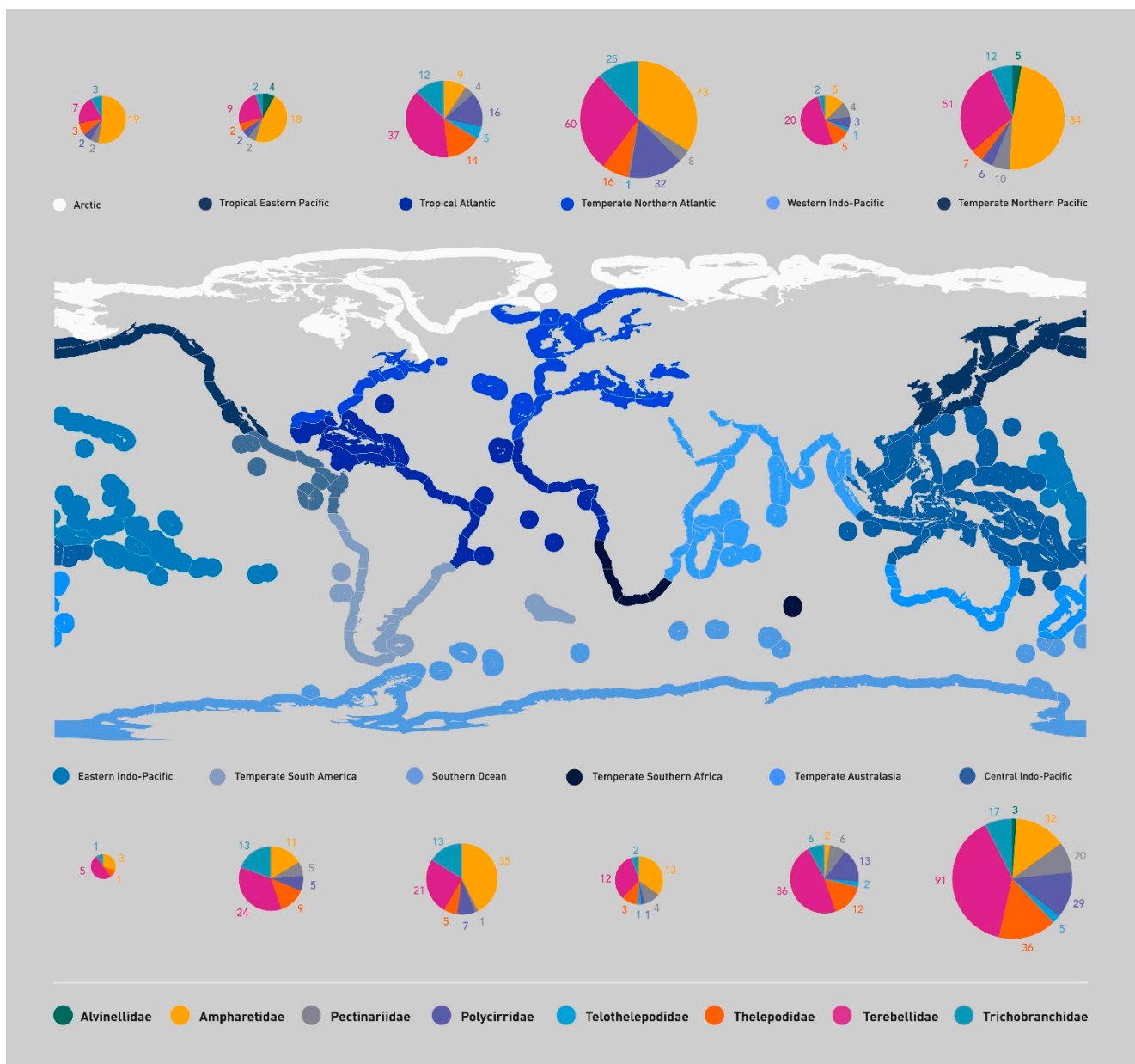


Figure 8. Marine Ecoregions of the World following [60] with number of species of terebelliforms described from each realm.

The fauna from Europe, corresponding to part of the Temperate Northern Atlantic realm, has been the most thoroughly investigated in the Central Indo-Pacific, with 233 species of terebelliforms described from the region [99], as a figure 8 above for France, corresponding to the area from the South China Sea through the Pacific side of Indochina Peninsula, Philippines, Indonesia, Papua, Melanesia and Micronesia islands. North-western, Northern and Northeastern Australia, including the northern Great Barrier Reef (Figure 8) Northern Pacific and the world Antarctic realm, hot spots for many groups of marine animals and dedicated resources as the Central Atlantic [102]. The following most diverse areas are the others: Rapa Nui and Chonos in the Pacific, with Mexico, Brazil and Colombia and latter the Southern Ocean also investigated by Temperate Northern Atlantic (217 species), Eastern Indo-Pacific (177 species), Iberian Atlantic (95 species), Southern Ocean (82 species), Temperate Australasia (76 species) and Temperate South America (67 species) (Table 2 and Figure 8). In the last few decades, with large projects carried out, such as in Australia and New Zealand, in the case of Temperate Australasia, and Chile, Argentina and Brazil, in Temperate South America.

Table 2. Distribution of Terebelliformia around the world, following the marine regionalization created by Spalding et al. [10], and bathymetric variation of the terebelliform families, as well as the deepest records of each group.

	Alvinellidae	Ampharetidae	Pectinariidae	Polycirridae	Telothelepodidae	Thelepodidae	Terebellidae	Trichobranchidae
Realms by Spalding et al (2007)								
Arctic		19	2	2		3	7	3
Central Indo-Pacific	3	32	20	29	5	36	91	17
Eastern Indo-Pacific		3				1	5	1
Suthern Ocean		35	1	7		5	21	13
Temperate Australasia		2	6	13	2	12	36	6
Temperate Northern Atlantic		73	8	32	1	16	60	25
Temperate Northern Pacific	5	84	10	6		7	51	12
Temperate South America		11	5	5		9	24	13
Temperate Southern Africa		13	4	1	1	3	12	2
Tropical Atlantic		9	4	16	5	14	37	12
Tropical Eastern Pacific	4	18	2	2		2	9	2
Western Indo-Pacific		5	4	3	1	5	20	2
Bathymetric distribution								
Inter tidal to 100 m		72	20	66	14	57	87	34
100–500 m		52	5	9		6	13	21
500–1000		42	2	3		4	1	3
1000–2000	4	38		1		4	1	5
2000–3000	7	23	2			2		5
3000–4000	1	21				1	1	
4000–5000		25						3
5000–6000		9						4
6000–7000		1						
8000–9000		1						
9000–10,000		1						
Deeper records	<i>Alvinella pompejana</i> , 2593 m	<i>Anobothrus auriculantus</i> , 9584 m	<i>Petta assimilis</i> , –3000 m	<i>Polycirrus nonatoi</i> 1904 m	<i>Prathelepus anomalus</i> and <i>Rhinothelepus mexicanus</i> , 91 m (for both)	<i>Streblosoma chilensis</i> , 3950 m	<i>Pista torcuata</i> 4540 m	<i>Terebellides bulbosa</i> and <i>T. ginkgo</i> , –5200 m (for both)

On the other hand, the least diverse realms are also those with fewer taxonomists and frequently fewer economic resources. Western Indo-Pacific (including eastern Africa, Red Sea, Persian Gulf, Pakistan, India, Sri Lanka and the Indian side of the Indochina Peninsula) tally only 40 species. Temperate Southern Africa tallies only 37 species, in spite of the efforts by Day [90], but this last author reported many European species for South Africa, as did Fauvel [103], for the region of India and Sri Lanka. Tropical Eastern Pacific, which includes the Pacific side of Tropical America, comprises 38 species only and this is attributable to Mexican and Colombian researchers. Only 36 species are described from the Arctic, which is somewhat surprising, considering the Scandinavian and Russian scientists who have been working in the region since the 19th century, although many Northern European and North American species are reported for this region. Additionally, the Eastern Indo-Pacific realm, the poorest of all, including the region from Hawaii and Marshall Islands through Polynesia and the Mariana Islands to Easter Island, with only 10 species, but also with many records from the West Indo-Pacific (Table 2; Figure 8). We suggest that some of these patterns of diversity may just reflect the lack of sampling rather than a reflection of their true diversity.

As discussed below, many genera of terebelliforms are monotypic, several of which have never been sampled since they were first collected. These descriptions are very brief and do not mention several characters currently considered important for the taxonomy of the group. This is further complicated by the loss of the type of material or it is damaged in such a way that those characters cannot be assessed. The uncertainty about the identity of those genera obviously imposes several problems in regard to the knowledge on the distribution of those animals and several genera are considered as endemic to certain regions which may change as more studies are carried out.

Most of the non-monotypic genera of terebelliforms are widespread through [10] realms. One non-monotypic genus which apparently has a more restricted distribution is *Reteterebella* Hartman, 1963, with three species. The type species, *R. queenslandia* Hartman, 1963, described from Heron Island, Great Barrier Reef (Central Indo-Pacific), but apparently restricted to that region [37], *R. aloba* Hutchings and Glasby, 1988, from South Eastern Australia (Temperate Australasia) and *R. lirrff* Nogueira, Hutchings and Carrerette, 2015, described from Lizard Island, also on the Great Barrier Reef. The habitats in which *R. lirrff*

and *R. queenslandia* occur are very different, the first being found in crevices deep down in boulders, whereas *R. queenslandia* occurs on reef flat with its flimsy tube attached to the underside of boulders. However, it should be stressed that reefs between Heron and Lizard have not been well sampled.

Another genus *Hadrachaeta* Hutchings, 1977 is only known by the type species and has only been found in the front of mangroves in Broken Bay, NSW and Moreton Bay, Queensland and, despite extensive sampling in these habitats along the east coast of Australia, no other material of this species has been found (Hutchings, pers., comm.).

3.4.3. Distribution of Terebelliforms with Depth

There is no generally accepted definition of the deep sea. One can consider depths below the euphotic layer (i.e., 300 m) as a natural upper limit to the deep sea. Overall, the deep-sea remains poorly explored outside of specific areas, such as cold seeps, hydrothermal vents, and organic falls. The typical lifestyle of terebelliforms also makes their capture unlikely by the gear typically used to sample the deep sea. In particular, species that live buried in the sediment or attached to rocks are often missed by dredges and beam trawls used by most recent general study programmes. This was clearly demonstrated by Gunton et al. [104] who studied the polychaete fauna from depths off the east coast of Australia (1000–4000 m), and while ampharetids were very well represented, with over 300 specimens belonging to more than six species, 10 specimens and 2 species of pectinariids were also present and described (*Petta investigatoris* Zhang, Hutchings and Kupriyanova, 2019 and *P. williamsonae* Zhang, Hutchings and Kupriyanova, 2019), and far fewer specimens of Terebellidae s.l. were collected, representing four genera but all in poor condition.

The deepest record among Terebelliformia comes from a species of ampharetid *Anobothrus auriculatus* Alalykina and Polyakova, 2020, found at 9584 m depth (Table 2). Ampharetids are well represented in the abyss and in different deep-sea habitats, with more than half of the known ampharetid species occurring below 500 m deep (Table 2). Several ampharetids are exclusively found in the deep-sea, in addition to some specialised representatives associated with chemosynthetic environments, such as some known species of the genera *Amage* (1 species., at cold seep), *Amphisamytha* (7 species., at cold seeps and hydrothermal vents), *Anobothrus* (3 species., at cold seeps and hydrothermal vent), *Decemunciger* (1 species., on decaying wood), *Endecamera* (1 species., on decaying wood), *Glyphanostomum* (2 species, at cold seep and sedimented hydrothermal vents), *Grassleia* (1 species at sedimented vents and cold seeps), *Paramytha* (2 species on decaying bones and sedimented hydrothermal vents), and *Pavelius* (3 species at cold seep and sedimented hydrothermal vents) [105].

The alvinellids are restricted to hydrothermal vents. All the species are exclusively found at hydrothermal vents in the Eastern and Western Pacific (Table 2), but a species was recently reported from vents in the Indian Ocean [7]. As a result, alvinellids are exclusively found at depths greater than 1500 m and can reach ~3600 m (Table 2).

Hydrothermal vents and cold seeps are also home to some terebellid species described recently (e.g., *Neoamphitrite hydrothermalis* Reuscher et al. 2012, and *Streblosoma kaia* Reuscher, Fiege and Wehe, 2012, for hydrothermal vents, and *Pista shizugawaensis* Nishi and Tanaka, 2006 for cold seeps; see [106] (Table 2). The Telothelepodidae, in contrast, so far have only been found at shallow depths, the deepest records (~91 m) for *Parathelepus anomalus* (Londoño-Mesa, 2009) and *Rhinothelepus mexicanus* (Glasby and Hutchings, 1986) (Table 2). In general, most polycirrids are found in intertidal to shallow water habitats, the deepest record being for *Polycirrus nonatoi* Carrerette and Nogueira, 2013, found from ~30–1900 m deep (Table 2). Trichobranchidae are also well represented in the deep sea, frequently by a large number of species (Table 2), despite sometimes being considered low in abundance, belonging to the genus *Terebellides*; the deepest records come from *Terebellides bulbosa* Schüller and Hutchings, 2012 and *T. ginkgo* Schüller and Hutchings, 2012, ~5200 m deep for both, from animals collected at the Brazil Basin [107] (Table 2). This genus is highly

speciose, with many endemic species, while others can have wide distributions, indicating dispersion over long distances [107]. Both Pectinariidae and Thelepodidae are much more diverse intertidally to ~100 m, but in both families a few species adapted to the deep sea have been described, the deepest records being *Streblosomma chilensis* (McIntosh, 1885), for thelepodids, registered at ~4000 m deep off Chile, and the pectinariid *Petta assimilis* McIntosh, 1885, found ~3000 m deep, off Crozet Islands (Table 2).

3.5. Evolution of Methods Used to Describe Species

Earlier taxonomists in the 18th and 19th centuries worked with very rudimentary optical instruments, sometimes only a little more than a magnifying glass, capable of low magnifications. Nevertheless, albeit with limited resources, those authors did an amazing job. Except for the Alvinellidae, Telothelepodidae and Thelepodidae, all other families, 35% of the genera and 23% of the currently valid species of Terebelliformia, were described in the 18th and 19th centuries (see above). Those descriptions are frequently criticized for their simplicity, but they reflect the state of knowledge at those times, when the authors considered enough to define species characters which, nowadays, frequently do not allow even for the recognition of the genus. Additionally, it is noteworthy how, in spite of these instruments, some of those earlier descriptions included minutely detailed drawings of chaetae, showing structures which can only be clearly seen under the SEM, a technology that was obviously developed much later.

A great improvement on taxonomists' instruments came in the 20th century, first with more powerful compound optical microscopes, with techniques such as phase contrast, allowing for a much better visualization of chaetal ornamentation, together with better software to capture the images directly from the microscopes and process them, largely replacing traditional line drawings (Figure 9).

Then, from the end of the 20th century through to today, Scanning Electron Microscopy (SEM) provides a much better view of the surface of microscopic structures, such as chaetal ornamentation (Figure 9); Transmission Electron Microscopy (TEM) brought information on cellular ultrastructure; confocal microscopy allowed us to peer deep into the tissues and highlight specific organs; molecular tools became available to distinguish the taxa at the genetic level (DNA and RNA), providing much more detailed and complete descriptions.

All this has greatly increased our knowledge on the diversity of terebelliforms, as for all other polychaetes, with many more morphological and molecular characters available to characterise the taxa, allowing for the recognition of complexes of cryptic species and alien species, for example, opposing the traditional view of species with wide distributions or even cosmopolitan [5,92].

Molecular data are extremely useful to delimit new species or even identify valid species, however it must be accompanied by voucher specimens and preferably be obtained from animals from the type localities of the species, in the case of those already described. Molecular data of misidentified species can generate much confusion. Additionally, in most cases, type species of the genera were not sequenced yet and cannot be included in the resulting phylogenies, compromising all the results obtained. Molecular studies on Terebelliformia so far have resulted in 222,406 sequences available for Alvinellidae in Genbank (mostly transcriptomics and phylogenetic markers), 1011 for Ampharetidae, 1298 for Pectinariidae, 2588 for Terebellidae s.l., and 1476 for Trichobranchidae, considering mitochondrial and nuclear gene markers (Figure 10) (Table 3).

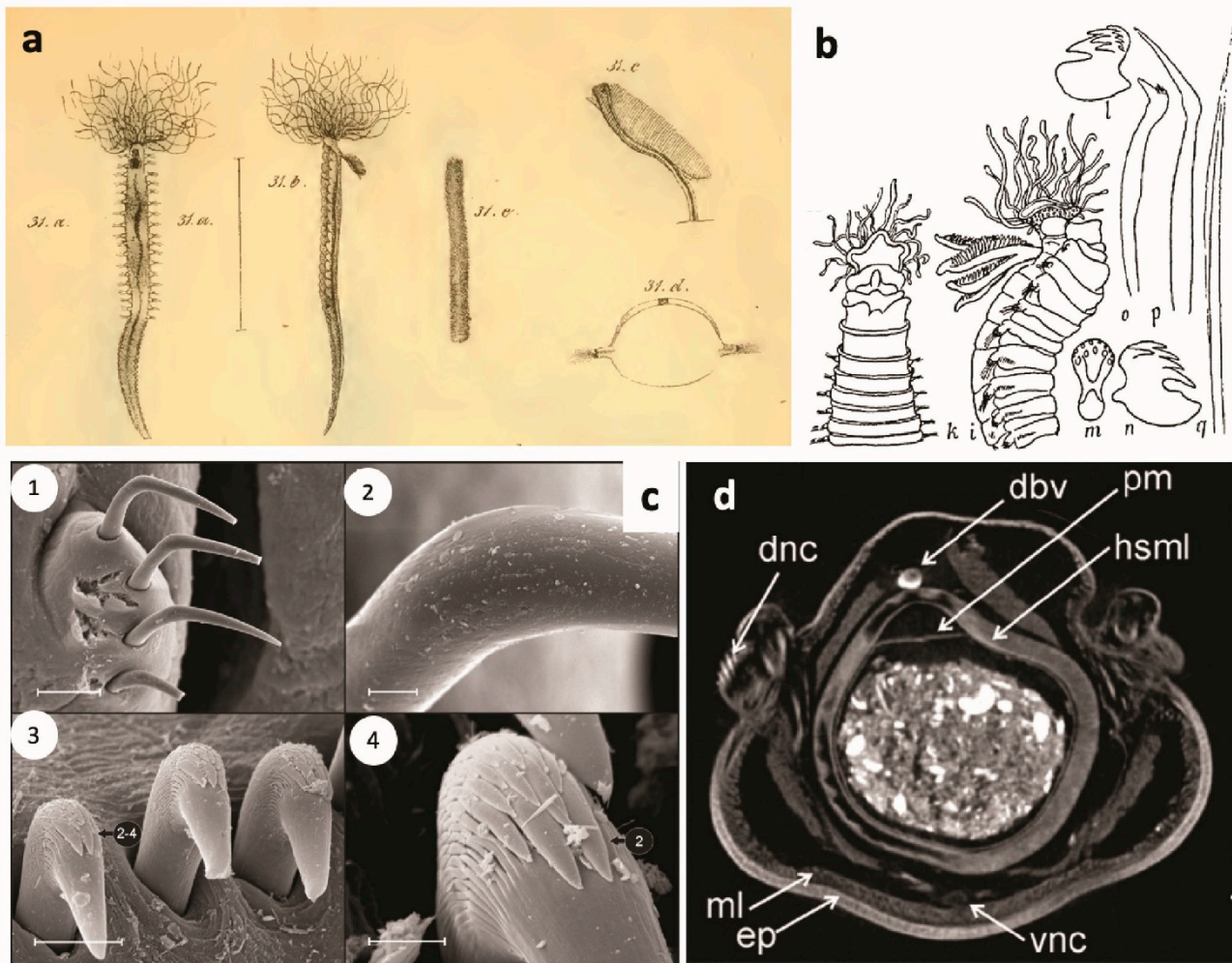


Figure 9. Evolution of appreciation of morphological traits important in taxonomy and techniques used, with *Terebellides stroemii* as an example. (a) Illustrations of the original description by Sars [108] (part of plate 13). (b) Later observations and key figures of the chaetae (setae), here summarized by Fauvel [86]. Key: i side view of anterior part; k ventral view; l–n, uncini front and side view; o, thoracic ventral hook; p, geniculate chaeta; q, dorsal chaeta. (c) Scanning Electron Microscopy of geniculate chaetae (1) and detail of the bend (2), thoracic uncini (3) and detail of the teeth (4) (Parapar et al. [109]). (d) Micro-computed tomography (μCT) allows cross sections to look at the anatomical level. Here, section at the level of thoracic chaetiger 9. dnc, dorsal notochaetae; dbv, dorsal blood vessel; hsml, hind stomach muscle layer; ml, muscle layer; pm, peritrophic membrane; vnc, ventral nerve chord. (Modified after Parapar and Hutchings [110]). Scale bars: a 50 μm, b 5 μm, c 10 μm, and d 3 μm.

Morphology-based polychaete taxonomy is largely based on external characters, particularly in Terebelliformia. Hesse [21] suggested a classification based on the structure of nephridia, however this requires dissection of the specimens, which is not feasible with museum material. However, a technique recently developed, computerized microtomography (μCT), scans the specimens and gives amazing 3D images of their internal anatomy (Figure 9) not causing any damage to the specimens, thus allowing type material to be largely replacing traditional line drawings (Figure 9). So far, few terebelliforms have been examined under the μCT, but as more are subjected to such analyses [111], additional morphological characters will certainly be found, increasing our knowledge on these animals. Then, from the end of the 20th century through to today, Scanning Electron Microscopy (SEM) provides a much better view of the surface of microscopic structures, such as chaetal ornamentation (Figure 9); Transmission Electron Microscopy (TEM) brought information on cellular ultrastructure; confocal microscopy allowed us to peer deep into the tissues and highlight specific organs; molecular tools became available to distinguish the

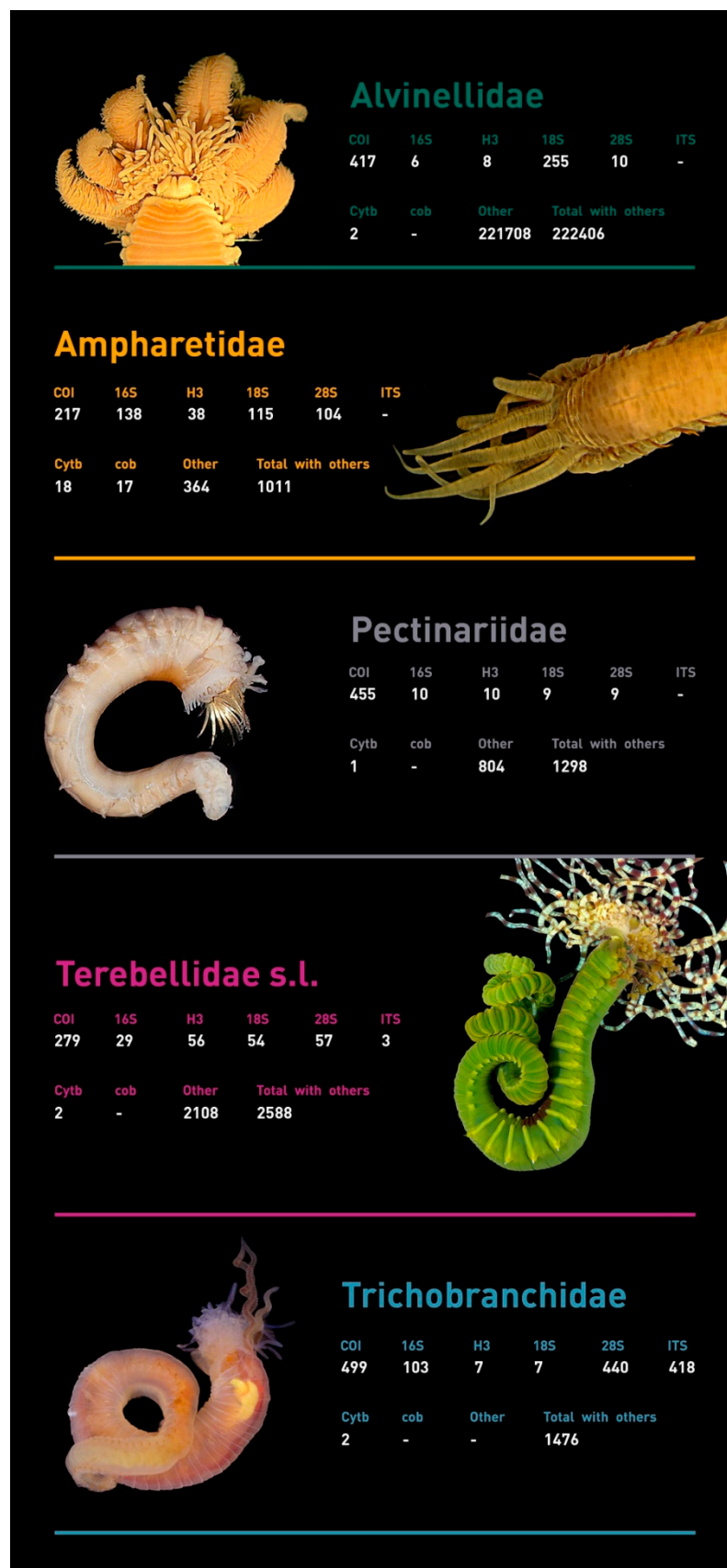


Figure 10. DNA sequences for Terebelliformia.

Table 3. Sequences available in Genbank for each main group of Terebelliformia.

	COI	16S	H3	18S	28S	ITS	Cytb	cob	Other	Total	% Sequences with Voucher
Alvinellidae	417	6	8	255	10	0	2	0	221,708	222,406	0.0
Ampharetidae	217	138	38	115	104	0	18	17	364	1011	53.9
Pectinariidae	455	10	10	9	9	0	1	0	804	1298	7.6
Terebellidae s.l.	279	29	56	54	57	3	2	0	2108	2588	19.7
Trichobranchidae	499	103	7	7	440	418	2	0	0	1476	793

3.6. Knowledge Gaps and Challenges for the Future

3.6.1. Poorly Known Regions of the World

As discussed above, some regions of the world have their local fauna of terebelliforms poorly known, as reflected by the low number of species originally described from those areas. In most cases, they correspond to poorly investigated areas of the world, such as the African coast (except for the Mediterranean part), Southern and Southeastern Asia, the western side of tropical America, corresponding to the Pacific Latin America shore, and all the Eastern Indo-Pacific realm, including the region from Hawaii and the Marshall Islands through Polynesia and the Mariana Islands to Easter Island. Those areas in most cases correspond to developing countries and/or with few institutions investigating invertebrate biodiversity. In some, however, the areas have been sampled and studied, but the identification of the specimens was made based on traditional monographs from other regions of the world, such as France [86,93], or South Africa [88], and resulting in many so called “cosmopolitan” species being recorded [92,112], whereas in fact they actually represent undescribed species. Even worse is that these names become incorporated into the ecological literature with no discussion as to the likelihood that a European species is present in China, for example (see [113]). With taxonomic studies of the fauna of Africa, India, China and other countries from SE Asia, and the Pacific side of America, the number of new species will certainly increase in the next decade or so and will mirror the tendency of the last decade (Figure 4).

Overall, the deep-sea also needs to be better explored, especially in areas that are not influenced by chemosynthetic local primary production. Better adapted gear for the sampling of sediment in which some species live may also be designed or adapted from other existing equipment.

Our knowledge of the deep-sea representatives of the terebelliforms, however, will soon expand as programmes are being conducted by many institutions around the world, such as the “Tropical Deep-Sea Benthos” series of cruises carried by the Museum National d’Histoire Naturelle, Paris, which have recently accessioned a large number of specimens to their collections. The use of tools, such as remotely operated vehicles (ROVs), has also allowed the targeted collection of deep-sea samples, and these are making their way to taxonomists around the world.

3.6.2. Species Complexes

Recently, with the rejection of cosmopolitanism [92] and the wide use of modern tools such as SEM imaging and molecular analysis, scientists have re-examined well-known species from well-known areas in Europe, resulting in the description of several cryptic species, as new to science. Consequently, the number of terebelliform species continues to increase, and many species previously considered widely distributed have become restricted to smaller areas. One of the best examples is *Terebellides stroemii*, reported from all around the world but almost certainly restricted to Norwegian waters [5]. These authors, using molecular data, showed the presence of more than 25 species in the Northeastern Atlantic alone, hidden behind this so-called “cosmopolitan” species. Parapar et al. [94] has just formally described five of these species identified by Nygren et al. [5]. By launching the Spaghetti project, Lavesque and collaborators are revising all French species of Terebellidae s.l. This project has allowed them to describe nine new species of Trichobranchidae [99],

three species of Thelepodidae [98] and eight species of Polycirridae [97] from French waters, an area historically well studied by early polychaetes workers (Audouin, Caullery, Fauvel, Gravier, Quatrefages, Rullier, Saint-Joseph, Savigny, etc.). A subsequent paper will document the diversity of Terebellidae from French waters (Lavesque et al. in prep.).

3.6.3. Taxonomic Issues Which Need to Be Resolved

Several genera of terebelliforms are monotypic, known only from the original descriptions, which do not include many characters important for the taxonomy of these groups, and type material is lost, damaged or cannot be located. In many cases, the material was collected by earlier expeditions and corresponds to species described, for example, by Grube, Müller, Lamarck, McIntosh, Chamberlin and Caullery. In some cases, the descriptions and illustrations are such that it is impossible to define the genus and, in these cases, they must be declared as *nomen dubium*, or indeterminate, at least until more material from the type of locality is collected and a neotype designated. Currently the genera *Paralanice* Caullery, 1944, *Opisthopista* Caullery, 1944 and *Spiroverma* Uchida, 1968, in the Terebellidae s.s., cannot be defined. Ebbe and Purschke [8] also list the monotypic genera, *Aryandes* Kinberg, 1866, *Rytocephalus* Quatrefages, 1866 and *Uschakovius* Laubier, 1973, as of doubtful affiliation. In some of the other cases, genera are not well known and Nogueira et al. [1] list those which could not be included in their phylogenetic study as the type material was either poorly preserved or too incomplete for scoring.

Another example is *Hadrachaeta* Hutchings, 1977. Although the type of locality has been extensively sampled through the years, since the original description, no additional specimens of *H. aspeta* Hutchings, 1977 have been obtained (Hutchings, pers. obs. [1]), and the type of material has been dissected several times, removing important diagnostic characters.

Another issue is whether some characters should be regarded as generic or species characters. These include the number of pairs of branchiae; in some genera, such as *Nicolea* Malmgren, 1866, they have two pairs, whereas in other genera the number of pairs is used to distinguish between species, such as in *Pista* Malmgren (2–3) and *Terebella* Linnaeus, 1767 (2–3, although the segment on which they occur can vary).

In *Pista*, the type of branching of the branchiae is a specific character. However, the genus *Pistella* which has only one pair of branchiae resembling some *Pista* species has recently been synonymised with *Pista* by Jirkov and Leontovich [63] but lacks the long-handled uncini characteristic of *Pista*. This is complicated by the type species of *Pista* (*Amphitrite cristata* Müller 1776) which was described as having one pair of branchiae, while Malmgren who erected the genus *Pista* and designated *P. cristata* (Müller 1776) as the type species, stated it has two pairs of branchiae, and no type material exists. However, this synonymy has between *Pista* and *Pistella* has not been accepted by other workers, and Hutchings et al. [2] record 76 species currently assigned to *Pista*, whereas the genus *Pistella* has four species.

Another issue which needs to be resolved is the development of long-handled uncini on thoracic neuropodia, which occur in several terebellid genera and their actual structure. Jirkov and Leontovich [63] have also suggested that all genera with long-handled uncini be synonymised with *Axionice* and that such structures are specific and not generic characters. This hypothesis has not been accepted but highlights the need for more developmental studies to actually study the development of the branchiae and the chaetae as the larvae settle and become juveniles. Similarly, the development and homologies of the peristomium and prostomium needs to be carefully investigated by developmental studies. Finally, the development of the anterior lateral lobes needs to be examined in detail, as their shape, orientation and the segment on which they occur appear to be very useful specific characters in many genera, although Jirkov and Leontovich [63] have suggested that all genera with large lateral lobes be synonymised, although they do not explain why this should happen.

A final issue concerns the genus *Pseudothelepus* Augener, 1918. Augener described this genus for *P. nyanganus* Augener, 1918, from the Tropical Atlantic coast of Africa. Later, Hartman [74] incorrectly synonymised *P. nyanganus* with *Sabellides oligocirra* Schmarda, 1861, described from the Caribbean, keeping the validity of the genus *Pseudothelepus* and changing the type species to *P. oligocirrus*. Unaware that the name was preoccupied, Hutchings [26] described an unusual thelepodid from Houtman Abrolhos Islands, Western Australia, as a new genus and species, which she named *Pseudothelepus binara* Hutchings, 1997. One of us (J.M.M.N.) examined the type of material of the three species and verified that all three are separate, valid species, rejecting the synonymy between *P. nyanganus* and *S. oligocirra*. However, both *P. nyanganus* and *S. oligocirra* are species of *Streblosoma*, and therefore *Pseudothelepus* is not valid. *Pseudothelepus binara*, in contrast, is a very different species, which justifies the erection of a new genus, since the original name is preoccupied, although that still requires phylogenetic confirmation.

So, in summary, not only will new species continue to be described around the world, but a more robust discussion needs to be had on the way in which generic and specific characters are defined, as well as better descriptions of those type species, which are currently inadequate. Ideally these descriptions will be based on neotypes and ideally with associated molecular data.

4. Discussion

As our taxonomic knowledge of this large group of polychaetes (both in terms of diversity and abundance) continues to increase, we need to develop online resources to make these data widely available to the wider biological community. Currently, online keys to the families are being developed and will be uploaded when completed (Kupriyanova et al. in prep.), which include all annelid families and genera as well as Australian species. Similar guides need to be developed for other parts of the world and the views that old monographs such as [86,93] and [88] should not be used and instead retained as historical documents [112] should become widely accepted.

An initiative in Australia could be developed elsewhere. The Atlas of Living Australia (<https://www.ala.org.au/>) is regularly updated by all the State natural history museums who upload their registered collection onto ALA. These data are all specimen based and you can interrogate the data and download distribution maps, as shown in Figure 11, which shows all the terebellid s.l. data from around Australia and indicates the number of species recorded around the coast which have all been checked by Hutchings and her colleagues. Similar analyses could be carried out in other parts of the world, but one needs to check the validity of the original identifications.

For example, if such data from terebellids as a selective deposit feeding group are combined with other polychaete families, which are filter feeders, such as the sabellids/serpulids, and opportunistic feeders, such as nereidids, for which the taxonomic data are good, one would be able to characterise benthic communities. Such data would be invaluable when developing zoning plans for marine national parks, which currently are often based on physical parameters, such as depth, sediment type, surrogates, such as seagrass beds, sponge gardens, coral reefs, and with limited biological data, such as fisheries data. Yet, the benthic communities dominate these parks and play a crucial role in the marine ecosystem and are barely considered. The sort of data which can be extracted from ALA could provide valuable data to improve the representativeness of marine parks and help develop monitoring programs to ensure that such plans are effectively conserving their biodiversity. Critically important is the fact that climate change is impacting our marine communities.

If we, taxonomists, can provide this sort of data to ecologists, marine managers, this may enhance our ability to attract funds to continue our research and to facilitate the training and mentoring of the next generation of taxonomists.

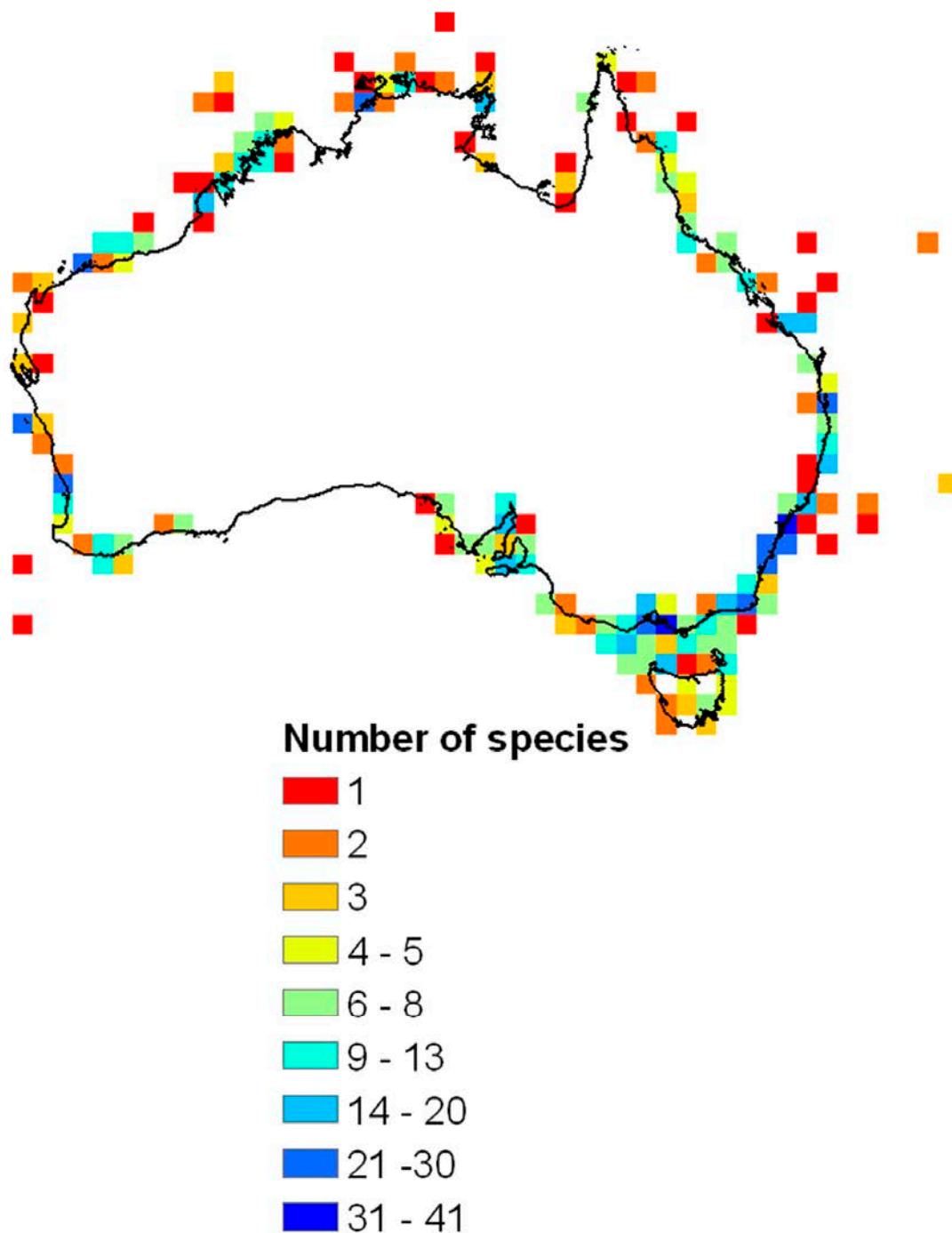


Figure 11. The distribution of terebellids ss. species around Australia based on data from ALA.

Supplementary Materials: The following are available online at <https://www.mdpi.com/1424-2818/13/2/60/s1>.

Figure 11. The distribution of terebellids ss. species around Australia based on data from ALA.

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CHAPITRE 1

Lavesque N., Hutchings P., Daffe G., Nygren A., Londoño-Mesa M.H. (2019). A revision of the French Trichobranchidae (Polychaeta), with descriptions of nine new species. *Zootaxa* 4664(2): 151-190*



Terebellides lilasae Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019

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A revision of the French Trichobranchidae (Polychaeta), with descriptions of nine new species

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Abstract

Trichobranchidae from French waters are revised based on material available in French marine stations and newly collected specimens. This research is the first part of the “Spaghetti Project” aiming to revise French species of terebellids and trichobranchids. It confirms the absence of the so-called cosmopolitan species *Terebellides stroemii* from French waters, and describes eight new species of *Terebellides*: *T. bonifi* n. sp., *T. ceneresi* n. sp., *T. europaea* n. sp., *T. gentili* n. sp., *T. gralli* n. sp., *T. lilasae* n. sp., *T. parapari* n. sp. and *T. resomari* n. sp. and one species of *Trichobranchus*: *T. demontaudouini* n. sp. using both morphological and molecular tools. An identification key for all European species of Trichobranchidae is provided.

Key words: Taxonomy, Systematic, Morphology, Molecular, Taxonomic key

Introduction

Trichobranchidae is a common family of tubicolous, deposit feeding polychaetes, found from shallow to shelf depths (Hutchings & Peart 2000), in all biogeographic regions (Garraffoni & Lana 2004). This family was considered, according to some authors (Fauvel 1927, Day 1967, Garraffoni & Lana, 2004) as a subfamily of Terebellidae; nevertheless, results obtained by Glasby *et al.* (2004) after a phylogenetic analysis of the clade Terebelliformia, have supported the hypothesis that Trichobranchidae is a valid distinct family. Currently, and after several synonymizations, only three genera are considered valid: *Octobranchus* Marion & Bobretzky, 1875, *Terebellides* Sars, 1835 and *Trichobranchus* Malmgren, 1866 (Hutchings *et al.* 2017).

The genus *Octobranchus* Marion & Bobretzky, 1875 comprises 10 valid species (Hutchings *et al.* 2017) with only two species known from European waters, *Octobranchus floriceps* Kingston & Mackie, 1980 (type locality: Northern North Sea), and *Octobranchus lingulatus* (Grube, 1863) (type locality: Adriatic Sea, and occurring in French Mediterranean waters) (Fauvel 1927).

The genus *Terebellides* Sars, 1835 is the most speciose within the family Trichobranchidae, with 52 currently valid species (Hutchings *et al.* 2017). However, the diversity within this genus is largely underestimated and several new species have almost certainly been misidentified as the cosmopolitan species *Terebellides stroemii* Sars, 1835 described from Norway (Nygren *et al.* 2018). Indeed, its distinctive large branchial structure made them recognizable, ‘easy to identify’ and has led to years of misidentifications (Parapar & Hutchings 2014; Hutchings & Kupriyaynova 2018). The diversity of *Terebellides* is still far from being well known (Parapar *et al.* 2014) and our study confirms that *T. stroemii* is probably absent from French waters, even though it was the only species recorded in France

belonging to the genus (Fauvel 1927; RESOMAR – French marine stations and observatories network – database, <http://resomar.cnrs.fr/bases/index.php>). In Europe, six species have been described or reported to date: *Terebellides atlantis* Williams, 1984 (type locality: New England slope), *T. bigeniculatus* Parapar, Moreira & Helgason, 2011 (type locality: Northwestern Iceland), *T. gracilis* Malm, 1874 (type locality: Skagerrak), *T. mediterranea* Parapar, Mikac & Fiege, 2013 (type locality: Northern Adriatic Sea), *T. shetlandica* Parapar, Moreira & O'Reilly, 2016 (type locality: between Shetland and Norway), and the type species of the genus, *T. stroemii* (type locality: Southwestern Norway). A recent study using molecular tools demonstrated the presence of more than 25 species in Northeastern Atlantic (Nygren *et al.* 2018). As few sequences could be linked to currently described species, a major revision of the genus is required.

Finally, the genus *Trichobranthus* Malmgren, 1866 includes 11 valid species (Hutchings *et al.* 2017). In French waters, *Trichobranthus glacialis* Malmgren, 1866 (type locality Spitzbergen, Arctic Ocean) is the only representative of the genus currently reported (Fauvel 1927; RESOMAR database). A second species, *Trichobranthus roseus* (Malm, 1874) (type locality: Western Sweden), also occurs in Europe (Gil 2011).

In 2016, the RESOMAR Benthic Team organized a workshop (Arcachon by Mario H. Londoño-Mesa) and a national taxonomic course (Caen by Pat Hutchings) on Terebellida (commonly called spaghetti worms). After discussions and observations of different specimens, participants realized that several species in French waters were erroneously identified, and certainly include undescribed ones. In this context, the first author decided to launch the “Spaghetti Project” aiming to revise French species of terebellids and trichobranchids. This collaborative project involves all benthic taxonomists of marine stations and includes newly collected material as well as material already available from the French marine stations (see Acknowledgements section). During the first part of the “Spaghetti Project”, we undertook a comprehensive survey of Trichobranthidae, and found three genera represented by eleven species, nine of which are herein described as new. A taxonomic key for European species of Trichobranthidae is provided.

Material and methods

Morphological observations. Specimens were collected during different research programs or specific samplings (see Acknowledgements) along the French coasts (North Sea, English Channel, Bay of Biscay and Mediterranean Sea) (Fig. 1) using Van Veen and Hamon grabs. For morphological analyses, specimens were fixed in 4% formaldehyde seawater solution; then, transferred to 70% ethanol. Methyl green, which can be washed out, was used to observe glandular areas. For molecular studies, the posterior part of the body (about 10 segments) was removed from several fresh specimens and fixed in 96% ethanol, with the remaining part of the body fixed in formaldehyde seawater solution.

Preserved specimens were examined under a Nikon SMZ25 stereomicroscope and a Nikon Eclipse E400 microscope, and photographed with a Nikon DS-Ri 2 digital camera. Measurements were made using the NIS-Elements Analysis software, with width corresponding to the widest segments with parapodia in the thoracic anterior region (about segment 10). Dehydrated specimens used for examination with scanning electron microscopy (SEM) were prepared by critical point drying, coated with gold and examined and photographed with a Hitachi TM3030 at Arcachon Marine Station, and with a JEOL JSM 6480LA at Macquarie University, Sydney.

Description of new species are based on the holotype and paratypes variations are given in brackets. The studied material is deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Australian Museum, Sydney (AM). Additional material is lodged in the collection housed at the Arcachon Marine Station (SMA).

Molecular data and analyses. Sub-samples for DNA analysis were removed from live specimens, placed in ethanol 96% and frozen at -20°C. Rest of bodies were fixed for morphological examination in order to link vouchers to material examined. Extraction of DNA was done with QIAamp DNA Micro Kit (QIAGEN) following protocol supplied by the manufacturers. The COI (cytochrome c oxidase subunit I), 16S and ITS genes were amplified using different primers: 16SANNF (GCGGTATCCTGACCGTRCWAAGGTA) (Sjölin *et al.* 2005) or 16SARL (CGCCTGTTTATCAAAAACAT), together with 16SBRH (CCGGTCTGAACTCAGATCACGT) for 16S rDNA (Palumbi 1996); LCO1490 (GGTCAACAAATCATAAAGATATTGG) and HCO2198 (TAAACTTCAGGGT-GACCAAAAATCA) (Folmer *et al.* 1994), or COIE (TATACTTCTGGGTGTCCGAAGAATCA) (Bely & Wray, 2004) for COI; and ITS58SF (GAATTGCAGGACACATTGAAC) and ITS28SR (ATGCTTAAATTCAGCGGGT)

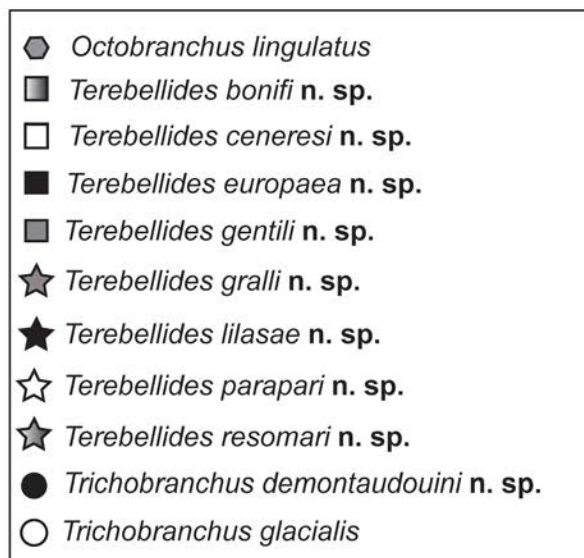
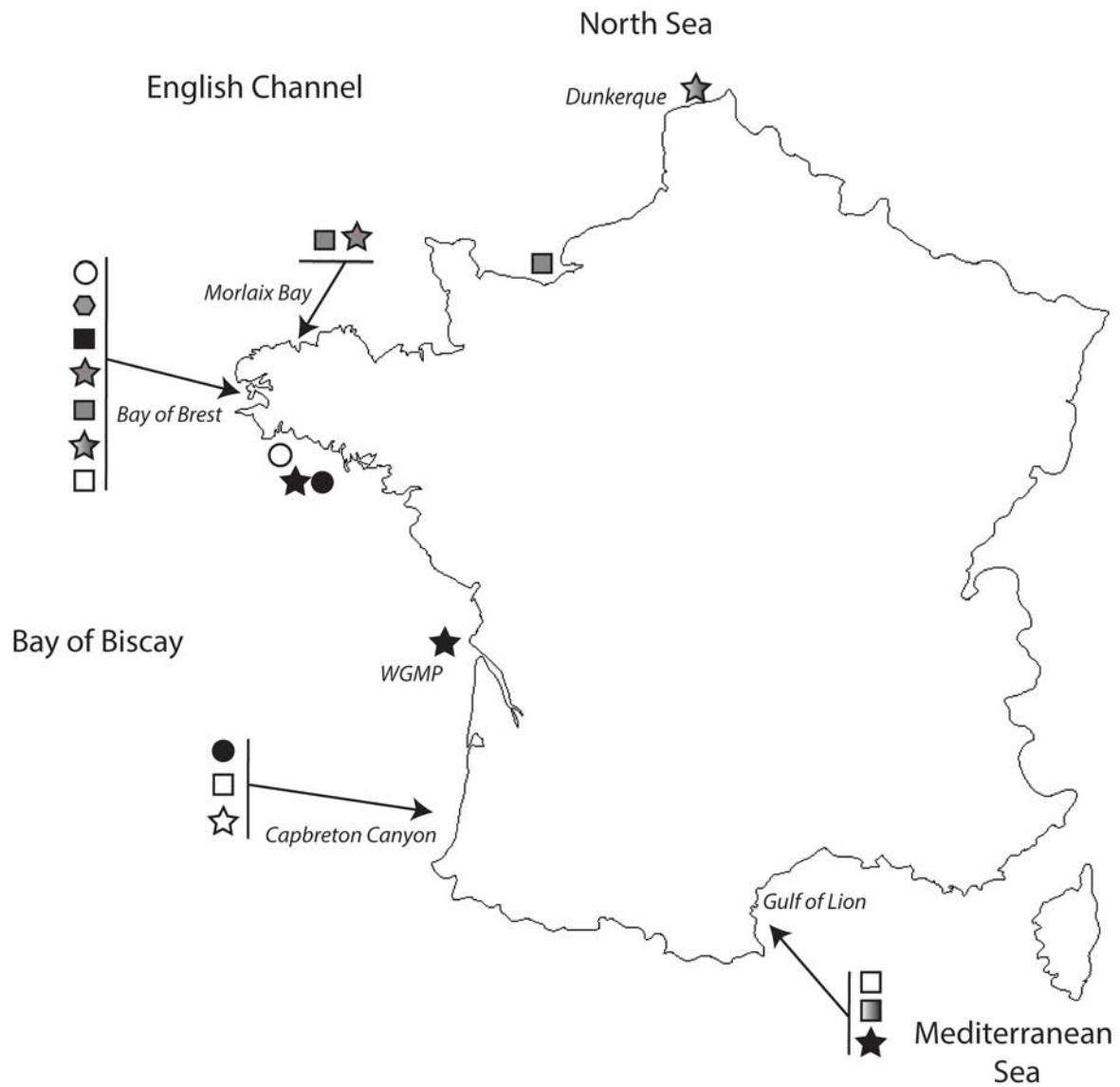


FIGURE 1. Schematic distribution of the different Trichobranchidae species along the French coasts. Text in italic represents type locality of new species. Abbreviation: WGMP, West Gironde Mud Patch.

(Nygren *et al.* 2009) for ITS2. The PCR (Polymerase Chain Reaction) was realised with Gotaq G2 Flexi DNA Polymerase (PROMEGA), with 50 μ L mixtures contained: 10 μ L of 5X Colorless GoTaq® Reaction Buffer (final concentration of 1X), 1.5 μ L of MgCl₂ solution (final concentration of 1.5mM), 1 μ L of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 0.5 μ L of each primer (final concentration of 1 μ M), 0.2 μ L of GoTaq® G2 Flexi DNA Polymerase (5U/ μ L), 1 μ L template DNA and 33.8 μ L of nuclease-free water. The temperature profile was as follows for 16S: 94°C/600s—(94°C/60s-59°C/30s-72°C/90s) *40 cycles—72°C/600s—4°C, for COI: 94°C/600s—(94°C/40s-44°C/40s-72°C/60s) *5 cycles -(94°C/40s-51°C/40s-72°C/60s) *35 cycles—72°C/300s—4°C. Amplified PCR products were analysed by electrophoresis in a 1 % p/v agarose gel stained with ethidium bromide and were sent to GATC Biotech Company to complete double strain sequencing, using same set of primers as used for PCR.

Overlapping sequence (forward and reverse) fragments were merged into consensus sequences and aligned using Clustal Omega (Sievers *et al.* 2011). For COI, sequences were translated into amino acid alignment and checked for stop codons to avoid pseudogenes. All sequences obtained in this study were deposited in GenBank (Table 1).

Bayesian analyses were run in MrBayes version 3.2 (Ronquist *et al.* 2012) with 5 million generations, with GTR+G+I model for COI and 16S. Maximum likelihood analyses were performed in raxmlGUI (Stamatakis 2014). In RAXML, we used the same models as in MrBayes, and node support was assessed with 1000 bootstrap replicates. COI and 16S tree-based analysis were obtained with valid European species from Nygren *et al.* (2018), and available sequences of *Terebellides* species obtained in this study. Sequences of *Trichobranthus glacialis* and *Thelepus* sp. were used as outgroup (Table 1).

Tabl E 1. List of sequenced specimens with voucher specification and Genbank accession numbers for 16S, COI and ITS2 genes.

Species	Voucher	16S	COI	ITS2
<i>Octobranthus cf. lingulatus</i>	SMA_Octo_08			MN219541
<i>Terebellides bonifi</i> n. sp.	MNHN-IA-TYPE 1860	MN219521		
<i>Terebellides ceneresi</i> n. sp.	SMA_BAN_11	MN219522		
<i>Terebellides europa</i> n. sp.	MNHN-IA-TYPE 1867	MN219523	MN207179	
	SMA_BR_10	MN219524	MN207180	MN219542
	MNHN-IA-TYPE 1868		MN207181	MN219543
	MNHN-IA-TYPE 1869	MN219525		
	SMA_SP_10	MN219526	MN207182	
<i>Terebellides gralli</i> n. sp.	MNHN-IA-TYPE 1878	MN219527		MN219544
<i>Terebellides lilasae</i> n. sp.	SMA_VOG8C2-A	MN219528	MN207183	
	SMA_VOG8C2-B	MN219529	MN207184	MN219545
	SMA_VOG8C2-C	MN219530	MN207185	
	SMA_BR_42	MN219531	MN207186	MN219546
	SMA_BAN_07	MN219532		
<i>Terebellides</i> sp.	SMA_BAN_17	MN219533		
<i>Terebellides</i> sp.	SMA_BR_23	MN219534	MN207187	
<i>Terebellides</i> sp.	SMA_BR_25	MN219535		
<i>Terebellides</i> sp.	SMA_BR_33	MN219536	MN207188	
<i>Terebellides</i> sp.	SMA_BR_35	MN219537		
<i>Thelepus</i> sp.	SMA_Thele_01	MN219538		
<i>Trichobranthus glacialis</i>	SMA_Tricho_08	MN219539	MN207189	MN219540

Abbreviations

AM	Australian Museum (Sydney, Australia)
COI	Cytochrome c Oxidase subunit I
MNHN	Muséum National d'Histoire Naturelle (Paris, France)
MG	Methyl green
RESOMAR	French Marine Stations and Observatories Network
SEM	Scanning electron microscope

SG	Segment
SMA	Station Marine Arcachon (Arcachon, France)
TC	Thoracic chaetiger
ZMB	Zoologisches Museum, Museum für Naturkunde der Humbolt-Universität, (Berlin, Germany)

Results

Taxonomic Account

Family Trichobranchidae Malmgren, 1866

Genus *Octobranchus* Marion & bobretzky, 1875

Type species: *Terebella lingulata* Grube, 1863 (*Octobranchus lingulatus* (Grube, 1863) by monotypy).

Octobranchus lingulatus (Grube, 1863)

Figure 2

Terebella lingulata Grube, 1863: 56–57, pl. 6 fig. 1.—Fauvel, 1927: 290, fig. 101 a–g.—Sardá, 1984: 129, fig. 3.—Hutchings & Peart, 2000: Table 2.

Octobranchus giardi Marion & Bobretzky, 1875: 87–90, pl. 10 fig. 21, pl. 11 fig. 21.

Material examined: MNHN-IA-PNT 91, one specimen, incomplete specimen, gravid, Northeast Atlantic Ocean, Brittany, Bay of Brest, station ZC, 48°18'55"N, 4°21'53"W, 5 m depth, May 2018. MNHN-IA-PNT 92, one specimen, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, station BK, 48°21'28"N, 4°26'38"W, 7 m depth, May 2018. MNHN-IA-PNT 93, one specimen, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, station ZC, 48°18'55"N, 4°21'54"W, 1.3 m, October 2016. MNHN-IA-PNT 94, 3 specimens (2 complete), Northeast Atlantic Ocean, Brittany, Bay of Brest, station ZC, 48°18'55"N, 4°21'54"W, 1.3 m, October 2016, mounted for SEM. AM W.50785, 3 incomplete specimens, Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'54"W, 1.3 m depth, June 2016.

Comparative material examined: ZMB Verm Q-5048, *Terebella lingulata* Grube 1863, holotype, described from Lussin Piccolo, Croatia, Adriatic Sea.

Description. Specimens very small. Complete specimens ranging from 3.59 to 6.32 mm in length, and 0.39 to 0.88 mm in maximum width in thoracic region. Complete specimens with 19 thoracic segments (16 TC) and between 23 and 24 abdominal neurochaetigers.

Thorax uniformly tapered, narrowing posteriorly, without clear boundary between thorax and abdomen (Fig. 2A). Buccal tentacles of two types: longer with ciliated depression on distal end, and shorter bulbous (Fig. 2C–D). Prostomium compact; tentacular membrane semicircular, projecting anteriorly (Fig. 2A–B). Eyespots present, arranged in two dorsal and two lateral patches, with 8–10 brown eyespots in each patch. Upper lip long, well developed, semicircular; lower lip poorly developed. Peristomium projecting as a bifurcated process, below the lower lip (Fig. 2A).

Four similar pairs of branchiae (SG2–5), basally thick, terminating in a filiform annulated process (Fig. 2B–C). First and fourth pairs inserted more dorsally, second and third pairs inserted more laterally (second pair more lateral than third one) (Fig. 2C). Lateral sides of branchiae basally with dense tufts of cilia between rings of the filiform process (Fig. 2C).

Lateral lobes present on SG2–5, as membranous collars. Second segment reduced ventrally, with two small lateroventral lobes (Fig. 2B). SG3 with large lateroventral lobes (auricular shape), connected ventrally by a collar, largely obscure those on second segment; inner surface slightly ridged. SG4 with a similar, though less well-developed lateroventral lappet, with a well-developed ventral collar. Segment 5 with a small dorsolateral lappet (Fig. 2B).

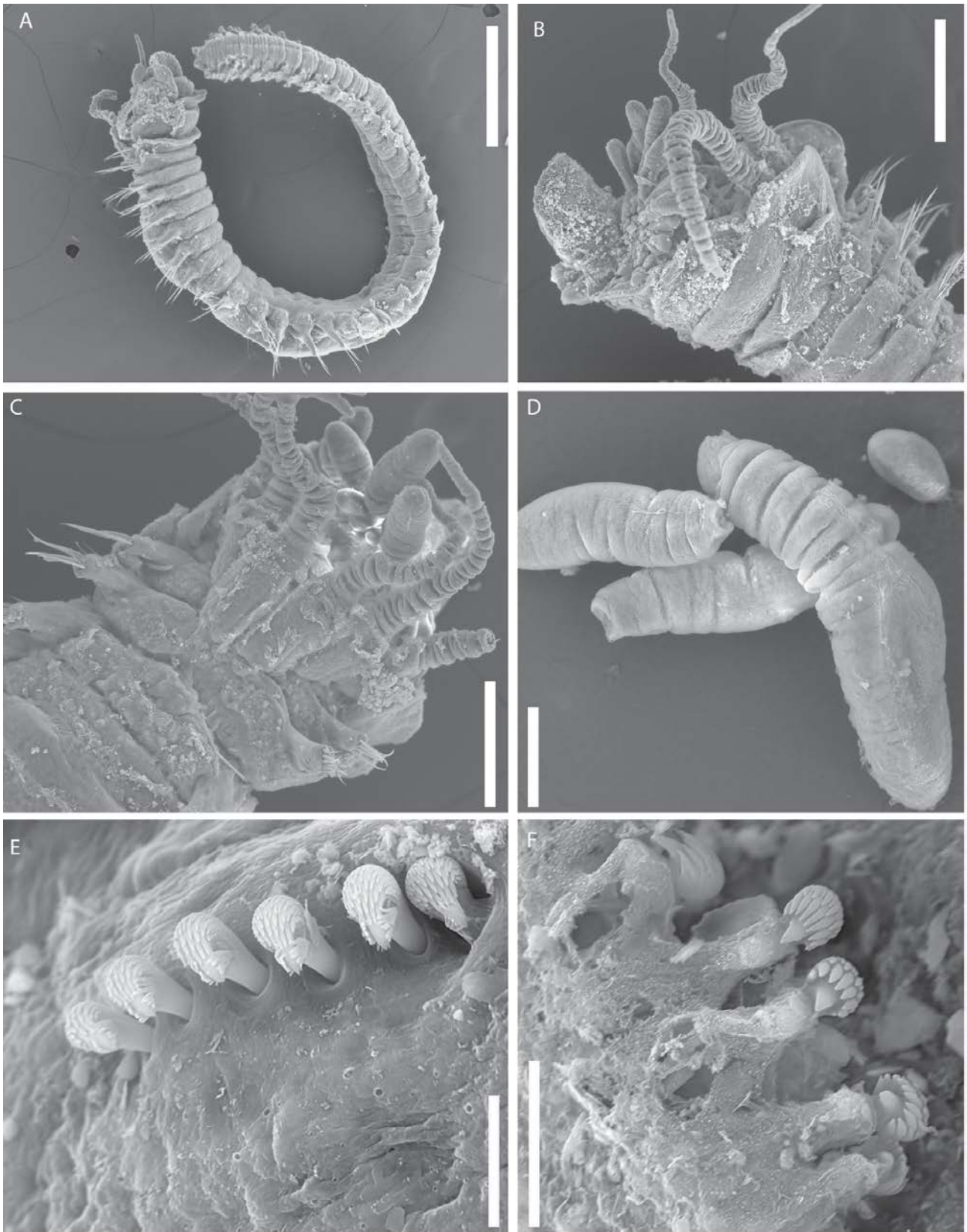


FIGURE 2. *Octobranchus lingulatus* (Grube, 1863) SEM, MNHN-IA-PNT 94A. Entire worm, lateral view **b**. Anterior region, lateral view; **C**. Anterior region, dorsal view; **D**. Buccal tentacles; **E**. Uncini, thoracic chaetiger; **F**. Uncini, abdominal chaetiger. Scales: A=500 μ m, B=250 μ m, C=125 μ m, D=50 μ m, E–F=10 μ m.

Sixteen pairs of notopodia, on SG4–19, elongate and well developed, first one always smaller than subsequent ones (Fig. 2A–C). Notochaetae of two sizes ($n = 9–12$), arranged in two rows, bilimbate with small limbus.

Neuropodia present as sessile pinnules from TC4 (SG7) to pygidium, with uncini arranged in a single row along body. Thoracic neuropodia with 6–10 uncini per torus. Uncini acicular with large main fang surmounted by five crests of denticles and beard below main fang (Fig. 2E). Abdominal neuropodia, as erect pinnules paddle-shaped, with 10–15 uncini per torus. Abdominal uncini with three rows of teeth above main fang, each row with numerous teeth (Fig. 2F).

Nephridial papillae not visible. Pygidium lobulated with two short anal cirri (Fig. 2A).

Remarks. We have compared our specimens with the holotype of *Terebella lingulata* Grube 1863 (ZMB Verm Q-5048, Zoologisches Museum, Museum für Naturkunde der Humbolt-Universität, Berlin) described from Lussin Piccolo, Croatia, Adriatic Sea. Holotype is in two parts and damaged. There are neither branchiae nor buccal tentacles remaining, and shape of lateral lobes is difficult to observe. Nevertheless, the main characteristics of French material matches with holotype. Our specimens differ only by the size (6.3 mm max instead of 7–10 mm for *O. lingulatus* (Hutchings & Peart, 2000) and shape of thoracic uncini and buccal tentacles. Thoracic uncini show beard below main fang which is reported here for the first time for the species. Moreover, a third row of teeth above the main fang of abdominal uncini is present, but visible only under SEM. This denticulation of thoracic uncini has an important taxonomic value and this character should be checked on new material of *O. lingulatus* from the type locality. Following Fauvel (1927) and Gil (2011), buccal tentacles are of one type, long grooved and spatulate. In French specimens, they are of two types: longer ones with ciliated depression situated on distal end, followed by an array of short bulbous ones (but latter could just be retracted long ones or not fully developed ones). Finally, Hutchings & Peart (2000) based on original figure of Grube (1863), reported that all described species of the genus, except *Octobranchus myunnus* Hutchings & Peart 2000, have “all pairs of notopodia of similar size”. This is not the case in either the French specimens of *O. lingulatus*, or on holotype, on which the first notopodia is always smaller than subsequent ones.

Habitat. In *Asparagopsis armata* and *Posidonia* spp. (Sardá 1984); in *Laminaria ochroleuca* (Parapar *et al.*, 1993), coastal maerl (rhodolith) beds (this study).

Type locality. Lussin Piccolo, Croatia, Adriatic Sea.

Distribution. Northeastern Atlantic Ocean (Madeira, Spain, France) (Kingston & Mackie, 1980; Parapar *et al.*, 1993; and this study); Mediterranean and Adriatic seas (Kingston & Mackie, 1980). These new records from Brittany represent a northerly expansion for this species and the first records for French Atlantic waters (Fig. 1).

Genus *Terebellides* Sars, 1835

Type species: *Terebellides stroemii* Sars, 1835

Terebellides bonifi n. sp.

Figures 3–4, Table 2

Type material: Holotype: MNHN-IA-TYPE 1859, gravid, incomplete, Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018. **Paratypes:** MNHN-IA-TYPE 1860, one specimen, complete (posterior part used for molecular analysis), Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018; MNHN-IA-TYPE 1861, one specimen, complete, Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018. MNHN-IA-TYPE 1862, one specimen, gravid, complete, Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018, mounted for SEM. All type specimens fixed with 96% alcohol.

Description. Relatively large species, with incomplete holotype 29.8 mm long (22.2–24.3) and 1.8 mm (1.8–2 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compacted towards pygidium.

Prostomium compact; eyespots absent; large upper lip surrounding mouth with many buccal tentacles (Fig. 3B–D). Buccal tentacles of 2 types, uniformly cylindrical and with expanded tips, spatulate (Fig. 3C–D). Lower lip forming an expanded structure below upper lip (Fig. 2B, D). SG1 and 2 short, only visible ventrally; following segments with lobes as ventral collars (Fig. 2B). Lateral lappets on SG3–6 (TC1–4), continuing ventrally in TC1–5,

largest on TC1 and declining in size posteriorly (Figs 3B, D & 4A). Conspicuous dorsal rounded projection on TC1–3 (Figs 3B, D & 4A). Presence of oval glandular lateral region on TC3 (Fig. 3D).

Branchiae arising as a single structure from TC1, reaching TC4 (TC3), consisting of single elongate and annulated stalk placed mid-dorsally (Figs 3A–D & 4A), 2 pairs of lobes, fused for about 1/2 of length, lower pair thinner. Upper lobes with about 45 tightly packed lamellae (Figs 3A–D & 4A–B). Anterior lamellae of each branchia with short conical papillae, visible under stereomicroscope (Figs 3C & 4A–B). Distal region of upper lobes with short projections, lower lobes with long projections (Fig. 3C–D). Anterior branchial projection (5th lobe) present (Figs 3A–B, D & 4A).

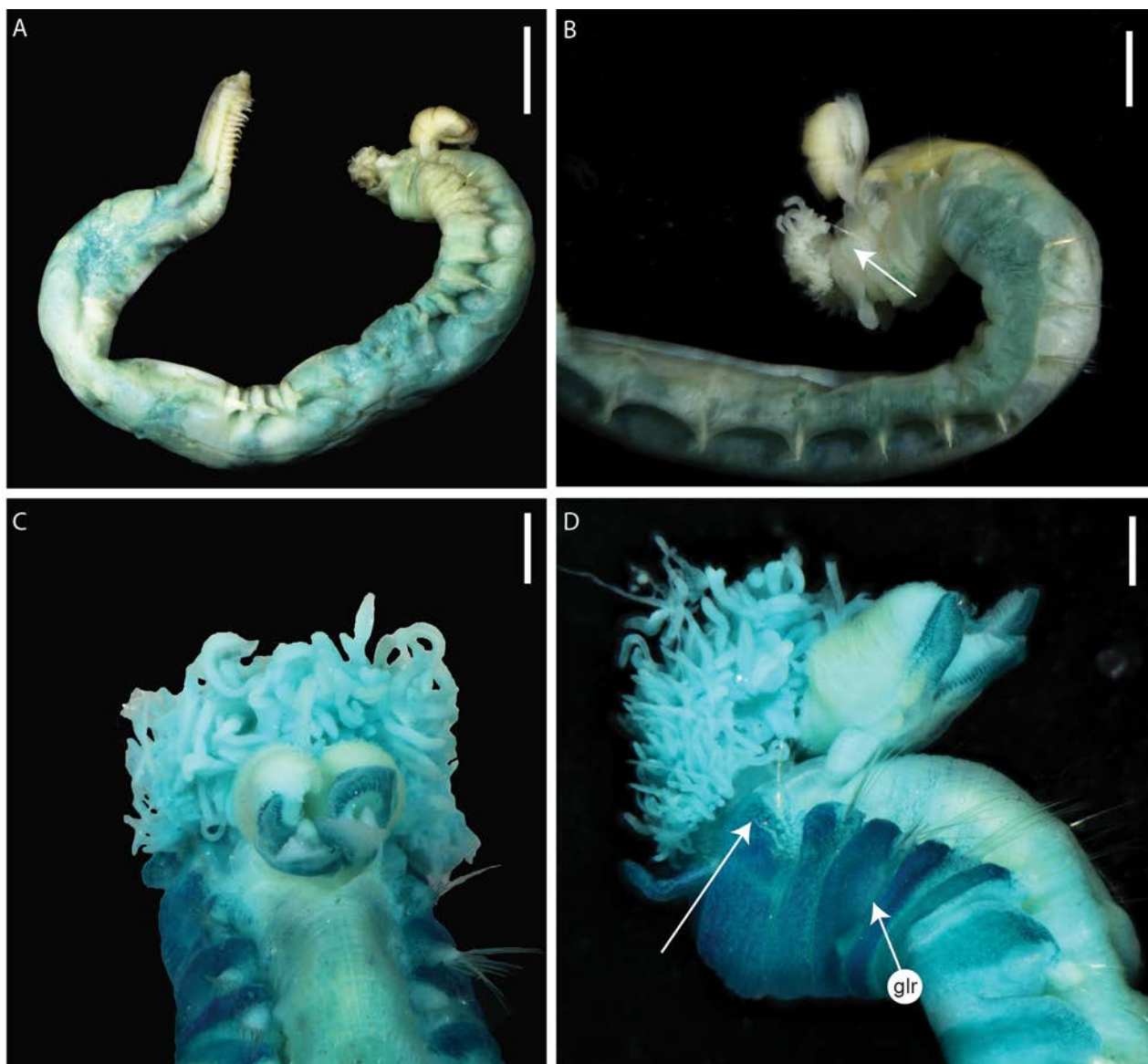


FIGURE 3. *Terebellides bonifi* n. sp. paratype MNHN-IA-TYPE 1861 (A), paratype MNHN-IA-TYPE 1860 (B), holotype MNHN-IA-TYPE 1859 (C–D) **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, dorsal view, methyl green staining; **D.** Anterior part, lateral view, methyl green staining. Abbreviation: glr, glandular lateral region. Arrow indicate conspicuous dorsal rounded projection of TC1. Scales: A=2 mm, B=1 mm, C–D=0.5 mm.

Eighteen pairs of thoracic notopodia (SG3–20). First notopodium slightly longer than subsequent notopodia; notochoetae from TC1 about same size as ones from subsequent notopodia, and transversally aligned (Fig. 3D). All notochoetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6 (SG8) to pygidium; uncini arranged in single rows from TC7. First thoracic neuropodium (TC6) provided with 5–7 sharply bent acute tipped, geniculate chaetae. All subsequent thoracic neuropodia with about 12–15 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks provided with long, thin and pointed main fang. Three or four

teeth above the main fang, surmounted by a row of three to five short denticles and an upper crest of several minute denticles (Fig. 4C). About 32 abdominal neuropodia as erect pinnules, paddle-shaped with entire margin provided with about 40 uncini; uncini with four pointed teeth above main fang, surmounted by a row of three short pointed teeth and an upper crest of minute teeth (Fig. 4D).

Two pairs of globular nephridial papillae, located latero-posteriorly to base of each notopodium of TC4 and TC5. Pygidium crenulated, as a funnel-like depression.

Methyl green staining pattern. First 4TC stain solid; TC5 and TC11 with distinct stripes; ventral faces of lobes stained dark blue; glandular region blue (Fig. 3C–D).

Etymology. The species is named after Paulo Bonifácio, *alias* Bonif, for his friendship and for being an excellent and fascinating worms' teacher to NL.

Habitat. Mud, about 90 m depth.

Type locality. Western Mediterranean Sea (Gulf of Lion), France (Fig. 1).

Distribution. Only known from type locality.

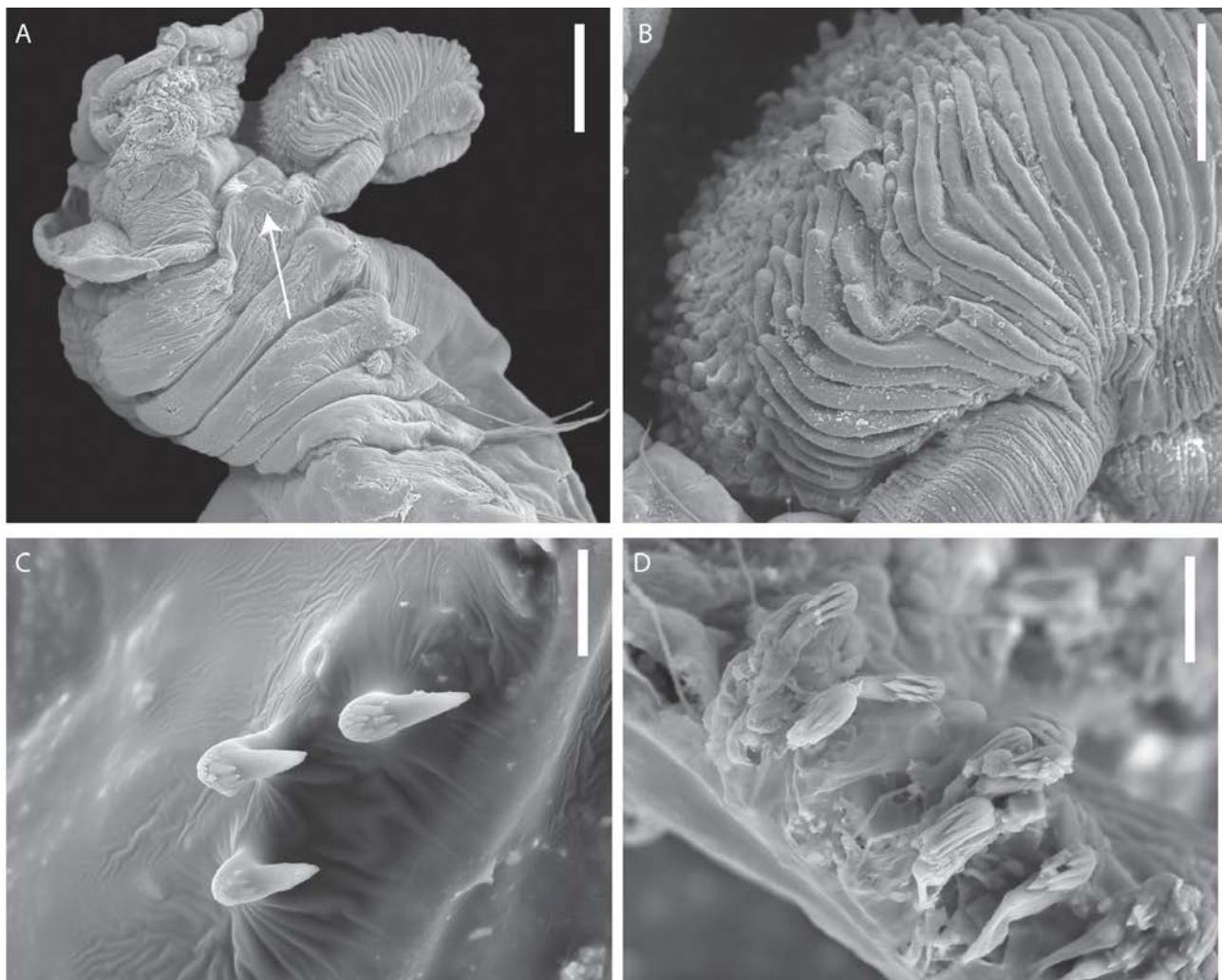


FIGURE 4. *Terebellides bonifi* n. sp. SEM paratype MNHN-IA-TYPE 1862 **A.** Anterior part, lateral view; **b.** Papillar projections on edge of anterior branchial lamellae, lateral view; **C.** Uncini, thoracic chaetiger; **D.** Uncini, abdominal chaetiger. Arrow indicate conspicuous dorsal rounded projection of TC1. Scales: A=500 μ m, B=200 μ m, C=15 μ m, D=15 μ m.

Remarks. *Terebellides bonifi* n. sp. is characterized by the papillar projections pointing over the edge of the branchial lamellae. By this characteristic, *T. bonifi* n. sp. is similar to *T. europea* n. sp., *T. gentili* n. sp., *T. lilasae* n. sp., *T. resomari* n. sp. and *T. stroemii* from Adriatic Sea (Parapar *et al.* 2013) (see *T. lilasae* n. sp. remarks). Among these species, *T. bonifi* n. sp. is similar to *T. europea* n. sp., in having papillar projections on anterior lamellae only, but differs from this species by the presence of an oval glandular region on TC3 (instead of undulating one for *T. europea* n. sp.) and presence of rounded conspicuous dorsal projection on TC1–3. The presence of oval glandular

region *T. bonifi* n. sp. is similar of that present in *T. lilasae* n. sp. and *T. stroemii* from Adriatic. However, these species differ by the absence of papillar projections on posterior branchial lamellae in *T. bonifi* n. sp. (presence on most of the lamellae *T. lilasae* n. sp. and *T. stroemii* from Adriatic), and by the shape of papillar projections, conical for *T. bonifi* n. sp., and rounded for *T. lilasae* n. sp. and *T. stroemii* from Adriatic.

Molecular results, based on material available for this study, show that *T. bonifi* n. sp. appears to be absent from Northern waters (Fig. 23).

***Terebellides ceneresi* n. sp.**

Figures 5–6, Table 2

Type material: **Holotype:** MNHN-IA-TYPE 1863, complete, Northeast Atlantic Ocean, Bay of Biscay, P34, 43°33'31"N, 1°43'49"W, 112 m depth, May 2018; **Paratypes:** MNHN-IA-TYPE 1864, one specimen, complete, Northeast Atlantic Ocean, Bay of Biscay, P36, 43°34'58"N, 1°42'01"W, 126 m depth, May 2018; AM W.51400, one specimen, complete, Northeast Atlantic Ocean, Bay of Biscay, P37, 43°33'31"N, 1°43'49"W, 129 m depth, May 2018; MNHN-IA-TYPE 1865, one specimen, complete, Northeast Atlantic Ocean, Bay of Biscay, P36, 43°35'0"N, 1°42'02"W, 125 m depth, May 2018.

Additional material examined: SMA_BAN_11, one specimen, complete (posterior part used for molecular analysis), Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018, mounted for SEM; SMA_BAN_20, one specimen, complete, Mediterranean Sea, Gulf of Lion, Ibis183, 42°30'30"N, 3°09'06"E, 40 m depth, December 2018; SMA_BAN_03, one specimen, complete, gravid, Mediterranean Sea, Gulf of Lion, A90, 42°32'40"N, 3°16'05"E, 90 m depth, August 2010, mounted for SEM; SMA_BR_34, incomplete, Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55" N, 4°21'53" W, 5 m depth, May 2018; AM W.51401, one specimen, complete, gravid, Mediterranean Sea, Gulf of Lion, A90, 42°32'40"N, 3°16'05"E, 90 m depth, August 2010; AM W.51402, one specimen, incomplete, Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018.

Description. Small species, holotype 14.2 mm long (14.2–16.5 mm) and 1.1 mm (0.8–1.1 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compacted towards pygidium.

Prostomium compact; eyespots absent; large upper lip surrounding mouth with many buccal tentacles (Fig. 5B, D). Buccal tentacles of 2 types, short cylindrical and very long tentacles, spatulate (Fig. 5D). Lower lip forming an expanded structure below upper lip. SG 1 and 2 short, only visible ventrally; following segments with lobes as ventral collars (Fig. 5D). Lateral lappets on SG3–7 (TC 1–5), continuing ventrally, largest on TC1–4 and declining in size posteriorly (Figs 5A–C). No conspicuous dorsal rounded projection on anterior chaetigers. Glandular lateral region absent on TC3 (Fig. 5C).

Branchiae arising as a single structure from TC1, reaching TC7 (TC8), consisting of a single elongate and annulated stalk placed mid-dorsally (Figs 5B–C & 6A), two pairs of lobes, not fused, lower pair narrower (Fig. 6A). Upper lobes with about 25 tightly packed lamellae (Figs 5A & 6A). Both sides of branchial lamellae provided with several parallel rows of cilia and tufts of cilia on outer edge (Fig. 6A–B). Branchiae provided without any papillar projections pointing over the edge of the branchial lamellae (Fig. 6B). Distal region of lower lobes with short terminal pointed projections (Fig. 6A). Anterior branchial projection (5th lobe) absent (Fig. 6A).

Eighteen pairs of thoracic notopodia (SG3–20). First notopodium on TC1 well-developed, same size as on subsequent notopodia, notopodia placed in a straight line; notochoetae from TC1 much smaller (or absent) than following notochoetae (Figs 5A–C & 6A). All notochoetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6 (SG8) to pygidium; uncini arranged in single rows from TC7. First thoracic neuropodium (TC6) provided with about five to six sharply bent acute tipped, geniculate chaetae. All subsequent thoracic neuropodia with 7–10 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks provided with long, thin and pointed main fang appearing bent terminally giving an 'eagle head' appearance (Fig. 6C). Three or four teeth above the main fang, surmounted by a row of four to five short denticles and an upper crest of several smaller denticles (Fig. 6C). About 30 abdominal neuropodia as erect pinnules paddle-shaped with entire margin provided with about 20 uncini; each with four to six pointed teeth above main fang, surmounted by a row of four or five short pointed teeth and an upper crest of minute teeth (Fig. 6D).

Nephridial papillae not seen. Pygidium blunt, as a funnel-like depression.

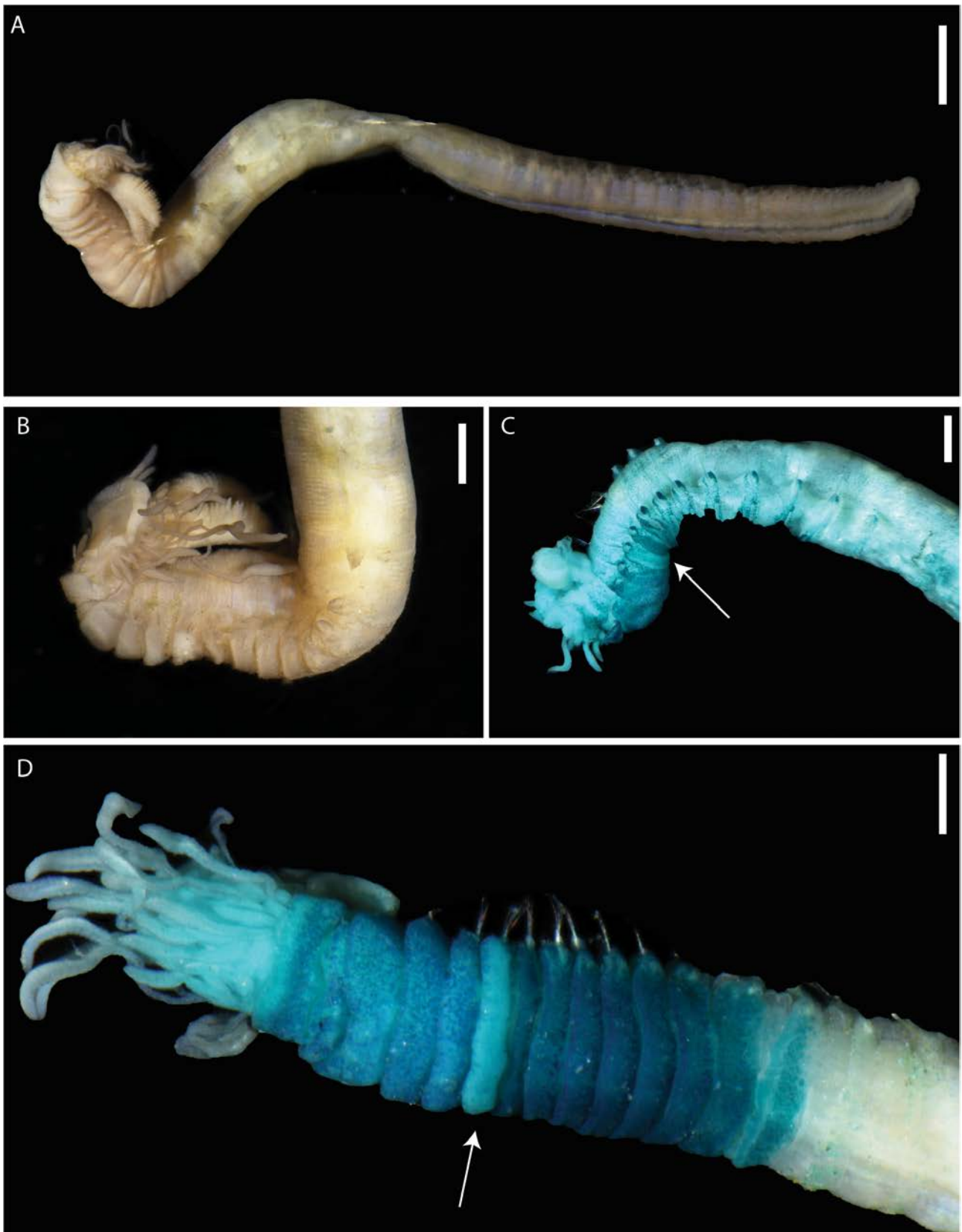


FIGURE 5. *Terebellides ceneresi* n. sp. holotype MNHN-IA-TYPE 1863 (A, C), additional material SMA_BAN_09 (C) and paratype MNHN-IA-TYPE 1864 (D) **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, lateral view, methyl green staining; **C.** Anterior part, ventral view, methyl green staining. Arrows indicate ventral band on TC4. Scales: A=1 mm, B–C=0.5 mm, D=0.25 mm.

Methyl green staining pattern. First 10 TC stain solid, except TC4 much lighter (Fig. 5D); TC11 and TC12, stain with distinct stripes, fading towards posterior thoracic region (without staining, first four chaetigers slightly lighter than following ones) (Fig. 5D).

Etymology. The species is named in honour of the CNRS (French National Center for Scientific Research) that celebrates, in 2019, 80 years since its foundation.

Habitat. Mud to sandy mud, from 90 to 140 m depth, coastal maerl (rhodolith) beds.

Type locality. Near Capbreton Canyon, Bay of Biscay, Northeast Atlantic Ocean, France.

Distribution. Northeast Atlantic Ocean (Bay of Biscay), Western Mediterranean Sea (Gulf of Lion), France (Fig. 1).

Remarks. *Terebellides ceneresi* n. sp. is very similar to specimens of *T. gracilis* from the Adriatic Sea (Parapar *et al.* 2013), in being of small size, without rounded dorsal projection or glandular region in CH3, the absence of notochaetae on first chaetiger in smaller specimens and short notochaetae on first chaetiger for larger ones and in having the same very distinctive MG staining pattern. The two species differ only by the presence of an ‘eagle head’ appearance of thoracic uncini of *T. ceneresi*. However, *T. ceneresi* n. sp. is clearly different from the holotype of *T. gracilis* (Parapar *et al.*, 2011). Indeed, *T. gracilis* is a larger species (32 mm vs 16 mm for gravid specimens of *T. ceneresi* n. sp.), with a 5th lobe present (absent in *T. ceneresi* n. sp.), with up to 22 uncini in thoracic chaetigers (instead of 8 in *T. ceneresi* n. sp.), with posterior region of lobes with pointed projections (instead of absence or very short projections in *T. ceneresi* n. sp.), with MG compact colouration from CH1 to CH10 (instead of whitish bands from CH1 to CH4, especially on CH4 in *T. ceneresi* n. sp.) (Table 2).

Molecular results, based on material available for this study, show that *T. ceneresi* n. sp. appears to be absent from Northern waters (Fig. 23).

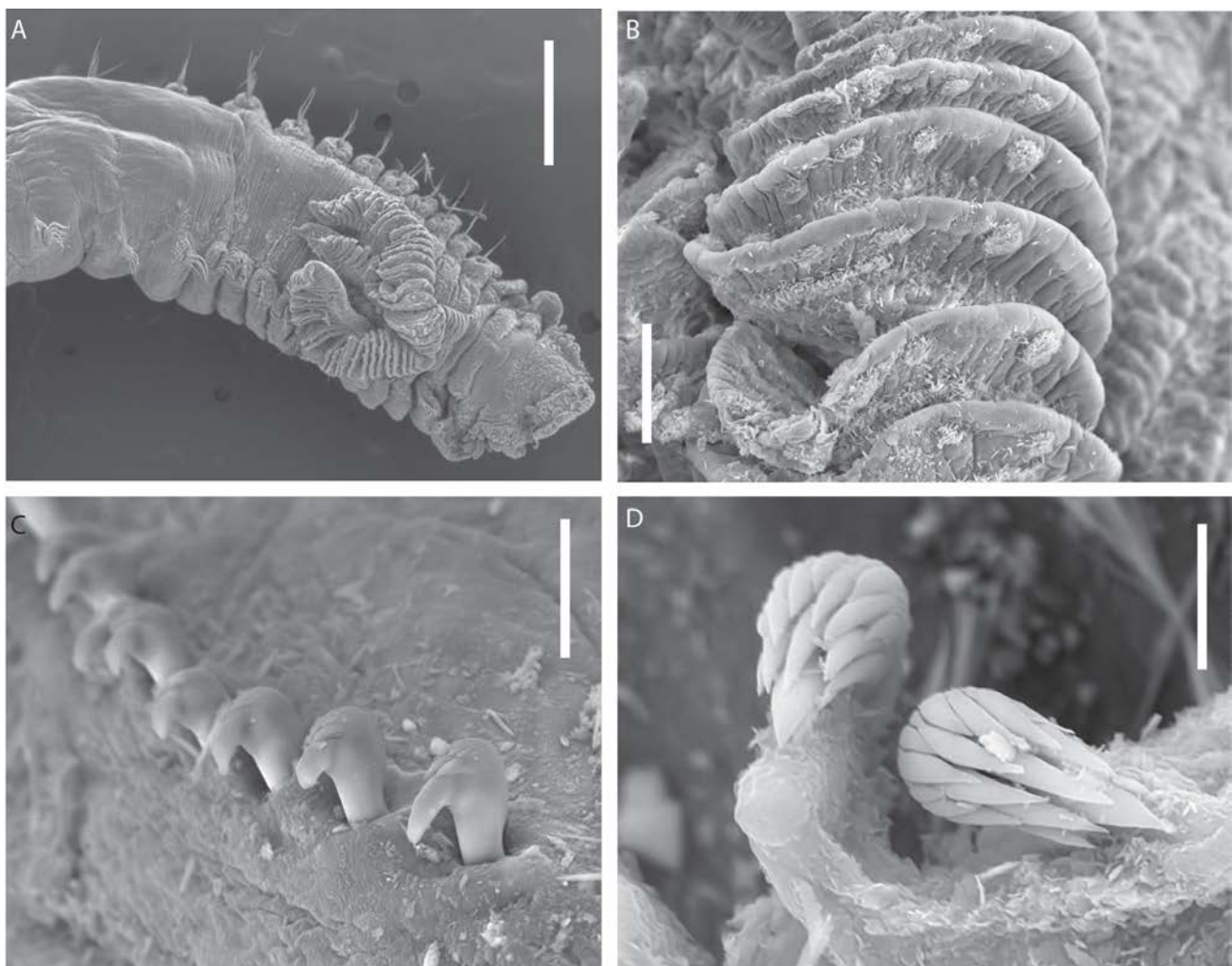


FIGURE 6. *Terebellides ceneresi* n. sp. SEM additional material SMA_BAN_03. **A.** Anterior part, dorsal view; **b.** detail of branchial lamellae, dorsal view; **C.** Uncini, thoracic chaetiger; **D.** Uncini, abdominal chaetiger. Scales: A=600 μ m, B=80 μ m, C=20 μ m, D=6 μ m.

Terebellides europaea n. sp.

Figures 7–8, Table 2

Type material: Holotype: MNHN-IA-TYPE 1866, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'54"W, 1.3 m depth, January 2016. **Paratypes:** MNHN-IA-TYPE 1867, complete specimen (posterior part used for molecular analysis), Northeast Atlantic Ocean, Brittany, Bay of Brest, VC, 48°18'59"N, 4°23'28"W, 2.2 m depth, July 2017; MNHN-IA-TYPE 1868, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'53"W, 5 m depth, May 2018; MNHN-IA-TYPE 1869, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Brittany, Bay of Brest, BK, 48°21'28"N, 4°26'38"W, 7 m depth, May 2018, mounted for SEM.

Additional material examined: SMA_BR_10, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Brittany, Bay of Brest, VC, 48°18'59"N, 4°23'28"W, 2.2 m depth, July 2017. SMA_SP_10, complete, (posterior part used for molecular analysis), Northeast Atlantic Ocean, Spain, Ria de Ferrol, 43°28'N, 8°14'W, 40 m depth, June 2017.

Description. Small size species, with holotype 16.9 mm long (15.4 mm) and 2.1 mm (1.5–2.2 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compacted towards pygidium.

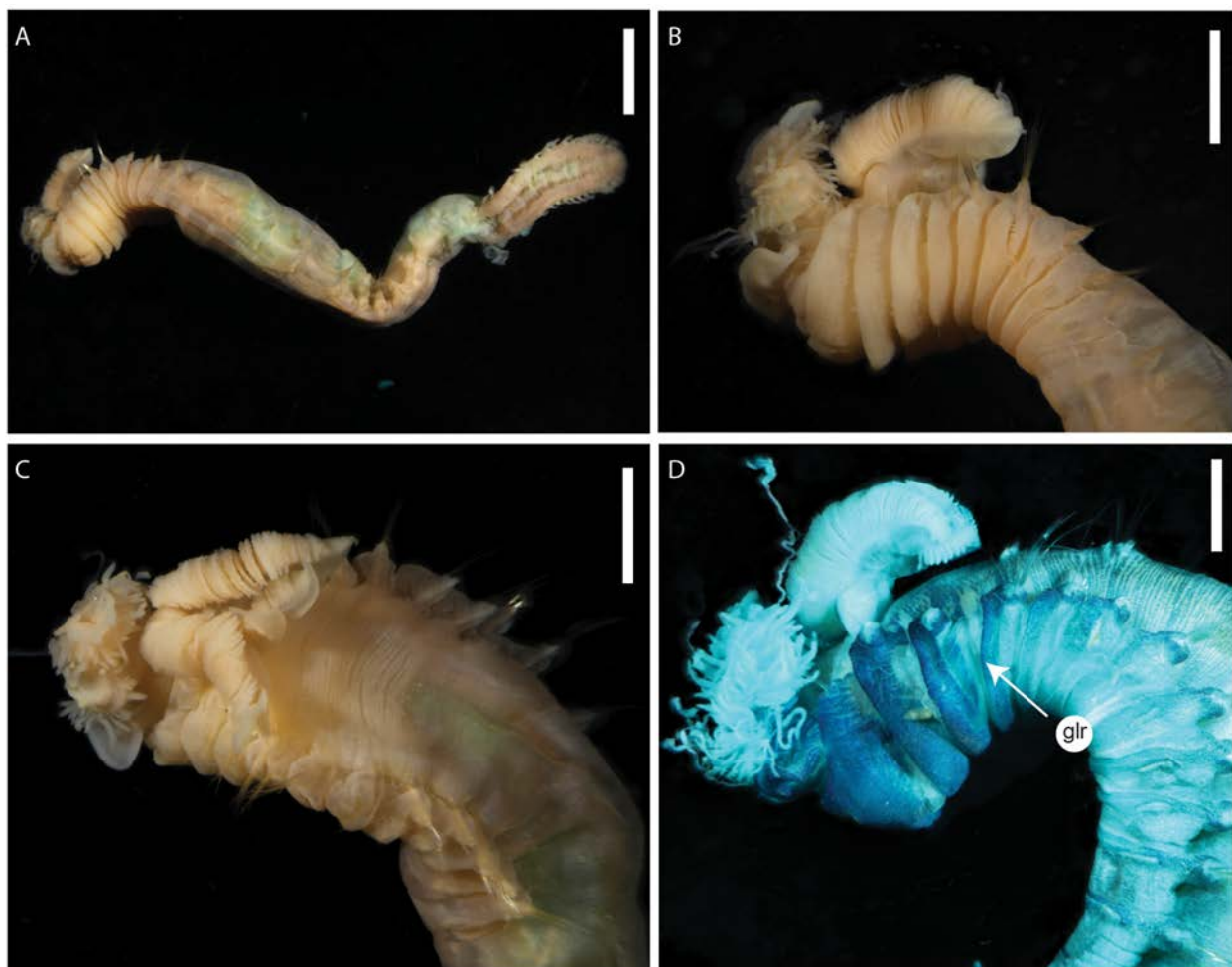


FIGURE 7. *Terebellides europaea* n. sp. holotype MNHN-IA-TYPE 1866 (A–C), paratype MNHN-IA-TYPE 1867 (D). **A.** Entire worm, ventro-lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, dorsal view; **D.** Anterior part, lateral view, methyl green staining. Abbreviation: glr, glandular lateral region. Scales: A=2 mm, B–D =1 mm.

Prostomium compact; eyespots absent; large upper lip surrounding mouth with many buccal tentacles (Figs 7B–D & 8A). Buccal tentacles of two types, uniformly cylindrical and with expanded tips, spatulate (Fig. 8A). Lower lip forming an expanded structure below upper lip (Figs 7A–B & 8A). S1 and S2 short, only visible ventrally; following segments with lobes as ventral collars (Fig. 7A–B). Lateral lappets on SG3–6, (TC 1–5), continuing ven-

trally in TC1–6, largest on TC1 and 2 and declining in size posteriorly. No conspicuous dorsal rounded projection on anterior chaetigers. Postero-lateral undulating glandular region on TC3 (Fig. 7D).

Branchiae arising as a single structure from TC1 and reaching TC6 (TC4), consisting of a single elongate and annulated stalk situated mid-dorsally, made up of two pairs of lobes fused on 1/2 of length, lower pair thinner (Fig. 7C). Posterior region of upper terminal pointed projections and of lower lobes with long pointed projections (Fig. 7B–C). Upper lobes provided with about 50 well packed lamellae, lamellae of different width and size (Figs 7B–C & 8A–B). Both sides of branchial lamellae provided with well-marked parallel rows of cilia, no tufts of cilia on outer edge (Fig. 8A–B). Presence of rounded papillar projections over the edge of anterior branchial lamellae (Figs 7B–C & 8A–B). Anterior branchial projection (5th lobe) present (Figs 7A–B, D & 8A).

Eighteen pairs of thoracic notopodia (SG3–20; TC1–18). Notopodia present from TC1 well-developed; notochoetae of TC1 slightly longer in length than following notochoetae. All notochoetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6 (SG 8) to pygidium, with uncini arranged in a single row from TC7. First thoracic neuropodia (TC6) provided with four (3–5) sharply bent acute tipped to almost straight, geniculate chaetae. All subsequent thoracic neuropodia with about 10–17 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks provided with long, thin and pointed main fang, straight terminally. Three or four teeth above the main fang, surmounted by a row of five to six short denticles and an upper crest of several minute denticles (Fig. 8C). Abdomen with 33 neuropodia as erect pinnules paddle-shaped with entire margin provided with about 30 uncini; each with four pointed teeth above main fang, surmounted by a row of three to five short pointed teeth and an upper crest of minute teeth (Fig. 8D).

Two pairs of elongated nephridial papillae, located latero-posteriorly to base of each notopodium of TC4 and TC5. Pygidium blunt.

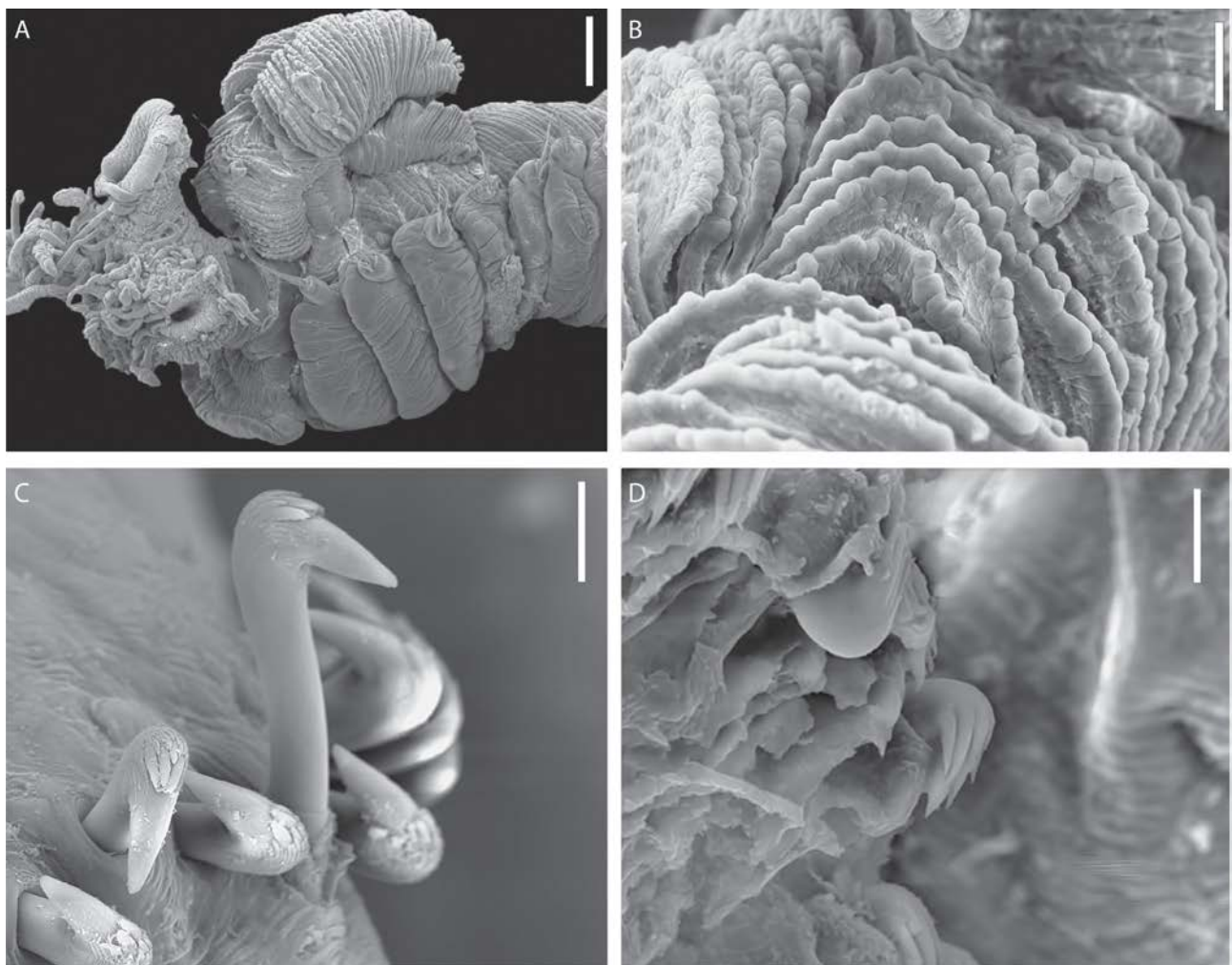


FIGURE 8. *Terebellides europaea* n. sp. SEM paratype MNHN-IA-TYPE 1869A. **a.** Anterior part, lateral view; **b.** Papillar projections on edge of anterior branchial lamellae, lateral view; **c.** Uncini, thoracic chaetiger; **d.** Uncini, abdominal chaetiger. Scales: A=500 μ m, B=250 μ m, C=15 μ m, D=9 μ m.

Methyl green staining pattern. Solid from TC1 to TC9, with distinct stripes from TC10 to about TC12, distinct white antero-ventral lines from TC5 to TC9; white glandular region on TC3, with central line more intensive stained and lateral deep ridges (Fig. 7D).

Etymology. Species name refers to the wide distribution of the species in Europe from the south of the Bay of Biscay (Spain) to North of Norway.

Habitat. Coastal maerl (rhodolith) beds, 2–11 m depth (this study), from mud to gravels, 8–102 m depth (Nygren *et al* 2018).

Type locality. Bay of Brest, Brittany, France.

Distribution. Bay of Biscay (Bay of Brest, Trévignon, Ria of Ferrol) (this study), Kattegat, Skagerrak, North Sea, Irish Sea, Celtic Sea and Norwegian coast and shelf (Nygren *et al.* 2018)

Remarks. Except *T. stroemii* from Adriatic Sea (Parapar *et al.* 2013) (see *T. lilasae* **n. sp.** Remarks), *Terebellides europaea* **n. sp.** differs from other previously known European species by the presence of papillar projections pointing over the edge of the branchial lamellae. In this character, *T. europaea* **n. sp.** is also similar to *T. bonifi* **n. sp.**, *T. gentili* **n. sp.**, *T. lilasae* **n. sp.** and *T. resomari* **n. sp.** Among these species, only *T. gentili* **n. sp.**, shares the same undulating glandular region on TC3. However, these two species differ in the shape of papillar projection (widely spaced, small and elongated for *T. gentili* **n. sp.**, rounded and only present on anterior lamellae for *T. europaea* **n. sp.**), by the size (<16 mm for *T. europaea* **n. sp.**, >30 mm for *T. gentili* **n. sp.**) and the presence of terminal filaments on the lower lobes for *T. europaea* **n. sp.**, (pointed projections only for *T. gentili* **n. sp.**) (Table 2).

Based on 16S and COI sequences, *T. europaea* **n. sp.** is identical to clade 6 from Nygren *et al.* (2018, Fig. 10). In this study, authors suggested that this clade could be *T. stroemii*. However, based on our observations, we are now confident that *T. europaea* **n. sp.** is different from *T. stroemii* which should not be associated with clade 6. Indeed, *T. europaea* **n. sp.** differs from *T. stroemii* by the presence of papillar projections over the edge of anterior branchial lamellae (absence for *T. stroemii*), the shape of glandular region on TC3 (undulating with lateral ridges for *T. europaea* **n. sp.**, oval for *T. stroemii*), the absence of both “eagle-shaped” thoracic uncini and rounded dorsal projection on TC1–5 (presence for *T. stroemii*) (Table 2). Next step will be to define which clade corresponds to the true *T. stroemii*. This is complicated by the fact that Sars did not designate a holotype and the exact locality is fairly vague and we know from Nygren *et al.* (2018) that more than one species can occur in the same location.

Terebellides gentili **n. sp.**

Figures 9–10, Table 2

Type material: Holotype: MNHN-IA-TYPE 1870, complete, gravid, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N, 3°51'58"W, 17 m depth, March 2015. **Paratypes:** MNHN-IA-TYPE 1871, one specimen, incomplete, gravid, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N, 3°51'58"W, 17 m depth, March 2015; MNHN-IA-TYPE 1872, one specimen, complete, English Channel, Brittany, Morlaix Bay, Château du Taureau, 48°40'26"N, 3°53'02"W, 12 m depth, August 2015; MNHN-IA-TYPE 1873, one specimen, complete, gravid, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N, 3°51'58"W, 17 m depth, March 2015, mounted for SEM; AM W.51395, one specimen, incomplete, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N, 3°51'58"W, 17 m depth, March 2018.

Additional material examined: AM W.51396, one specimen, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, MF1, 48°18'05" N, 4°19'26"W, 2 m depth, January 2016; SMA_ROS_08, one specimen, complete, gravid, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N, 3°51'58"W, 17 m depth, October 2014. SMA_BR_08, complete, gravid, Northeast Atlantic Ocean, Brittany, Bay of Brest, Camaret, 48°17'48"N, 4°34'59"W, 15 m depth, March 2015; SMA_OUI_02, one specimen, complete, English Channel, Bay of Seine, 49°26'05"N, 0°11'00"W, 30 m depth, April 2018.

Description. Large species, with holotype 30.4 mm long (15.1–31.9 mm) and 2.8 mm (1.5–2.8 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compacted towards pygidium.

Prostomium compact; eyespots absent; large upper lip surrounding mouth with many buccal tentacles (Figs 9C–D & 10A). Buccal tentacles of 2 types, uniformly cylindrical and with expanded tips, spatulate (Fig. 10A). Lower lip forming an expanded structure below upper lip (Figs 9A–D & 10A). SG1 and 2 short, only visible ventrally; following segments with lobes as ventral collars (Figs 9A–B, D & 10A). Lateral lappets on SG3–6, (TC1–4),

continuing ventrally in TC1–5, largest on TC1 and declining in size posteriorly. No conspicuous dorsal rounded projection on anterior chaetigers. Elongated glandular lateral region on TC3, with ventral portion pointed anteriorly (Fig. 9B, D).

Branchiae arising as a single structure from TC1, reaching TC6 (TC5), consisting of a single elongate and annulated stalk placed mid-dorsally (Figs 9A–D & 10A), two pairs of lobes, fused for about 1/2 of length, lower pair thinner (Fig. 9C). Upper lobes with 50 to 70 tightly packed lamellae (Figs 9A–D & 10A). Both sides of branchial lamellae provided with several parallel rows of cilia and tufts of cilia on outer edge (Fig. 10B). Most of individual lamellae of each branchia with widely spaced elongated small projecting papillae, visible under stereomicroscope (Fig. 10A–B). Distal region of both upper and lower lobes with long terminal pointed projections (Figs 9B–C & 10A). Anterior branchial projection (5th lobe) present (Figs 9A–C & 10A).

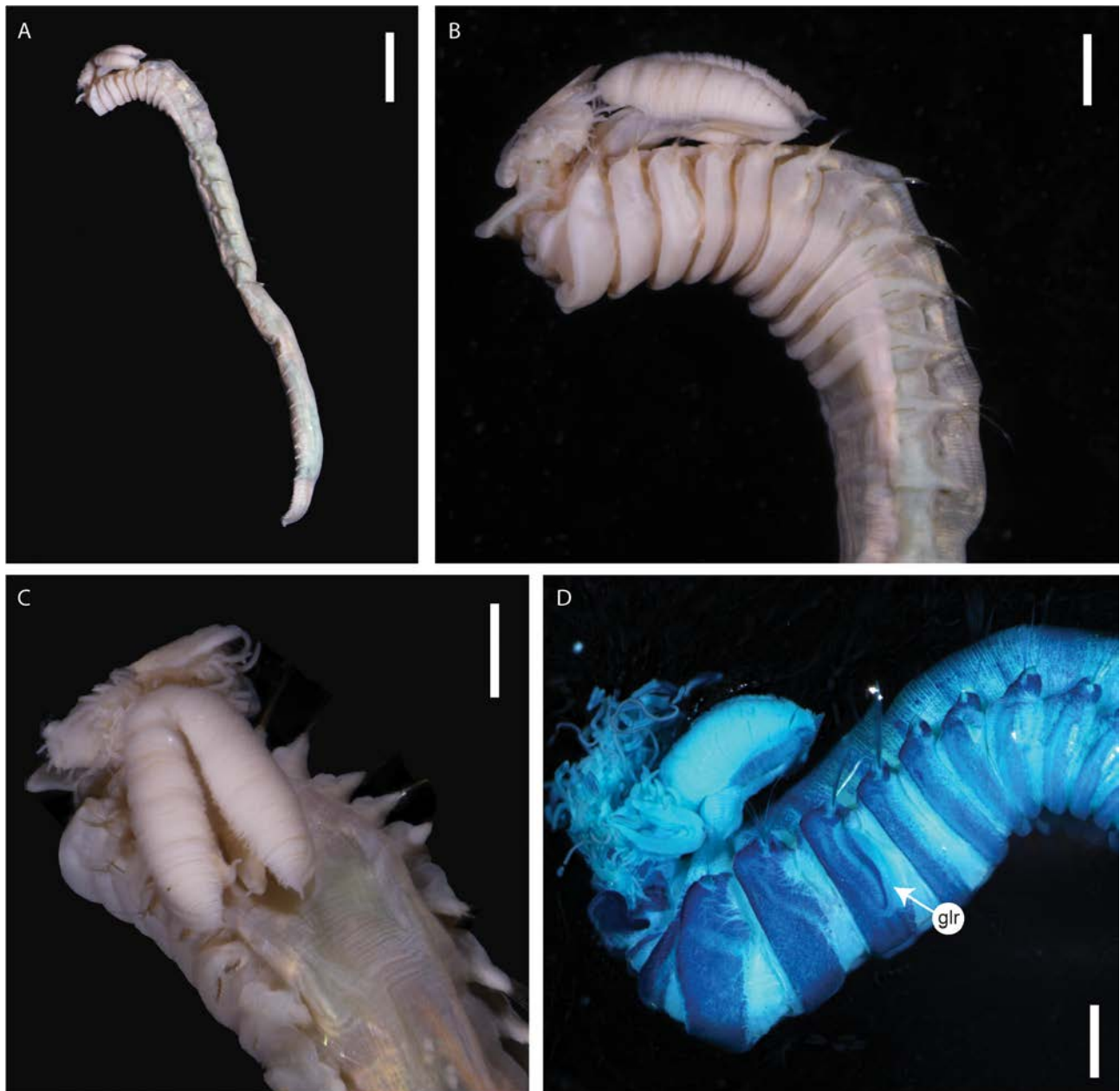


FIGURE 9. *Terebellides gentili* n. sp. holotype MNHN-IA-TYPE 1870 (A–C) and paratype MNHN-IA-TYPE 1871 (D) **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, dorsal view; **D.** Anterior part, lateral view, methyl green staining. Abbreviation: glr, glandular lateral region. Scales: A=4 mm, B–D=1 mm.

Eighteen pairs of thoracic notopodia (SG3–20). First notopodium slightly smaller than subsequent notopodia; notochaetae from TC1 slightly smaller in length than following notochaetae, and transversally aligned (Figs 9B, D & 10A). All notochaetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6

(SG8) to pygidium; uncini arranged in single rows from TC7. First thoracic neuropodium (TC6) provided with four to six sharply bent acute tipped, geniculate chaetae. All subsequent thoracic neuropodia with about 11–15 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks provided with long, thin and pointed main fang, straight terminally. Three or four teeth above the main fang, surmounted by a row of five to six short denticles and an upper crest of several smaller denticles (Fig. 10C). About 30 abdominal neuropodia as erect pinnules paddle-shaped with entire margin provided with about 30 uncini; each with four pointed teeth above main fang, surmounted by a row of three short pointed teeth and an upper crest of minute teeth (Fig. 10D).

Two pairs of flattened nephridial papillae, located dorso-posteriorly to each notopodium from TC4 to TC5. Pygidium blunt, as a funnel-like depression.

Methyl green staining pattern. Stained with distinct stripes on each notopodial segments, from CH1 to CH12, bands becoming narrower and more widely spaced (stripes of first four chaetigers more or less visible depending on contraction of chaetigers); elongated whitish glandular region on TC3 with central line more intensive stained (Fig. 9D).

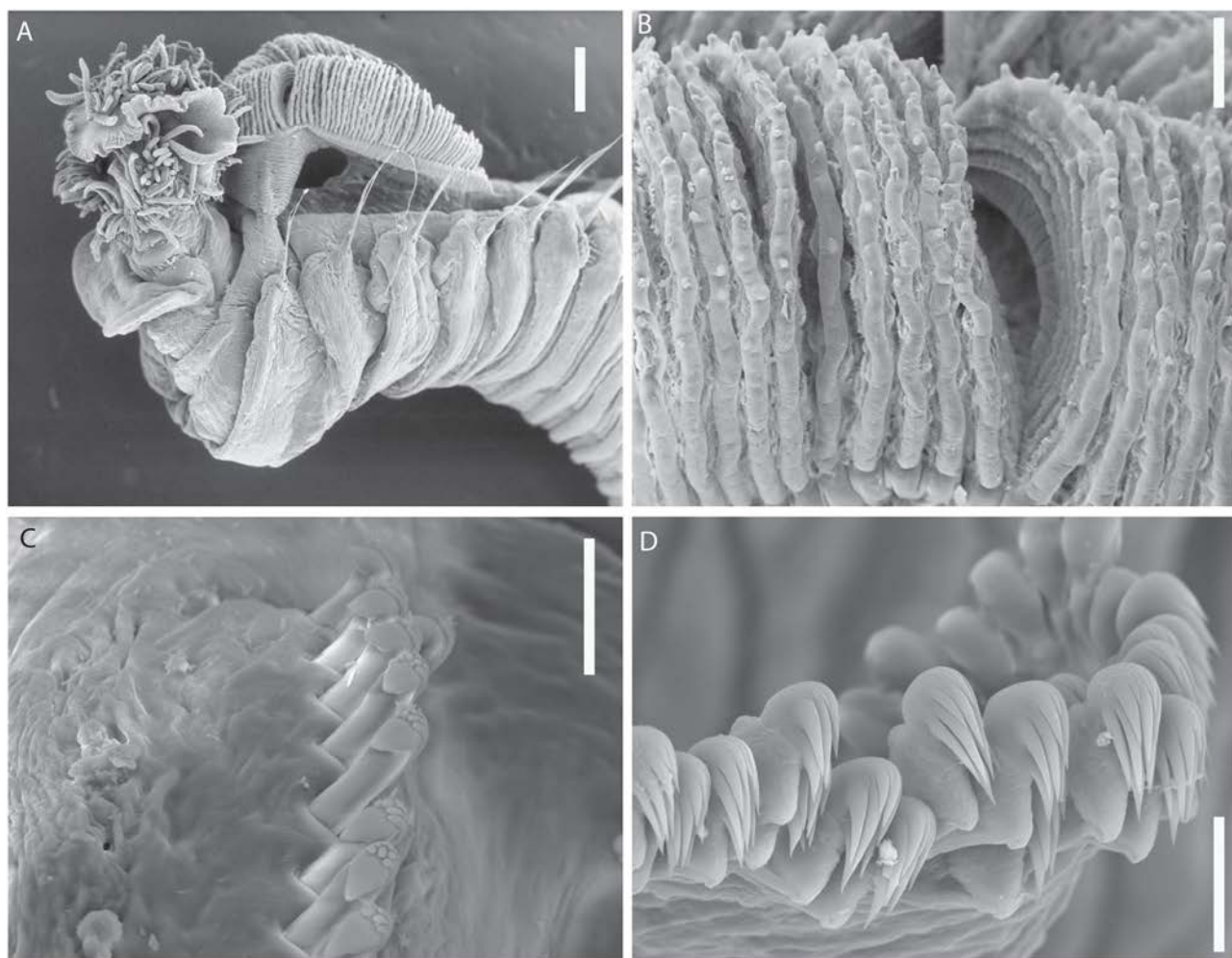


FIGURE 10. *Terebellides gentili* n. sp. SEM paratype MNHN-IA-TYPE 1873 **A.** Anterior part, lateral view; **b.** Papillar projections on edge of branchial lamellae, lateral view; **C.** Uncini, thoracic chaetiger; **D.** Uncini, abdominal chaetiger. Scales: A=400 μ m, B=90 μ m, C=25 μ m, D=15 μ m.

Etymology. The species is named after Dr. Franck Gentil, for his many contributions to benthic ecology of English Channel. This species name was chosen in agreement with Céline Houbin and Caroline Broudin, from Roscoff laboratory, who were mentored by FG for many years.

Habitat. Coastal fine sands and maerl (rhodolith) beds, from 2 to 35 m depth.

Type locality. Morlaix Bay, English Channel, France.

Distribution. Bay of Biscay (Bay of Brest), English Channel (Morlaix and Bay of Seine), France, NE Atlantic (Fig. 1).

Remarks. Except *T. stroemii* from Adriatic Sea (Parapar *et al.* 2013) (see *T. lilasae* **n. sp.** remarks), *Terebellides gentili* **n. sp.** differs from other European previously known species by the presence of papillar projections pointing over the edge of the branchial lamellae. This character is similar to that present in *T. gentili* **n. sp.** and *T. bonifi* **n. sp.**, *T. europaea* **n. sp.**, *T. lilasae* **n. sp.** and *Terebellides resomari* **n. sp.** Among these species, only *T. europaea* **n. sp.**, shares the presence of an undulating glandular region on TC3. However, *T. gentili* **n. sp.** differs from *T. europaea* **n. sp.** by the presence of papillar projections on most of the branchial lamellae (instead of anterior lamellae only for *T. europaea* **n. sp.**), by the shape of papillar projections (small, elongated and widely spaced for *T. gentili* **n. sp.**, rounded for *T. europaea* **n. sp.**), by the degree of fusion of lobes (1/2 of length for *T. gentili* **n. sp.**, not fused for *T. europaea* **n. sp.**), the presence terminal projections of lower lobes (short and pointed for *T. gentili* **n. sp.**, short filaments for *T. europaea* **n. sp.**) and by the MG pattern (striped from TC1 to TC12 for *T. gentili* **n. sp.**, compact from TC1 to TC9 for *T. europaea* **n. sp.**) (Table 2).

Terebellides gralli **n. sp.**

Figures 11–12, Table 2

Type material. Holotype: MNHN-IA-TYPE 1874, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, ME2, 48°18'31"N, 4°21'56"W, 1 m depth, June 2016. **Paratypes:** MNHN-IA-TYPE 1875, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'54"W, 1.3 m depth, January 2016; MNHN-IA-TYPE 1876, two complete specimens, Northeast Atlantic Ocean, Brittany, Bay of Brest, HA, 48°19'18"N, 4°24'11"W, 2 m depth, June 2016, mounted for SEM; MNHN-IA-TYPE 1877, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, LC3, 48°18'39"N, 4°21'22"W, 1.4 m depth, January 2016; AM W.52079, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, VC, 48°18'59"N, 4°23'28"W, 2.2 m depth, October 2015; MNHN-IA-TYPE 1878, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'53"W, 5 m depth, May 2018.

Additional material: SMA_ROS_02, one specimen, incomplete, gravid, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N, 3°51'58"W, 17 m depth, March 2018.

Description. Small size species, with holotype 18.9 mm long (8.3–19.8 mm) and 1.2 mm (0.8–1.4 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compacted towards pygidium.

Prostomium compact; eyespots absent; large upper lip surrounding mouth with many buccal tentacles (Fig. 11A–D). Buccal tentacles of 2 types, uniformly cylindrical and with expanded tips, spatulate (Figs 11B–D & 12A–B). Lower lip forming an expanded structure below upper lip (Fig. 11A–C). S1 and S2 short, only visible ventrally; following segments with lobes as ventral collars (Fig. 11A–C). Lateral lappets on SG3–6 (TC1–5), continuing ventrally in TC1–5, largest on TC1 and 2 and declining in size posteriorly. No conspicuous dorsal rounded projection on anterior chaetigers. Postero-lateral crescent moon-shaped glandular region on TC3 (Fig. 11B–C).

Branchiae arising as a single structure from TC1 and reaching TC4 (TC6), consisting of a single elongate and annulated stalk situated mid-dorsally, made up of two pairs of lobes fused on less than 1/2 of length, lower pair thinner (Figs 11B, D & 12B). Posterior region of upper lobes with long pointed projections and lower lobes with short terminal pointed projections (Figs 11B, D & 12B). Upper lobes provided with about 40 well packed to loosely fused lamellae, lamellae of different width and size (Figs 11A–D & 12A–B). Both sides of branchial lamellae provided with five to six well-marked parallel rows of cilia, no tufts of cilia on outer edge. Absence of papillar projections over the margins of the branchial lamellae (Fig. 11A–B). Anterior branchial projection (5th lobe) present (Fig. 11A–C).

Eighteen pairs of thoracic notopodia (SG3–20; TC1–18). Notopodia present from TC1 well-developed; notochoetae of TC1 slightly shorter in size than following notochoetae. All notochoetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6 (SG 8) to pygidium, with uncini arranged in a single row from TC7. First thoracic neuropodia (TC6) with three or four (6) sharply bent acute tipped, geniculate chaetae. All subsequent thoracic neuropodia with about 8–12 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks with long, thin and pointed main fang, straight terminally. Three or four teeth above the main fang, surmounted by a row of four to five short teeth and an upper crest of several smaller denticles (Fig. 12C). Abdomen with 25–30 neuropodia as erect pinnules paddle-shaped with entire margin with about 25 uncini; each with four pointed teeth above main fang, surmounted by a row of three to five pointed teeth and an upper crest of minute teeth (Fig. 12D).

Three pairs of globular nephridial papillae, located latero-posteriorly to base of each notopodium of TC1, TC4 and TC5 (Fig. 11D). Pygidium crenulated, as a funnel-like depression (Fig. 11A).

Methyl green staining pattern. Solid to TC4, with distinct stripes from TC5 to about TC11, distinct white antero-ventral lines from TC5 to TC9; white glandular region on TC3 (Fig. 11C–D).

Etymology. The species is named after Dr. Jacques Grall, for his many contributions to benthic ecology of maerl beds, for his friendship and his role of mentor for the young generation of French benthic ecologists. Indeed, this species name was chosen in agreement with Vincent Le Garrec and Gabin Droual, from Brest laboratory, who collected many specimens for us and who are supervised by Jacques Grall.

Habitat. Coastal maerl (rhodolith) beds, 1–5 m depth.

Type locality. Bay of Brest, Brittany, France.

Distribution. Bay of Biscay (Bay of Brest), English Channel (Morlaix Bay) (Fig. 1).

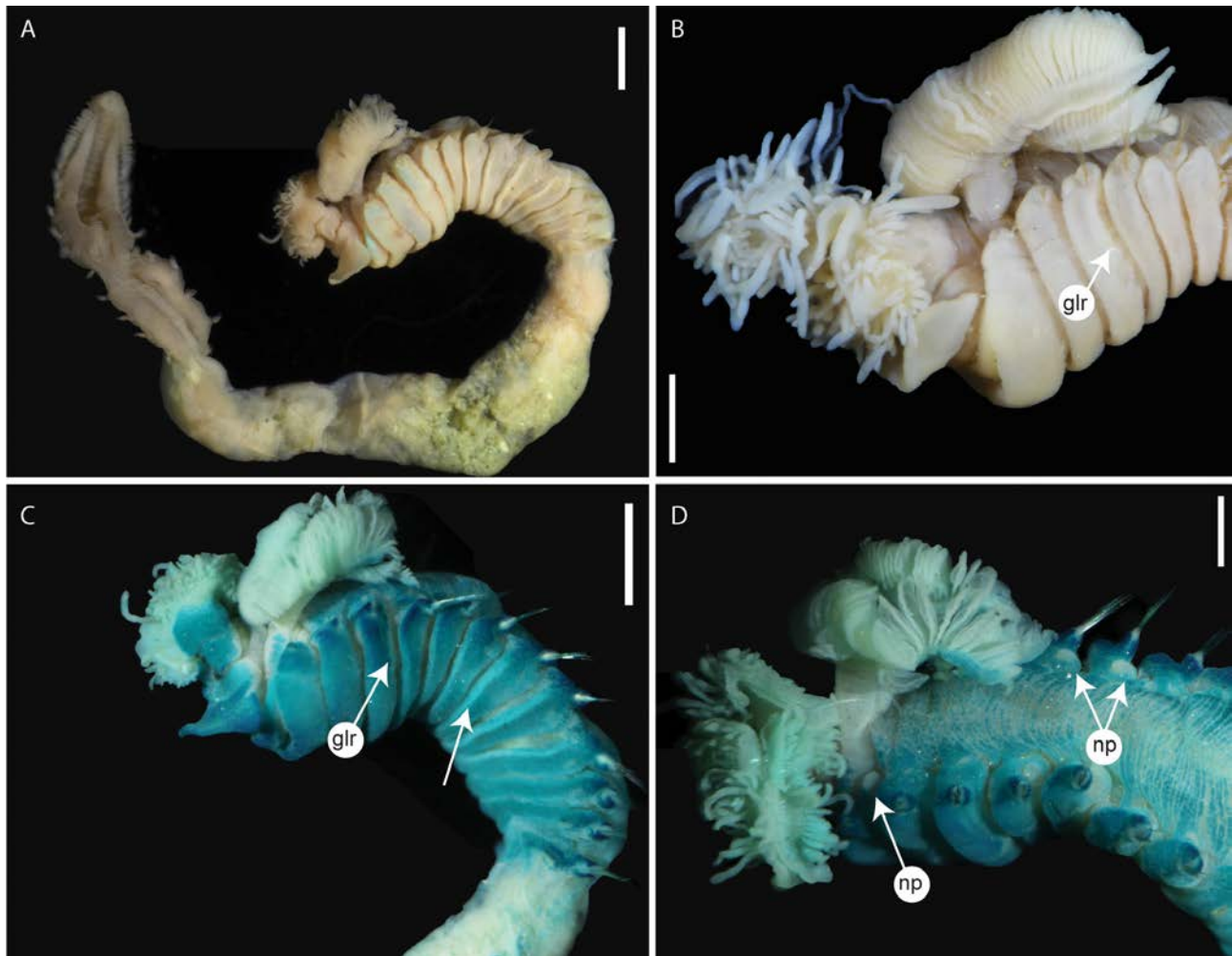


FIGURE 11. *Terebellides gralli* n. sp. holotype MNHN-IA-TYPE 1874 (A, C–D), paratype MNHN-IA-TYPE 1875 (B) **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, lateral view, methyl green staining; **D.** Anterior part, dorsal view, methyl green staining. Abbreviation: glr, glandular lateral region; np, nephridial papillae. Arrow indicates antero-ventral band. Scales: A, C=1 mm, B, D=500 μ m.

Remarks. *Terebellides gralli* n. sp. is similar to *T. parapari* n. sp. in having a small size (<20 mm), the presence of a glandular region on TC3 and the absence of projecting papillae on lamellae of the branchiae. However, these two species can be differentiated by the presence of pointed terminal projections on branchial lobes for *T. gralli* n. sp. (presence of filaments for *T. parapari* n. sp.), by the size of notochaetae (longer on the first chaetiger for *T. parapari* n. sp., slightly shorter for *T. gralli* n. sp.), the shape of the glandular region (J-shaped for *T. parapari* n. sp. vs crescent moon-shaped for *T. gralli* n. sp.) and the presence of a 5th lobe for *T. gralli* n. sp. (absence for *T. parapari* n. sp.). *Terebellides gralli* n. sp. is also very similar to *T. atlantis* in having a small size (<20 mm), two pairs of lobes not fused and provided with pointed projections and in lacking projecting papillae on lamellae of

branchiae. However, *T. gralli* n. sp. differs from *T. atlantis* by the presence of glandular regions both on TC3 and 5th branchial lobe (Table 2).

For now, and based on molecular results from Nygren *et al.* (2018), *T. gralli* n. sp. seems to be absent from Northern waters.

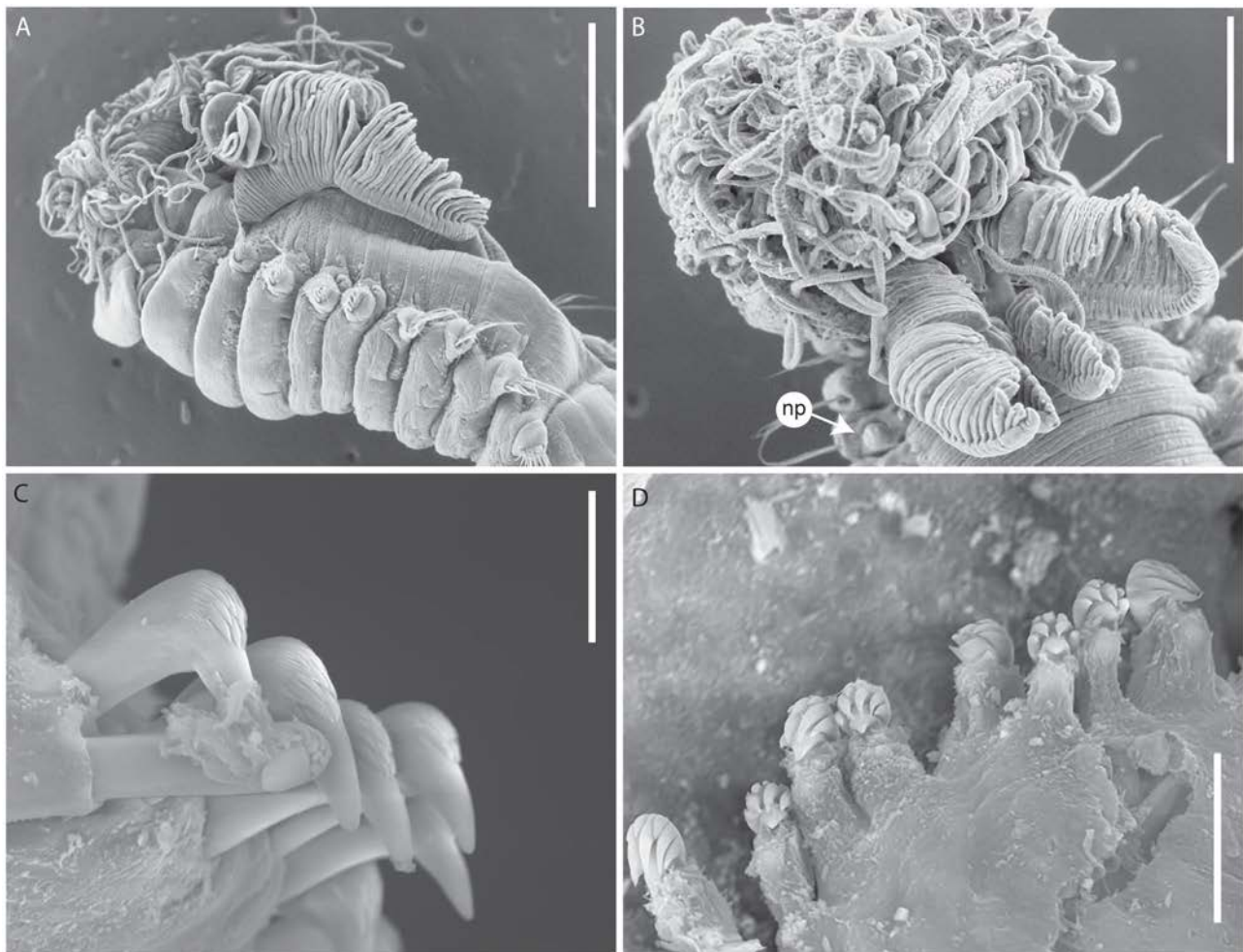


FIGURE 12. *Terebellides gralli* n. sp. SEM paratype MNHN-IA-TYPE 1876 **A.** Anterior part, lateral view; **b.** Anterior part, dorsal view; **C.** Uncini, thoracic chaetiger; **D.** Uncini, abdominal chaetiger. Abbreviation: np, nephridial papillae. Scales: A=1 mm, B=500 μ m, C–D=0.15 μ m.

Terebellides lilasae n. sp.

Figures 13–14, Table 2

Type material: Holotype: MNHN-IA-TYPE 1879, complete, Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-8, 45°38'55"N, 01°45'47"W, 62 m depth, 29 October 2016. **Paratypes:** MNHN-IA-TYPE 1880, complete, Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-8, 45°38'55"N, 01°45'47"W, 62 m depth, 29 October 2016; MNHN-IA-TYPE 1881, anterior part, Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-8, 45°38'55"N, 01°45'47"W, 62 m depth, 29 October 2016, mounted for SEM; MNHN-IA-TYPE 1882, complete, Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-4, 45°36'50"N, 01°49'37"W, 69 m depth, 16 August 2017; MNHN-IA-TYPE 1883, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-4, 45°36'50" N, 01°49'37" W, 69 m depth, 29 April 2018; AM W.51394, one specimen, complete, Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-3, 45°40'57"N, 1°41'30"W, 54 m depth, 27 October 2016, mounted for SEM; AM W.51450, one specimen, complete, Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-4, 45°38'55"N, 1°45'47"W, 69 m depth, 28 October 2016.

Additional material examined: SMA_VOG8C2-A, complete (posterior part used for molecular analysis),

Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-8, 45°38'55"N, 01°45'47"W, 61 m depth, 20 August 2017; SMA_VOG8C2-B, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-8, 45°38'55"N, 01°45'47"W, 61 m depth, 20 August 2017; SMA_VOG8C2-C, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Bay of Biscay, West Gironde Mud Patch, JERICO-8, 45°38'55"N, 01°45'47"W, 61 m depth, 20 August 2017; SMA_BR_42, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Northern Bay of Biscay, APP 5220, 47°28'51"N, 03°45'23"W, 85 m depth, May 2018; SMA_BAN_13, one specimen, gravid, complete, Mediterranean Sea, Gulf of Lion, Appeal I2, 42°45'18"N, 3°17'40"E, 83 m depth, September 2019; SMA_BAN_07, juvenile, Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018, entirely used for molecular analysis.

Description. Large species, holotype 35.2 mm long (34.6–55.9 mm) and 3.2 mm (2.3–3.8 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compacted towards pygidium.

Prostomium compact; eyespots absent; large upper lip surrounding mouth with many buccal tentacles (Fig. 13A–B, D). Buccal tentacles of 2 types, uniformly cylindrical, with expanded spatulate tips (Fig. 13B). Lower lip expanded, below upper lip (Fig. 13A–B, D). SG 1 and 2 short, visible ventrally; following segments with lobes forming ventral collars. Lateral lappets on SG3–6, thoracic chaetigers TC1–4 continuing ventrally, larger on TC1–2 and decreasing in size posteriorly (Fig. 13A–B, D). No conspicuous dorsal rounded projection on anterior chaetigers. Oval-shaped glandular lateral region on TC3 (Fig. 13D).

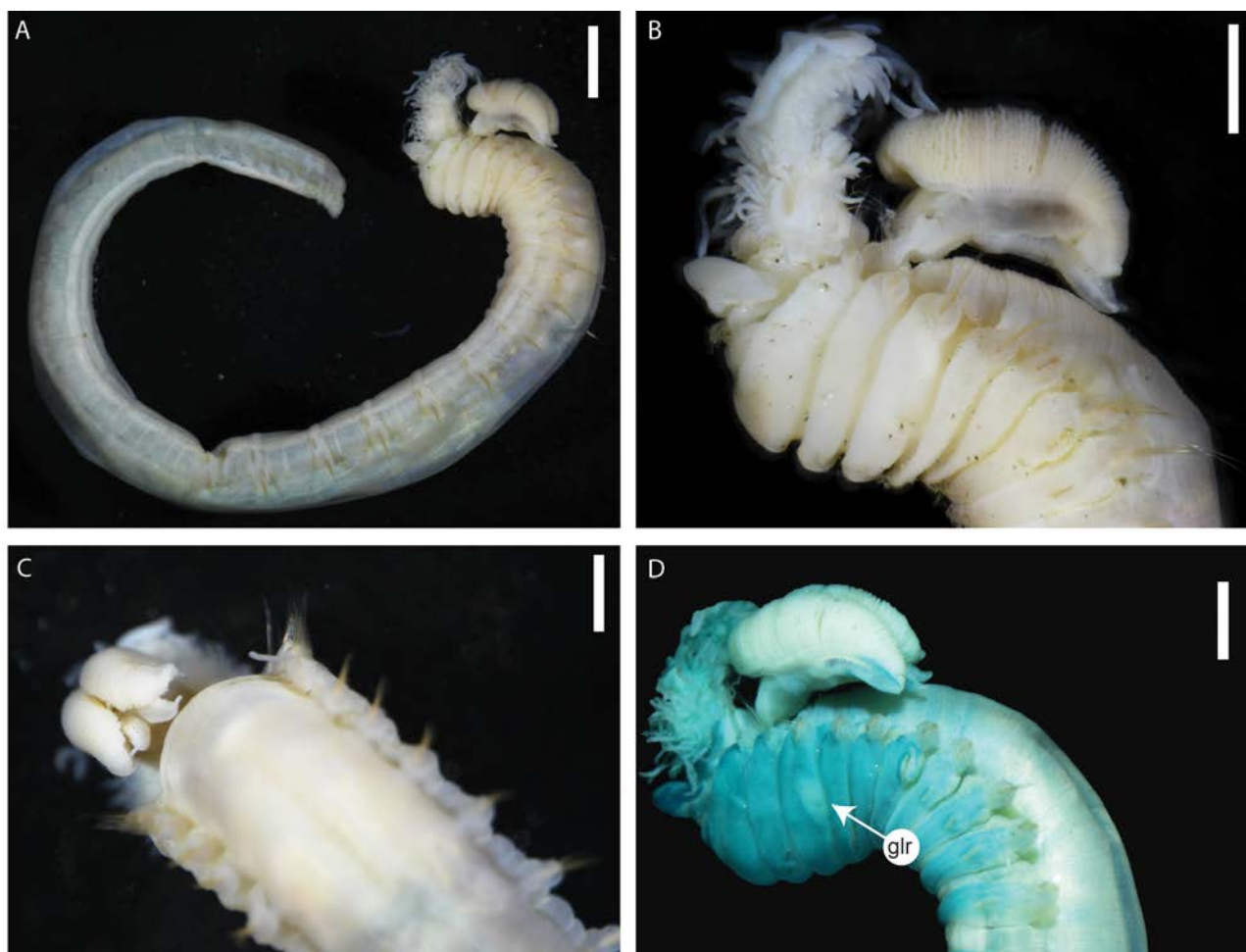


FIGURE 13. *Terebellides lilasae* n. sp. holotype MNHN-IA-TYPE 1879 **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, dorsal view; **D.** Anterior part, lateral view, methyl green staining. Abbreviation: glr, glandular lateral region. Scales: A=2 mm, B–D=1 mm.

Branchiae arising as a single structure between TC1–TC2, reaching TC5 (TC6), consisting of a single elongate and annulated stalk placed mid-dorsally (Figs 13A–B, D & 14A), two pairs of lobes, fused for about 3/4 of length, lower pair thinner (Figs 13C & 14A). Upper lobes with 60 to 80 tightly packed lamellae (Figs 13 A–B, D & 14A).

Both sides of branchial lamellae provided with several parallel rows of cilia, no tufts of cilia on outer edge (Fig. 14B). Margins of most of individual branchial lamellae with numerous rounded projecting papillae, visible under stereomicroscope (Figs 13B, D & 14A–B). Distal region of both upper and lower lobes with short terminal pointed projections for upper lobes and long terminal projections for lower lobes (Figs 13A–D & 14A). Anterior branchial projection (5th lobe) present (Figs 13A–B, D & 14A).

Eighteen pairs of thoracic notopodia (SG3–20). Notopodia on TC1 and TC2 inserted slightly more dorsally than subsequent notopodia; notopodia from TC1 smaller in size than following ones, and transversally aligned; noto chaetae from TC1 slightly longer (all of same length) than following noto chaetae (Fig. 13B). All noto chaetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6 (SG8) to pygidium; uncini arranged in single rows from TC7. First thoracic neuropodium (TC6) provided with six (5) sharply bent acute tipped, geniculate chaetae. All subsequent thoracic neuropodia with around 12–20 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks provided with long, thin and pointed main fang, straight terminally. Three or four teeth above the main fang, surmounted by a row of five to eight short teeth and an upper crest of several minute denticles (Fig. 14C). About 25 abdominal neuropodia as erect pinnules paddle-shaped with entire margin provided with about 36 uncini; uncini with three or five pointed teeth above main fang, surmounted by a row of five pointed short teeth and an upper crest of minute teeth (Fig. 14D).

Two pairs of globular nephridial openings, located dorsal to each notopodium from TC4 to TC5. Pygidium blunt, slightly crenulated, as a funnel-like depression.

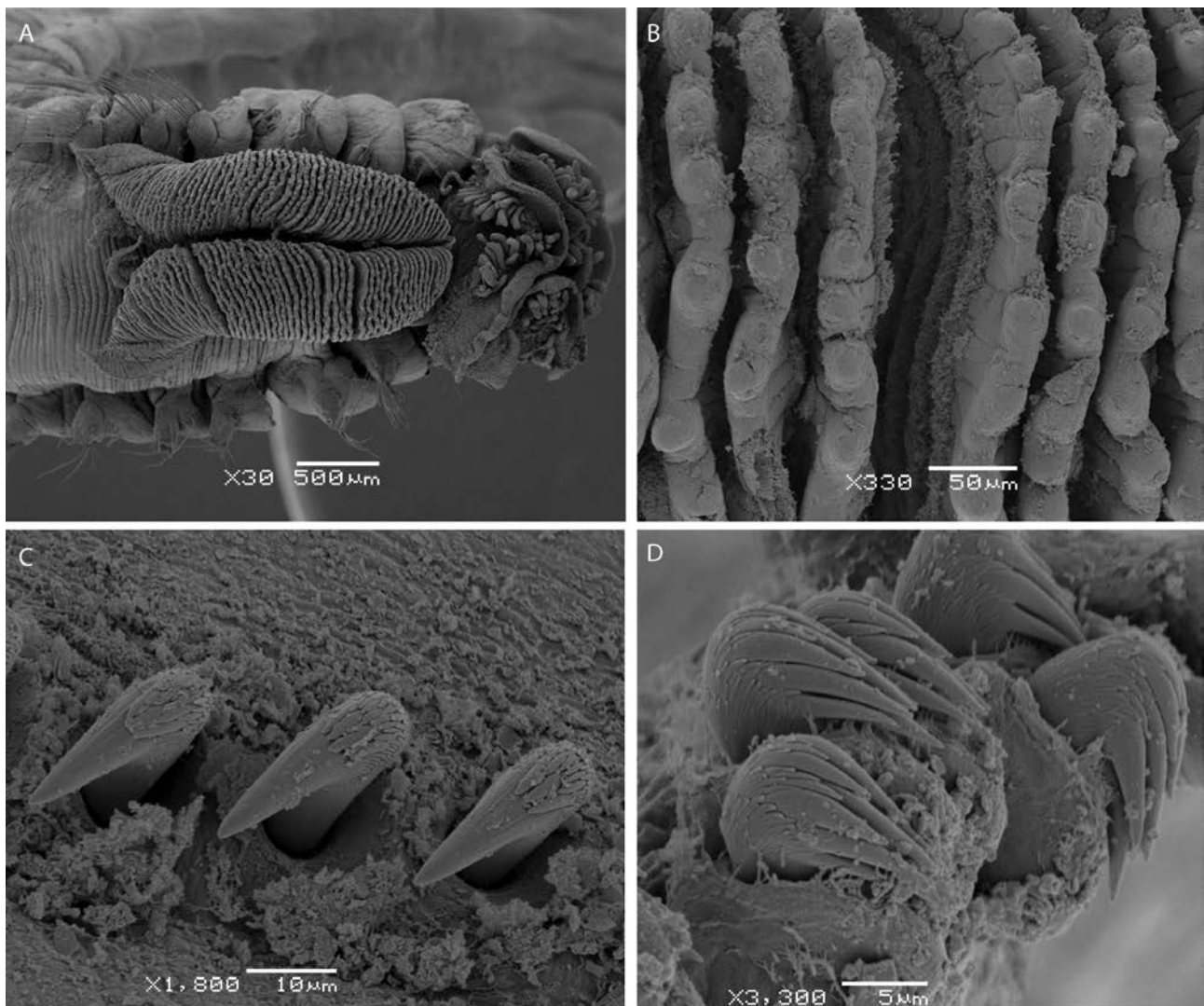


FIGURE 14. *Terebellides lilasae* n. sp. SEM paratype AM W.51394 **A.** Anterior part, dorsal view; **b.** Ciliation and papillar projection of branchial lamellae; **C.** Uncini, thoracic chaetiger; **D.** Uncini, abdominal chaetiger.

Methyl green staining pattern: First six TC stain solid; from TC7 to about TC11, stain with distinct stripes, fading towards posterior thoracic region, width of stained stripes decreases posteriorly (Fig. 13D); glandular region on TC3 white (except dorso-anterior region stained in blue) (Fig. 13D).

Etymology. The species is named after Lilas Lavesque, NL and GD' beloved daughter.

Habitat. in coastal mud and sandy mud, at 50–105 m depth.

Type locality. West Gironde Mud Patch, Bay of Biscay, France, NE Atlantic.

Distribution. Northeast Atlantic Ocean (Bay of Biscay, from south of Brittany to off Gironde estuary), Western Mediterranean Sea (Gulf of Lion), France (Fig. 1).

Remarks. Among the European previously known species, *Terebellides lilasae* n. sp. differs by the presence of papillar projections pointing over the edge of the branchial lamellae. By this character, *T. lilasae* n. sp. is similar to *T. bonifi* n. sp., *T. europaea* n. sp., *T. gentili* n. sp. and *T. resomari* n. sp. Among these last species, only *T. bonifi* n. sp., shares the presence of oval glandular region on TC3. However, *T. lilasae* n. sp. differs from *T. bonifi* n. sp. by the staining of the glandular region (mostly white for *T. lilasae* n. sp., dark blue for *T. bonifi* n. sp.), by the presence of papillar projections on most of the branchial lamellae (instead of anterior lamellae only for *T. bonifi* n. sp.) and the absence of conspicuous dorsal projections on TC1–3 (presence on *T. bonifi* n. sp.).

Based on the literature, *T. lilasae* n. sp. is similar to *T. stroemii* from Adriatic Sea (Parapar *et al.* 2013), in having a size greater than 30 mm, the same type of papillar projections pointing over the margins of the branchial lamellae and the same shape of glandular region on TC3. However, *T. lilasae* n. sp. differs by a few characters such as the number of lamellae on upper lobes (about 30 for Adriatic specimens vs about 60–80 for *T. lilasae* n. sp.), the length of branchiae (reaching TC3 vs TC6, respectively) and the number of abdominal uncinus (about 23 for Adriatic specimens vs about 36 for *T. lilasae* n. sp.). As suggested previously by Parapar & Hutchings (2014), specimens from the Adriatic Sea cannot belong to *T. stroemii*. They are more similar to *T. lilasae* n. sp. although they differ by a few characters. Further molecular analysis should permit to test if these variations are intra specific or if specimens from Adriatic belong to an undescribed species.

Finally, molecular results confirm that *T. lilasae* n. sp. is present from off Gironde estuary to North of the Bay of Biscay and the Mediterranean Sea. Molecular results, based on material available for this study, show that this species appears to be absent from Northern waters (Fig. 23).

Terebellides parapari n. sp.

Figures 15–16, Table 2

Type material: Holotype: MNHN-IA-TYPE 1884, complete specimen, gravid, Northeast Atlantic Ocean, Bay of Biscay, P40, 43°33'26"N, 1°41'37"W, 112 m depth, May 2018; **Paratypes:** MNHN-IA-TYPE 1885, one complete specimen, Northeast Atlantic Ocean, Bay of Biscay, P37, 43°33'31"N, 1°43'49"W, 129 m depth, May 2018; MNHN-IA-TYPE 1886, one complete specimen, Northeast Atlantic Ocean, Bay of Biscay, P31, 43°38'40"N, 1°35'05"W, 86 m depth, May 2018; MNHN-IA-TYPE 1887, one complete specimen, Northeast Atlantic Ocean, Bay of Biscay, P40, 43°33'26"N, 1°41'37"W, 112 m depth, May 2018; MNHN-IA-TYPE 1888, two complete specimen, Northeast Atlantic Ocean, Bay of Biscay, P40, 43°33'26"N, 1°41'37"W, 112 m depth, May 2018, mounted for SEM; AM W.51403, 4 complete specimens (2 of them gravid), Northeast Atlantic Ocean, Bay of Biscay, P35, 43°36'35"N, 1°40'35"W, 120 m depth, May 2018; AM W.51404, 3 complete specimens (2 of them gravid), Northeast Atlantic Ocean, Bay of Biscay, P36, 43°35'0"N, 1°42'02"W, 125 m depth, May 2018.

Description. Small species, holotype 13.4 mm long (6.2–14.1 mm) and 0.9 mm (0.6–0.9 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compact towards pygidium.

Prostomium compact; eyespots absent; upper lip with single anteriorly elongated projecting lobe surrounding mouth with many buccal tentacles (Figs 15C & 16A). Buccal tentacles of two types, uniformly cylindrical and with expanded tips, spatulate (Fig. 16B). Lower lip forming an expanded structure below upper lip (Fig. 15C). SG1 and 2 short, only visible ventrally; following segments with lobes as ventral collars (Figs 15A–C & 16B). Lateral lapets on SG3–7 (TC 1–5), continuing ventrally in TC1–5 (Figs 15C & 16B), largest on TC1–3 and declining in size posteriorly. No conspicuous dorsal rounded projection on anterior chaetigers. Small round glandular region on TC3, situated latero-dorsally (Fig. 15C).

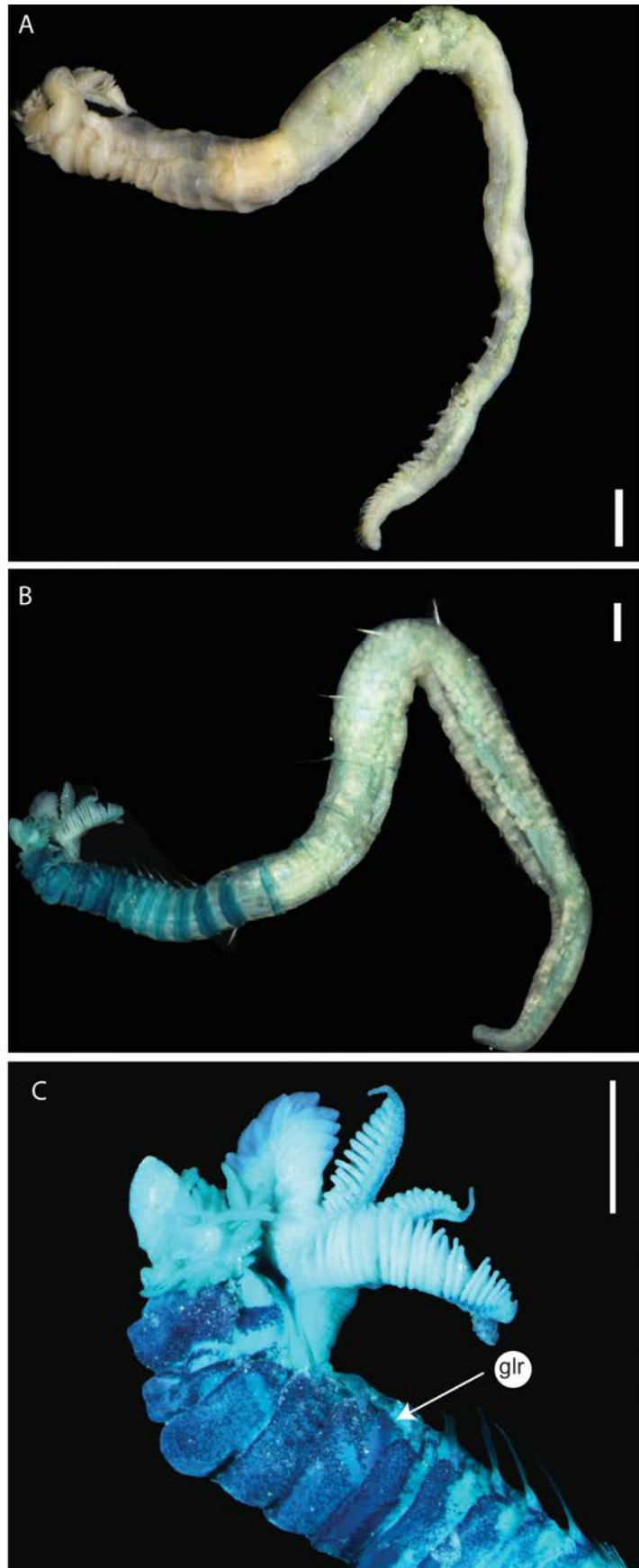


FIGURE 15. *Terebellides parapari* n. sp. paratype MNHN-IA-TYPE 1885 (A), holotype MNHN-IA-TYPE 1884 (B) and paratype MNHN-IA-TYPE 1886 (C). **A.** Entire worm, lateral view; **b.** Entire worm, lateral view, methyl green staining; **C.** Anterior part, lateral view, methyl green staining. Abbreviation: glr, glandular lateral region. Scales: 0.5 mm.

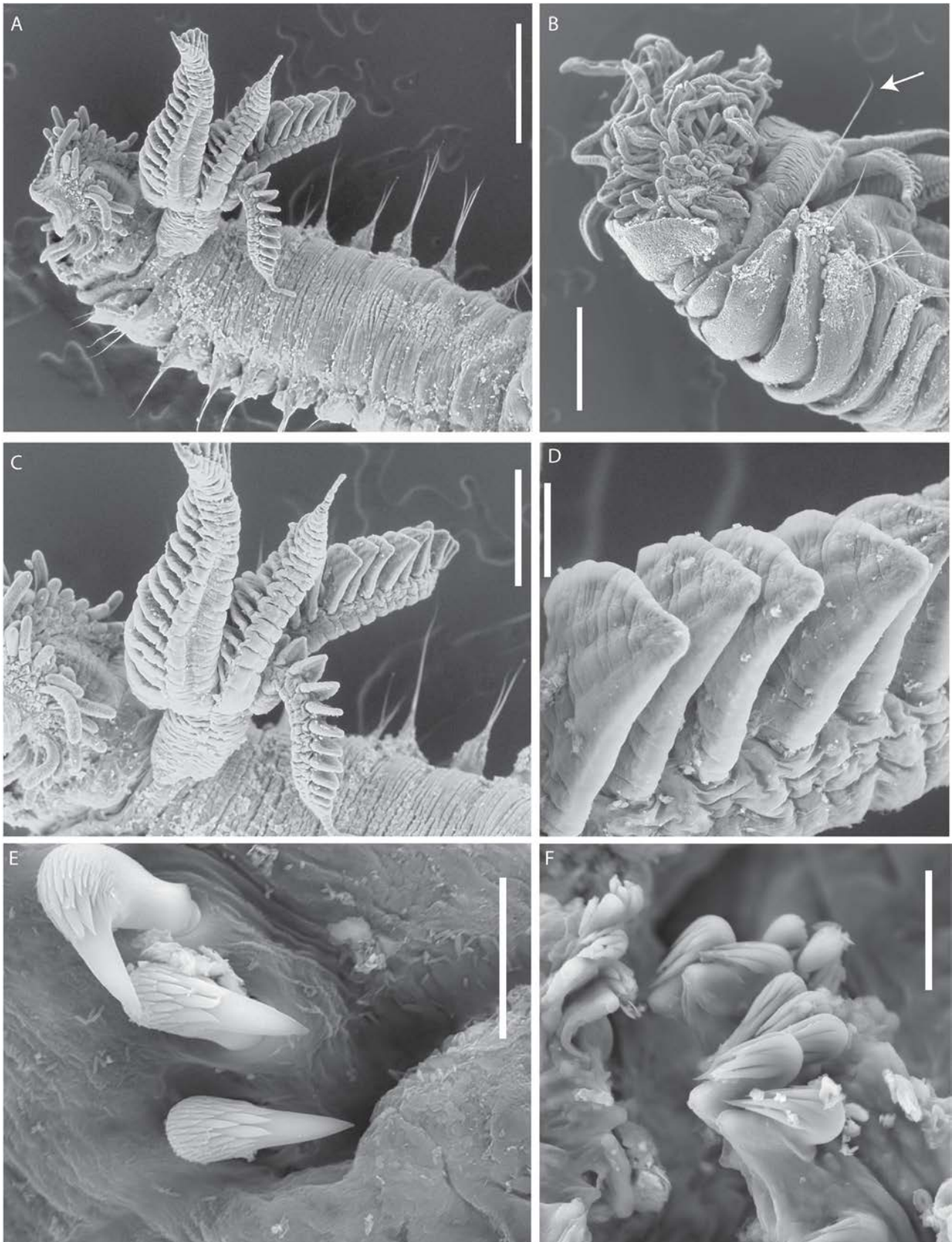


FIGURE 16. *Terebellides parapari* n. sp. SEM paratype MNHN-IA-TYPE 1888 (2 individuals). **A.** Anterior part, dorsal view (indiv1); **b.** Anterior part, lateral view (indiv2); **C.** Branchial lobes, dorsal view (indiv1); **D.** Detail of branchial lamellae, dorsal view (indiv1); **E.** Uncini, thoracic chaetiger (indiv1); **F.** Uncini, abdominal chaetiger (indiv2). Arrow indicates notochaetae of TC1 Scales: A–B=400 μ m, C=250 μ m, D=50 μ m, E=10 μ m, F=15 μ m.

Branchiae arising as a single structure from TC1, reaching TC4 (TC5), consisting of a single elongate and annulated stalk placed mid-dorsally (Figs 15A–C & 16A, C), two pairs of lobes, not fused, lower pair thinner (Figs 15B & 16A, C). Upper lobes with about 20 widely spaced lamellae (Figs 15C & 16A, C). Branchial lamellae, with mid-dorsal pointed tip (Fig. 16C–D), with sparse tufts of cilia. Branchiae provided without any papillar projections pointing over margins of the branchial lamellae (Fig. 16C–D). Distal region of upper lobes with small terminal pointed projections, lower lobes with short filaments (Figs 15A–C & 16A–C). Anterior branchial projection (5th lobe) absent (Fig. 16A, C).

Eighteen pairs of thoracic notopodia (SG3–20). First notopodium on TC1 well-developed, same size than subsequent notopodia; TC1 and TC2 situated more dorsally; notochaetae from TC1 longer than notochaetae from TC2, notochaetae from TC2 longer than following ones (Figs 15C & 16B). All notochaetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6 (SG8) to pygidium; uncini arranged in single rows from TC7. First thoracic neuropodium (TC6) provided with about three to four sharply bent acute tipped, geniculate chaetae. All subsequent thoracic neuropodia with about 10–12 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks provided with long, thin and pointed main fang, straight terminally. Two to four teeth above the main fang, surmounted by a row of three to five short teeth and an upper crest of several minute denticles (Fig. 16E). About 30 abdominal neuropodia as erect pinnules paddle-shaped with entire margin provided with about 15 uncini; uncini with three or four pointed teeth above main fang, surmounted by a row of three short pointed teeth and an upper crest of minute teeth (Fig. 16F).

Nephridial papillae not seen. Pygidium blunt, slightly crenulated, as a funnel-like depression.

Methyl green staining pattern. First 4 TC stain solid; from TC5 to about TC11, stain striped with space between stripes pale blue. Ventral part of TC4 stain darker (Fig. 15C). Presence of transverse diagonal white lines on lateral part of first three chaetigers (Fig. 15C). Glandular region whitish.

Etymology. The species is named after Dr. Julio Parapar, for his many contributions to the taxonomy of the *Terebellides* genus, especially in European waters and for his friendship.

Habitat. Mud to sandy mud, around 120 m depth.

Type locality. Near Capbreton Canyon, Bay of Biscay, Northeast Atlantic Ocean, France.

Distribution. Only known from type locality (Fig. 1).

Remarks. *Terebellides parapari* n. sp. is similar to *T. shetlandica* in having a relatively small size (*T. shetlandica*: 6–19 mm vs *T. parapari* n. sp.: 8–23 mm), lobes free from each other and filaments in each of lower lobes. Nevertheless, these filaments are much longer for *T. shetlandica* (about ½ of length of lower lobe for *T. shetlandica*, instead of less than ¼ of length for *T. parapari* n. sp.). These two species also differ by the presence of glandular region for *T. parapari* n. sp. (absent in *T. shetlandica*), absence of dorsal papillae on each thoracic and abdominal chaetiger for *T. parapari* n. sp. (present in *T. shetlandica*), by the size of notochaetae (longer on the first chaetiger for *T. parapari* n. sp., same length for *T. shetlandica*), by the shape of branchial lamellae (rounded for *T. shetlandica* and pointed for *T. parapari* n. sp.) and absence of cilia on branchial lamellae for *T. parapari* n. sp. (instead of presence of rows and tufts of cilia in *T. shetlandica*). Finally, these two species differ by the MG pattern (compact from CH1–4 and striped from CH5–11, with white latero-diagonal white lines on CH1–CH3 for *T. parapari* n. sp. vs compact from TC1–6 and striped from CH7–12 for *T. shetlandica*) (Table 2).

***Terebellides resomari* n. sp.**

Figures 17–18, Table 2

Type material: Holotype: MNHN-IA-TYPE 1889, complete specimen, North Sea, Dunkerque harbour, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016; **Paratypes:** MNHN-IA-TYPE 1890, one specimen, complete, North Sea, Dunkerque harbour, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016; MNHN-IA-TYPE 1891, one specimen, complete, North Sea, Dunkerque harbour, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016; MNHN-IA-TYPE 1892, one specimen, complete, North Sea, Dunkerque harbour, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016, mounted for SEM; MNHN-IA-TYPE 1893, one specimen, complete, North Sea, Dunkerque harbour, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016, mounted for SEM; AM W.51397, one specimen, complete, gravid, North Sea, Dunkerque harbor, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016; AM W.51398, one specimen, complete, North Sea, Dunkerque harbour, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016; AM W.51399, one specimen, complete, North Sea, Dunkerque harbour, 51°02'52"N, 2°21'14"E, 10 m depth, May 2016.

Additional material examined: SMA_BR_51, complete, Northeast Atlantic Ocean, Brittany, Bay of Brest, BK, 48°21'28"N, 4°26'38"W, 7 m depth, 2011.

Description. Large species, holotype 36.7 mm long (30.1–35.5 mm) and 3.4 mm (2.6–3.9 mm). Body tapering posteriorly with segments becoming increasingly shorter and more compacted towards pygidium.

Prostomium compact; eyespots absent; large upper lip surrounding mouth with many buccal tentacles, with dorsal lobe very elongated and with convoluted margins (Figs 17A–B & 18A, C). Buccal tentacles of two types, uniformly cylindrical and with expanded tips, spatulate. Lower lip forming an expanded structure below upper lip (Figs 17A–B, D & 18C). S1 and S2 short, only visible ventrally; following segments with lobes as ventral collars (Fig. 17A–B, D). Lateral lappets on SG3–7 (TC1–5), continuing ventrally in TC1–5, largest on TC1 and declining in size posteriorly (Fig. 17A–B, D). No conspicuous dorsal rounded projection on anterior chaetigers. Glandular lateral region on TC3 elongated, with lateral deep ridges (Fig. 17B, D).

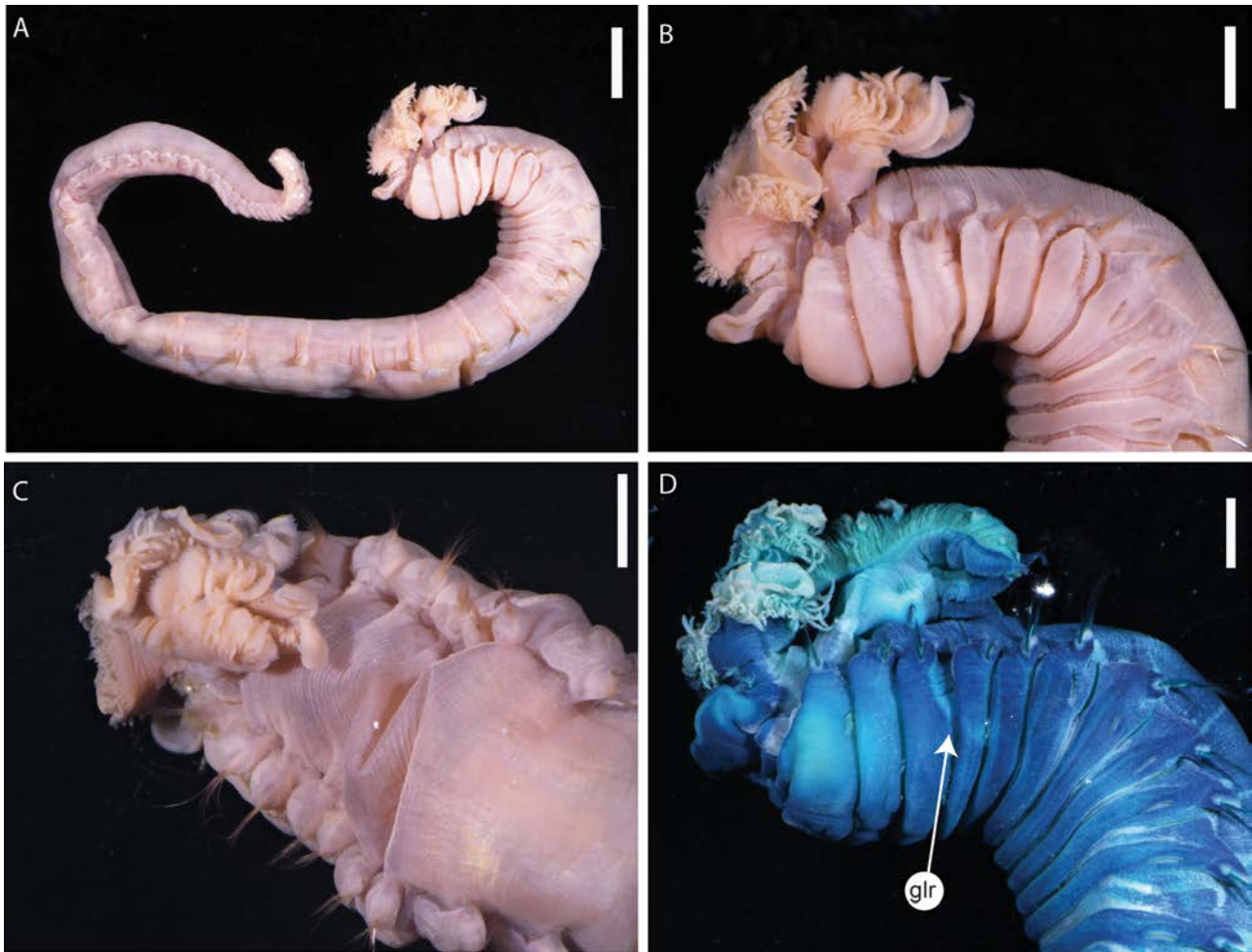


FIGURE 17. *Terebellides resomari* n. sp. holotype MNHN-IA-TYPE 1889 (A–C) and paratype MNHN-IA-TYPE 1890 (D) **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, dorsal view; **D.** Anterior part, lateral view, methyl green staining. Abbreviation: glr, glandular lateral region. Scales: A=2 mm, B–D=1 mm.

Branchiae arising as a single structure from TC1, reaching TC4 (TC5), consisting of a single elongate and annulated long stalk placed mid-dorsally (Figs 17A–D & 18A), two pairs of lobes, fused for less of half of length, lower pair thinner. Upper lobes with 50 to 60 not well-packed lamella, not uniform in height, slightly expanded at one end (Figs 17B–C & 18A–B.) Both sides of branchial lamellae provided with more than eight well-marked parallel rows of cilia, no tufts of cilia on outer edge (Fig. 18A–B). Margins of most of individual lamellae slightly convoluted with digitiform papillae, visible under stereomicroscope (Figs 17B–C & 18A–B). Distal region of upper with short terminal pointed projections and of lower lobes with long projections (Fig. 17A–D). Anterior branchial projection (5th lobe) present and very long (Fig. 17D).

Eighteen pairs of thoracic notopodia (SG3–20). First notopodium same size as subsequent notopodia; size of notopodia increasing posteriorly and notopodia becoming more erect; notochaetae from TC1 slightly smaller in length

than following notochaetae, and transversally aligned (Fig. 17B). All notochaetae simple capillaries, arranged in two rows. Neuropodia present as sessile pinnules from TC6 (SG8) to pygidium; uncini arranged in single rows from TC7. First thoracic neuropodium (TC6) provided with 6–7 (5) sharply bent acute tipped, geniculate chaetae. All subsequent thoracic neuropodia with about 20–25 uncini per torus arranged in one irregular row. Uncini as shafted denticulate hooks provided with long, thin and pointed main fang, straight terminally. Three or four teeth above the main fang, surmounted by a row of three to five short teeth and an upper crest of several minute denticles (Fig. 18D). About 35 abdominal neuropodia arising from raised glandular ridges on either side of mid-ventral groove, far posterior neuropodia very elongated, with entire margin provided with about 45 uncini; uncini with three pointed teeth above main fang, surmounted by a row of three short pointed teeth and an upper crest of minute teeth (Fig. 18E).

Two pairs of raised globular nephridial papillae, located dorso-posteriorly to each notopodium from TC4 to TC5. Pygidium blunt, as a funnel-like depression.

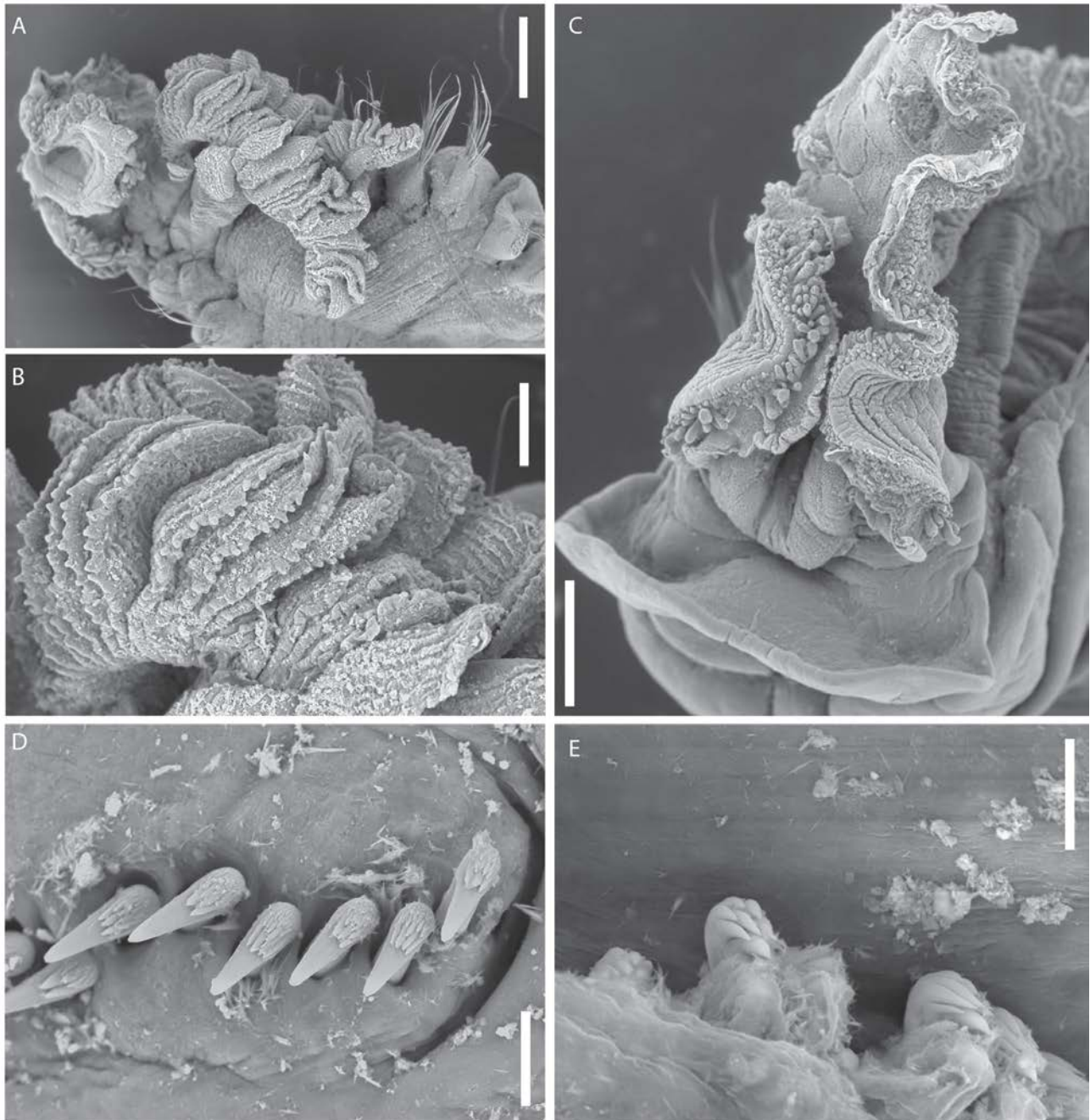


FIGURE 18. *Terebellides resomari* n. sp. SEM Additional material SMA_DUN_09 (A–B), SEM paratype MNHN-IA-TYPE 1893 (C) and SEM paratype MNHN-IA-TYPE 1892 (D–E) **A.** Anterior part, dorsal view; **b.** Papillar projections on edge of branchial lamellae, lateral view; **C.** Anterior part, frontal view; **D.** Uncini, thoracic chaetiger; **E.** Uncini, abdominal chaetiger. Scales: A–C=600 μ m, B=200 μ m, D=25 μ m, E=15 μ m.

Table 2. Distinguishing characters of species of *Terebellidae* (Polychaeta: Trichobranchidae). LL: lower lobes, Nos: number, UL: upper lobes.

	Reference (material examined)	Size range (mm)	Notochaetae TC1 (vs following ones)	TC3 glandular region (shape)	Nos thoracic uncini	Nos abdominal uncini (Nos abd. segments)	M/G pattern
<i>T. atlantis</i> Williams, 1984	Parapar <i>et al.</i> 2011 (new material)	8–18	same size	no	15	25 (25)	compact TC1–10 striped TC11–17
<i>T. bigeniculatus</i> Parapar, Moreira & Helgason, 2011	Parapar <i>et al.</i> 2011 (type material)	10–24	same size	no	8–10	20 (22)	compact SG1–11 striped SG12–14
<i>T. bonifi</i> n. sp.	this study (type material)	22–30	same size	yes (oval)	12–15	40 (32)	compact TC1–4 striped TC5–11
<i>T. ceneresi</i> n. sp.	this study (type material)	14–16	absent or much smaller	no	7–10	20 (30)	TC4 white, compact TC1–10 striped TC11–12
<i>T. europa</i> n. sp.	this study (type material)	15–17	slightly longer	yes (undulating, with lateral ridges)	13–17	30 (33)	compact TC1–9 striped TC10–12
<i>T. gentili</i> n. sp.	this study (type material)	20–32	slightly shorter	yes (undulating)	11–15	30 (30)	white antero-ventral lines (TC5–9) striped TC1–12
<i>T. gracilis</i> Malm, 1874	Parapar <i>et al.</i> 2011 (holotype)	32	same size	no	16–22	45 (43)	white TC1–4, compact TC5–10 striped TC11
<i>T. gralli</i> n. sp.	this study (type material)	8–20	slightly shorter	yes (crescent moon shape)	8–12	25 (30)	compact TC1–4 striped TC5–11
<i>T. lilasae</i> n. sp.	this study (type material)	34–37	same size	yes (oval)	12–20	36 (25)	white antero-ventral lines (TC5–9) compact TC1–6
<i>T. mediterranea</i> Parapar, Mikac & Fiege, 2013	Parapar <i>et al.</i> 2013 (type material)	23	longer	no	10–16	33 (32)	striped TC7–12 compact TC1–3
<i>T. parapari</i> n. sp.	this study (type material)	6–14	longer	yes (small round)	10–12	30 (15)	striped TC4–12 compact TC1–4
<i>T. resomari</i> n. sp.	this study (type material)	30–35	slightly shorter	yes (elongated with lateral ridges)	20–25	45 (35)	striped TC5–11 compact TC1–5
<i>T. shetlandica</i> Parapar, Moreira & O'Reilly, 2016	Parapar <i>et al.</i> 2016 (type material)	6–19	same size	no	8–10	6–12 (30)	striped TC6–12 compact TC1–6
<i>T. stroemii</i> Sars, 1835	Parapar & Hutchings, 2014 (neotype)	52	same size	yes (oval)	30	70 (36)	striped TC7–12 compact TC1–3 striped TC4–12

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Tabl E 2. (Continued)

	Presence of 5 th lobe	Branchiae length (Nos lamellae)	Fusion of lobes	Lobe tips	Presence of branchial papillae	Type locality	Depth range	Distribution
<i>T. atlantis</i> Williams, 1984	no	TC6 (20)	not fused	pointed	no	New England slope, USA	173–3000 m	Iceland, Norwegian Sea, Barent Sea, Greenland Sea
<i>T. bigenticulatus</i> Parapar, Moreira & Helgason, 2011	yes	TC4 (16)	1/3 of length	pointed	no	North-West Iceland	179–968 m	Norwegian coast, Barent Sea, Iceland
<i>T. bonifi</i> n.sp.	yes	TC4 (45)	1/2 of length	short pointed (UL), long pointed (LL)	yes (short conical, anteriorly only)	Gulf of Lion (Mediterranean Sea), France	90 m	only type locality
<i>T. ceneresi</i> n.sp.	no	TC7 (25)	not fused	short on LL only	no	Near Capbreton Canyon (Bay of Biscay), France	90–140 m	Bay of Biscay, Gulf of Lion (France)
<i>T. europa</i> n.sp.	yes	TC6 (50)	1/2 of length	short pointed (UL), long pointed (LL)	yes (rounded, anteriorly only)	Bay of Brest (Bay of Biscay), France	2–102 m	from Norwegian coasts to Bay of Biscay
<i>T. gentili</i> n.sp.	yes	TC6 (50–70)	1/2 of length	long pointed	yes (spaced, small and elongated)	Morlaix Bay (English Channel), France	2–17 m	English Channel, Bay of Biscay (France)
<i>T. gracilis</i> Malm, 1874	yes	TC4 (25)	1/3 of length	pointed	no	Bohuslän (North Sea), Sweden	68–2076 m	Skagerrak, Norwegian coast, Norwegian Sea, Iceland
<i>T. gralli</i> n.sp.	yes	TC4 (40)	less than 1/2 of length	long pointed (UL), short pointed (LL)	no	Bay of Brest (Bay of Biscay), France	2–3 m	only type locality
<i>T. lilasae</i> n.sp.	yes	TC5 (60–80)	3/4 of length	short pointed (UL), long pointed (LL)	yes (rounded)	West Gironde Mud Patch (Bay of Biscay), France	50–70 m	Bay of Biscay, Gulf of Lion (France)
<i>T. mediterranea</i> Parapar, Mikac & Fiege, 2013	yes	TC4 (40)	fused	pointed	no	North Adriatic Sea, Croatia	31 m	only type locality
<i>T. parapari</i> n.sp.	no	TC4 (20)	not fused	short pointed (UL), short filaments (LL)	no	Near Capbreton Canyon (Bay of Biscay), France	120 m	only type locality
<i>T. resomari</i> n.sp.	yes	TC4 (50–60)	less than 1/2 of length	short pointed (UL), long pointed (LL)	yes (digitiform)	Dunkerque (North Sea), France	10–15 m	North Sea, Bay of Biscay (France)
<i>T. shetlandica</i> Parapar, Moreira & O'Reilly, 2016	no	TC6 (20)	not fused	long pointed (LL), long filaments (LL)	no	East of the Shetland Islands (North Sea), Scotland	100–160 m	Kattegat, Skagerrak, North Sea, Norwegian Coast
<i>T. stroemii</i> Sars, 1835	yes	TC4 (80)	1/2 of length	short pointed	no	Bergensfjord (North Sea), Norway	55–110 m	Norwegian coasts (other localities doubtful)

Methyl green staining pattern. Stained with solid from TC1–TC5 (TC1 and TC2, poorly stained), striped from TC6 to about TC12, bands becoming slightly narrower and more widely spaced; glandular region on TC3 white (Fig. 17D).

Etymology. The species is named after the RESOMAR, French marine stations and observatories network (Réseau des Stations et Observatoires MARins) which organized the venue for the workshops of Mario Londoño-Mesa and Pat Hutchings in France and whose participants sent us all the material examined in this paper.

Habitat. Muddy sediments of harbour, from 10 to 15 m depth and maerl (rhodolith) beds (2–3 m depth).

Type locality. Dunkerque harbour, North Sea, France.

Distribution. North Sea (Dunkerque), Bay of Biscay (Bay of Brest), France, NE Atlantic (Fig. 1).

Remarks. Except *T. stroemii* from Adriatic Sea (Parapar *et al.* 2013) (see *T. lilasae* **n. sp.** Remarks), *Terebellides resomari* **n. sp.** differs from other European previously known species by the presence of papillar projections pointing over the edge of the branchial lamellae. By this characteristic, *T. resomari* **n. sp.** is similar to *T. bonifi* **n. sp.**, *T. europaea* **n. sp.**, *T. gentili* **n. sp.** and *T. lilasae* **n. sp.** Among these last species, *T. resomari* **n. sp.** differs by the presence of an elongated upper lip, of individually well separated branchial lamellae and of conical branchial papillae (Table 2).

Genus *Trichobranthus* Malmgren, 1866

Type species *Trichobranthus glacialis* Malmgren, 1866 by monotypy.

Trichobranthus glacialis Malmgren, 1866 by monotypy.

Figures 19–20

Trichobranthus glacialis,—Malmgren, 1866: 395–396, pl. 24 fig. 65.—McIntosh, 1922: 205–209, pl. 115 fig. 5, pl. 127 fig. 4.—Fauvel, 1927: 288–289, fig. 100a–h,—Holthe, 1986b: 164–165, fig. 77, map 76.—Hutchings & Peart, 2000: table 4.

Material examined: SMA_Tricho_02, two complete specimens, Northeast Atlantic Ocean, Brittany, Trévignon, MTR1, 47°47'30"N, 3°52'57"W, 11 m depth, February 2015; MNHN-IA-PNT 95, one specimen, anterior part, Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'54"W, 1.3 m depth, June 2016; MNHN-IA-PNT 96, one specimen, anterior part, Northeast Atlantic Ocean, Brittany, Bay of Brest, BK, 48°21'28"N, 4°26'38"W, 7 m depth, May 2018; MNHN-IA-PNT 97, one complete specimen, Northeast Atlantic Ocean, Brittany, Trévignon, MTR1, 47°47'30" N, 3°52'57" W, 11 m depth, February 2015; MNHN-IA-PNT 98, two specimens, Northeast Atlantic Ocean, Brittany, Bay of Brest, ZG, 48°17'19"N, 4°24'04"W, 2 m depth, June 2016, mounted for SEM; SMA_Tricho_05, one specimen, anterior part, Northeast Atlantic Ocean, Brittany, Bay of Brest, HA4, 48°19'18"N, 4°24'11"W, 2 m depth, June 2016, mounted for SEM; SMA_Tricho_14, two specimens, Northeast Atlantic Ocean, Brittany, Bay of Brest, BK, 48°21'28"N, 4°26'38"W, 7 m depth, May 2018, mounted for SEM; MNHN-IA-PNT 99, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'53"W, 5 m depth, May 2018; SMA_Tricho_08, complete (posterior part used for molecular analysis), Northeast Atlantic Ocean, Brittany, Bay of Brest, ZC, 48°18'55"N, 4°21'53"W, 5 m depth, May 2018.

Comparative material examined: BMNH 1923.3.22.47 (National History Museum, London). NMW.Z.2012.045.0072 and NMW.Z.2000.011.0102 (National Museum Wales, Cardiff). All specimens sampled in Norway.

Description. Medium size species, with length between 9.8 and 13.9 mm and width between 1.2 and 1.7 mm, thorax cylindrical, abdomen tapering (Fig. 19A).

Prostomium well developed, distal part extending transversely across base of upper lip, trilobed, with buccal tentacles originating laterally and mid-dorsally; long buccal tentacles of 2 types, thin and cylindrical, and thick and grooved (Figs 19C & 20A–B). Two groups of black or brown eyespots, forming two dorsolateral areas, situated dorsally on prostomium. Peristomium with one pair of large ventrolateral flaring lobes (Figs 19A, D & 20A), with ciliary ridges, midventrally fused to lower lip; lower lip short, upper lip hidden by buccal tentacles. SG1 dorsally inconspicuous, ventrally forming semicircular eversible process (Fig. 19C). SG2–4 with ventral crests anteriorly raised, larger than following ones (Fig. 19C); following segments with short ventral crests. Dorsum smooth. Ventral

groove absent. Three pairs of branchiae, on posterior parts of SG2–4, each pair with single long and thick filament (extending to TC3) (Figs 19B, D & 20 A–B); filaments wrinkled, with rounded tips (Figs 19B & 20B); pairs of branchiae progressively inserted mid dorsally (third pair with each filament joined) (Fig. 20B); filaments highly fragile and easily lost.

Notopodia starting from SG6, extending for 15 segments, trapezoidal shaped, laterally aligned; first two pairs shorter than subsequent ones; narrowly-winged long bilimbate notochaetae, narrowly bilimbate. Neuropodia starting from SG6, first thoracic neuropodia with few uncini, following ones with about 15 uncini per torus arranged in one irregular row; uncini with strong, distally blunt main fang and many rows of secondary teeth, presence of a sheath below main fang (Fig. 20C). About 45 abdominal neuropodia as erect pinnules paddle-shaped with distal margin provided with about 35 uncini; each with 2 rows of pointed secondary teeth above and laterally to main fang, surmounted by an upper crest of minute teeth (hardly visible) (Fig. 20D).

Nephridial papillae not seen. Pygidium bulbous and slightly crenulated (Fig. 19A).

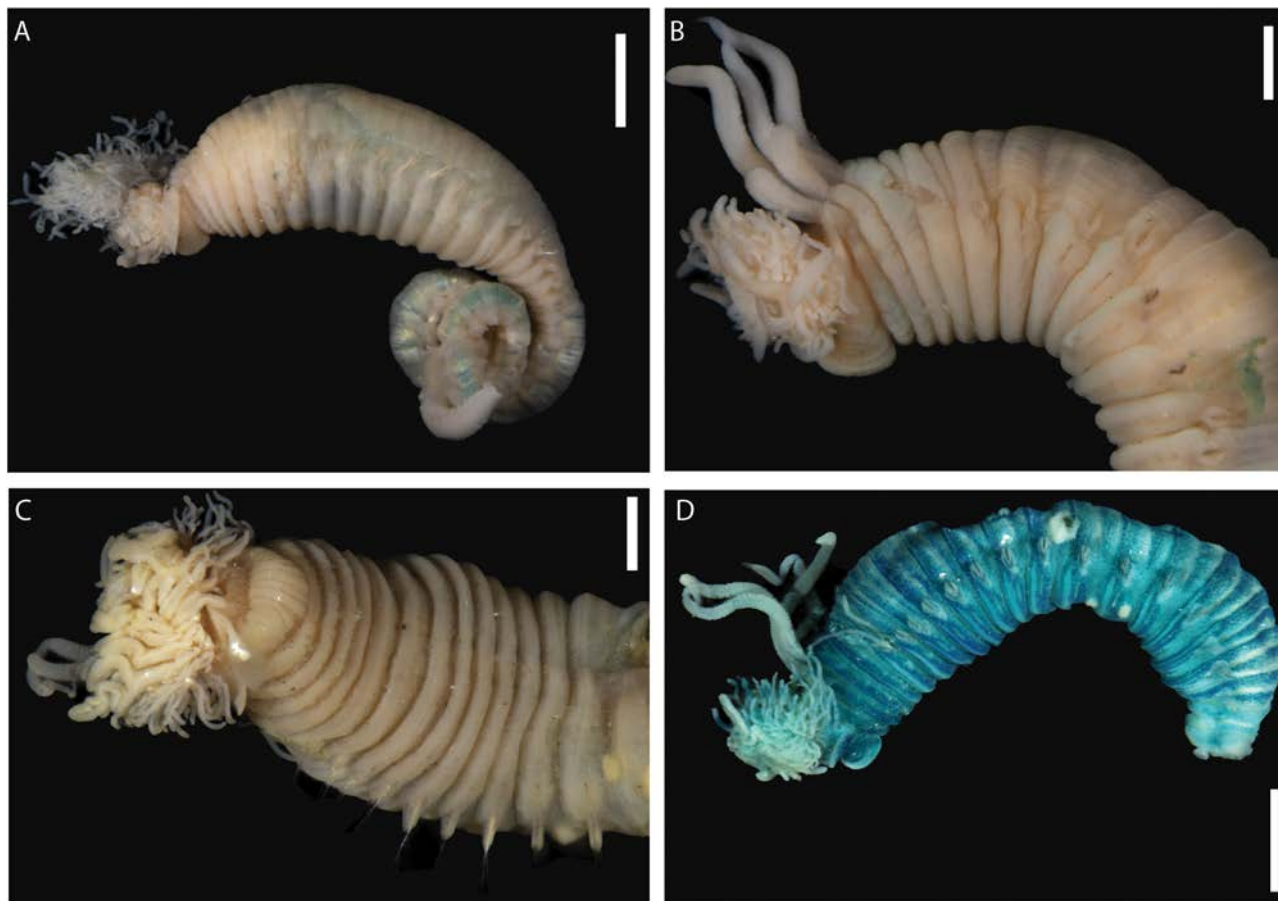


FIGURE 19. *Trichobranchus glacialis* Malmgren, 1866, MNHN-IA-PNT 97 (A), MNHN-IA-PNT 96 (B) and MNHN-IA-PNT 95 (C–D) **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, ventral view; **D.** Anterior part, lateral view, methyl green staining. Scales: A–D=1 mm, B–C=500 μ m.

Remarks. As pointed out by Garraffoni *et al.* (2005), the holotype of *T. glacialis* is not stored in any Swedish museum and is probably lost. In the absence of type material, we have compared our specimens with specimens from Norway: BMNH 1923.3.22.47, NMW.Z.2012.045.0072 and NMW.Z.2000.011.0102. The characteristics of French specimens correspond to those of Norwegian specimens but also to distinguishing characters summarized in Hutchings & Peart (2000, Table 4). Indeed, French specimens show three pairs of branchiae with 3rd inserted mid-dorsally, presence of eyespots, peristomium with a pair of large rounded thin and flexible lobes, presence of lateral lobes on segments 2 and 3, narrow double winged notochaetae, about 45 abdominal chaetigers, short abdominal neuropodia. To our knowledge, this study provides for the first time SEM plates for this species. SEM permitted to confirm the presence of a tuft of bristles along the lower surface of the main fang of thoracic uncini, as shown for *Trichobranchus bunnabus* Hutchings & Peart, 2000. SEM also permitted us to distinguish an upper crest of minute teeth above the two rows of pointed secondary teeth of abdominal uncini.

Habitat. On mud, sand and mixed bottoms, uppermost sublittoral to depths exceeding 2500 m (Holthe 1986), maerl (rhodolith) beds, from 2 to 15 m depth (this study).

Distribution. Reported widely from Northern Europe; Mediterranean, Adriatic and Aegean Seas; Western North Atlantic, North Pacific, South, West and East Africa; South America, Arctic and Antarctica (Hutchings & Peart, 2000; Gil, 2011); Northern part of the Bay of Biscay (Bay of Brest, Trévignon, Belle-Ile) (this study). However, molecular studies should be carried out to confirm this wide distribution and depth range.

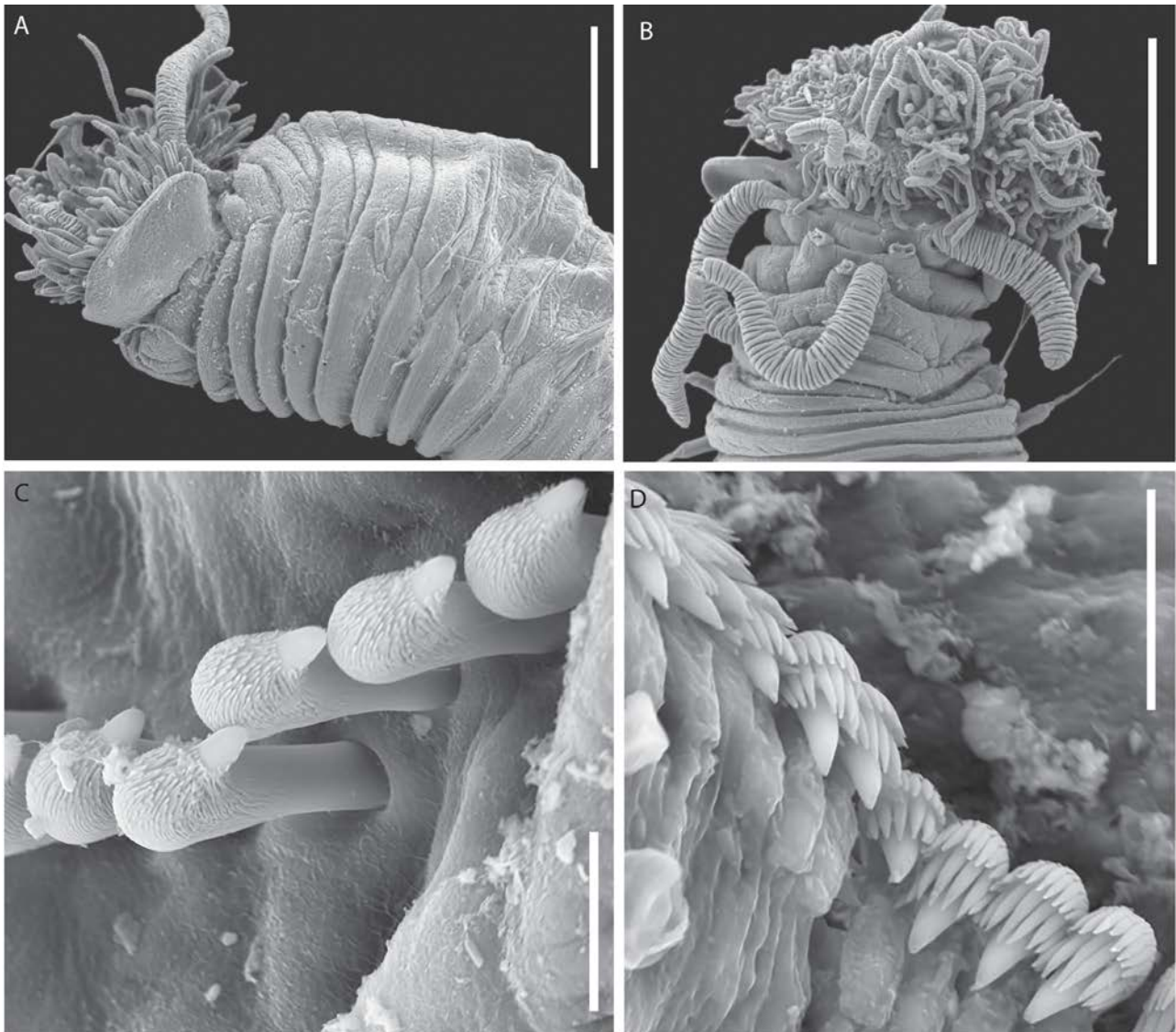


FIGURE 20. *Trichobranthus glacialis* Malmgren, 1866, SEM MNHN-IA-PNT 98 (A, D), SMA_Tricho_14 (B), BR_Tricho_05 (C) **A.** Anterior part, lateral view; **b.** Anterior part, dorsal view; **C.** Uncini, thoracic chaetiger; **D.** Uncini, abdominal chaetiger. Scales: A=500 μ m, B=1 mm, C–D=10 μ m.

***Trichobranthus demontaudouini* n. sp.**

Figures 21–22

Type material: Holotype: MNHN-IA-TYPE 1894, one complete specimen, Northeast Atlantic Ocean, Bay of Biscay, P40, 43°33'26"N, 1°41'37"W, 112 m depth, May 2018; **Paratypes:** MNHN-IA-TYPE 1895, one incomplete specimen, Northeast Atlantic Ocean, Bay of Biscay, P40, 43°33'26"N, 1°41'37"W, 112 m depth, May 2018, mounted for SEM; MNHN-IA-TYPE 1896, one incomplete specimen, Northeast Atlantic Ocean, Bay of Biscay, P37, 43°33'31"N, 1°43'49"W, 129 m depth, May 2018.

Additional material: SMA_Tricho_22, incomplete, Northeast Atlantic Ocean, Northern Bay of Biscay, APP

D3, 47°28'21" N, 03°29'35" W, 72 m depth, May 2018, mounted for SEM; AM W.52080, incomplete, Northeast Atlantic Ocean, Northern Bay of Biscay, APP D3, 47°28'21"N, 03°29'35"W, 72 m depth, May 2018; SMA_Tricho_25, incomplete, Northeast Atlantic Ocean, Northern Bay of Biscay, APP D1, 47°28'48"N, 03°39'20"W, 72 m depth, May 2018;

Description. Medium size species, holotype with length of 30.4 mm and width of 1.8 mm (1.2–1.6 mm), thorax cylindrical, abdomen tapering (Fig. 21A).

Prostomium well developed, distal part extending transversely across base of upper lip, trilobed, with buccal tentacles originating laterally and mid-dorsally; long buccal tentacles of two types, thin and cylindrical, and thick and grooved (Fig. 22B); eyespots present as two groups forming two dorsolateral bands situated on prostomium above origin of buccal tentacles (Fig. 21A–C). Peristomium with one pair of large ventrolateral flaring lobes (Fig. 21A), with ciliary ridges, midventrally fused to lower lip; lower lip short, upper lip hidden by buccal tentacles. Segment 1 dorsally inconspicuous, ventrally forming semicircular eversible process (Fig. 21D). SG2–4 with ventral crests anteriorly raised, larger than following ones; following segments with short ventral crests (Fig. 21D). Dorsum smooth. Ventral groove absent. Two pairs of branchiae, on segments 2 and 3 (Figs 21B–C & 22A–B), each pair with single long filament; filaments annulated, highly fragile (filament of second pair of holotype regenerating) (Fig. 21B), second pair originating slightly dorsally to first pair (Fig. 22B).

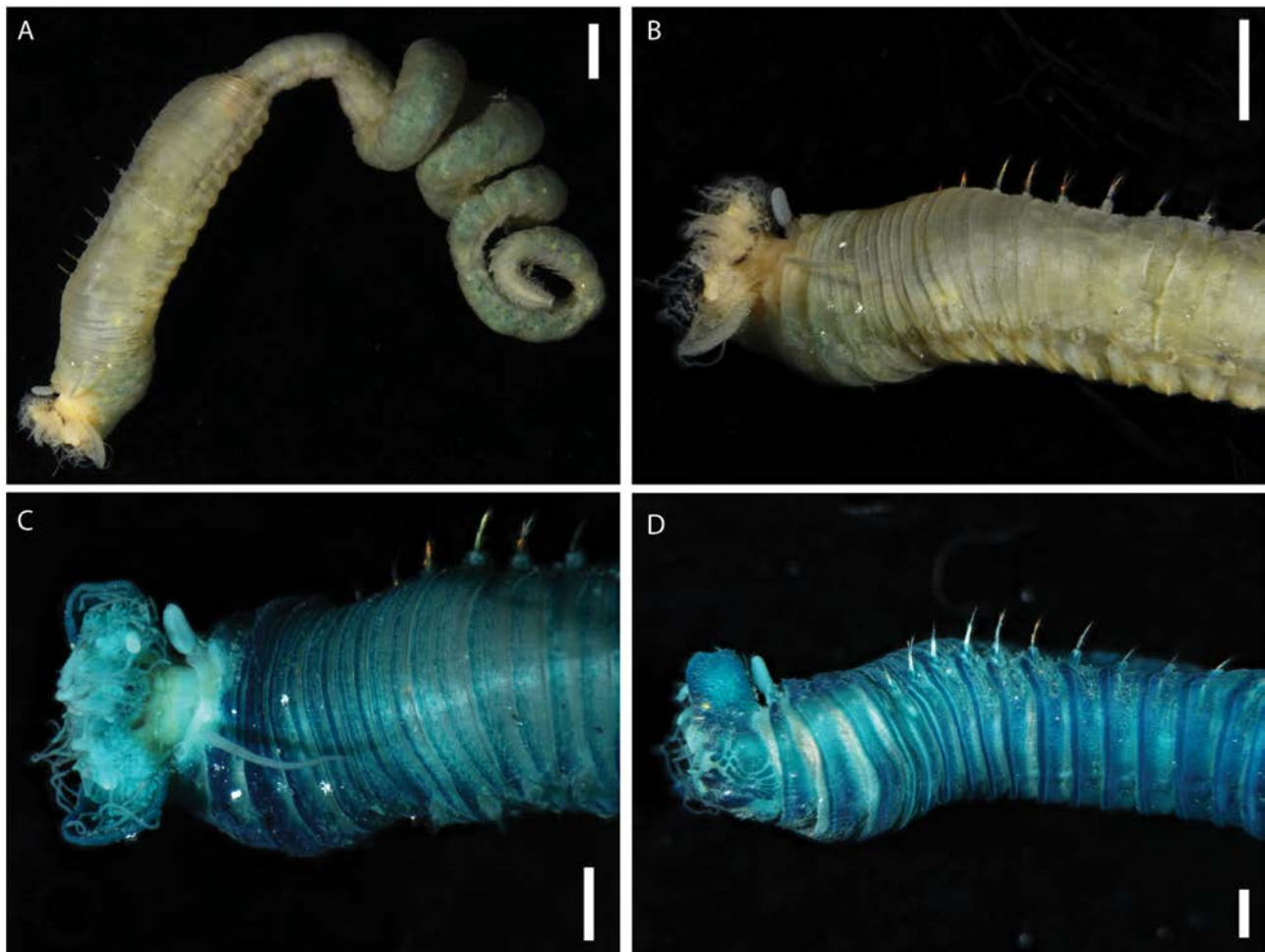


FIGURE 21. *Trichobranthus demontaudouini* n. sp. holotype MNHN-IA-TYPE 1894 **A.** Entire worm, lateral view; **b.** Anterior part, lateral view; **C.** Anterior part, dorsal view, methyl green staining; **D.** Anterior part, ventral view, methyl green staining. Scales: A–B=1 mm, C–D=500 μ m.

Notopodia starting from SG 6, extending for 15 segments, trapezoidal shaped; first three pairs shorter than subsequent ones, laterally aligned; narrowly-winged long bilimbate notochoetae, with narrow limbation on both margins. Neuropodia starting from SG 6, thoracic neuropodia with 15 to 25 uncini per torus arranged in one irregular row; uncini with strong, distally blunt main fang and many rows of secondary teeth, presence of a sheath below main fang (Fig. 22C). About 65 abdominal neuropodia as erect pinnules, paddle-shaped with distal margin

provided with about 35 uncini; uncini with three rows of pointed secondary teeth above and laterally to main fang, surmounted by an upper crest of minute teeth (only visible with SEM) (Fig. 22D). Pygidium with two short bulbs (Fig. 21A).

Remarks. In European waters, *Trichobranthus demontaudouini* n. sp. can be easily differentiated from *T. glacialis* by the presence of two pairs of branchiae, instead of three pairs. In this character, *T. demontaudouini* n. sp. is similar to *T. roseus*. However, *T. roseus* is characterized by the absence of eyespots and many secondary teeth on abdominal uncini (Holthe 1986:167, fig.78d; Nogueira 2008).

Etymology. The species is named after Dr. Xavier de Montaudouin, for his friendship, his permanent support and for his many contributions to French benthic research.

Habitat. Mud to sandy mud, 110–130 m depth.

Type locality. Near Capbreton Canyon, Bay of Biscay, Northeast Atlantic Ocean, France.

Distribution. Bay of Biscay, near Capbreton Canyon to South Brittany (Fig. 1).

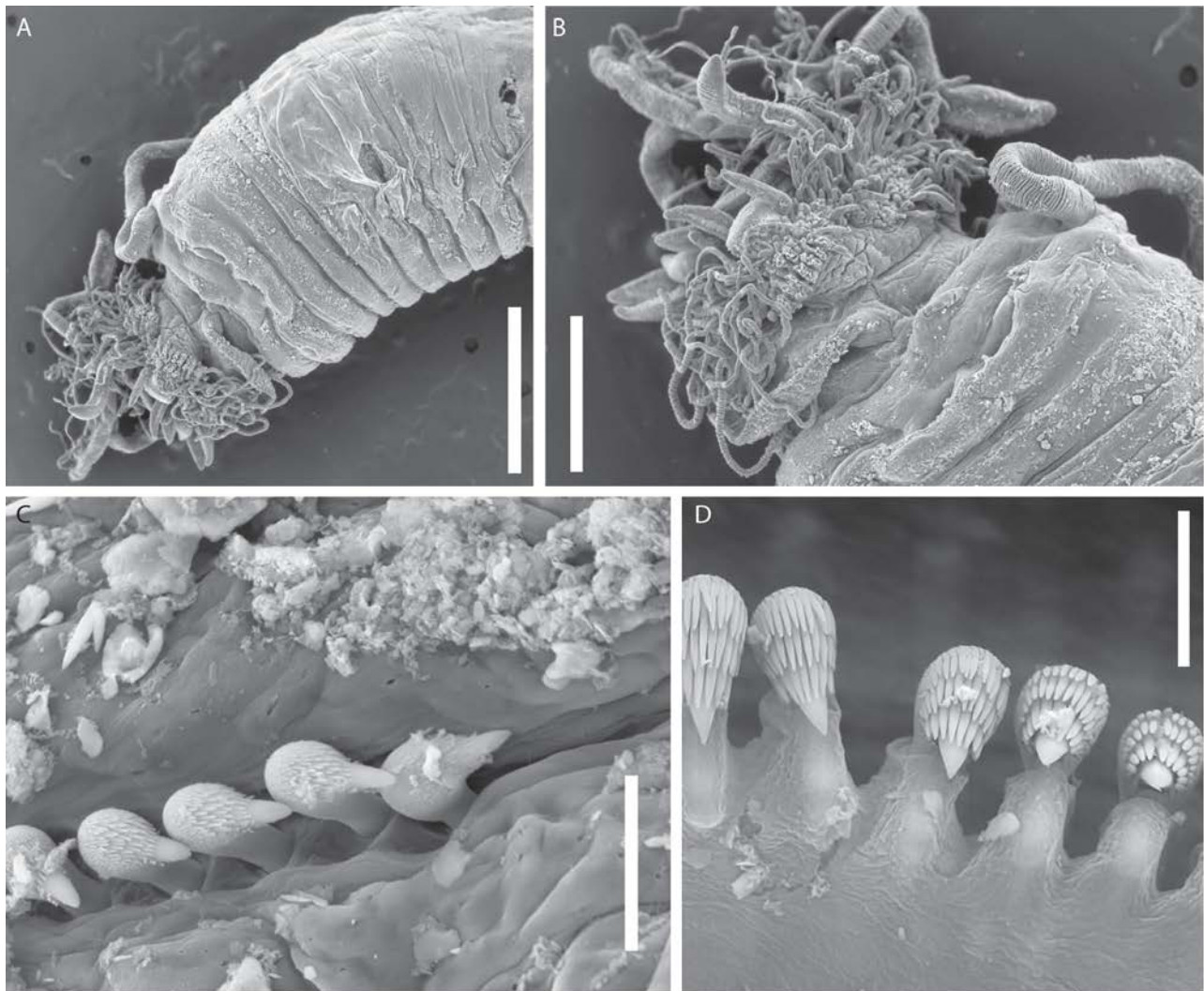


FIGURE 22. *Trichobranthus demontaudouini* n. sp. SEM paratype MNHN-IA-TYPE 1895 **A.** Anterior part, dorsal view; **b.** Head, dorsal view; **C.** Uncini, thoracic chaetiger; **D.** Uncini, abdominal chaetiger. Scales: A–B=1 mm, C–D=500 μ m.

Discussion

Prior to this study, only three species belonging to Trichobranchidae have been reported from French waters: *Terbellides stroemi*, *Trichobranthus glacialis* and *Octobranthus lingulatus*. The two last species seem to be present along the French coasts, even if some doubts persist, especially because their type locality are situated far from French Atlantic coasts (from Spitzbergen, Arctic Ocean for *T. glacialis* and from Croatia, Adriatic Sea for *O. lingulatus*). Moreover, as the holotype of *O. lingulatus* is in poor condition and holotype of *T. glacialis* seems to be

lost, neotypes for these two species should be designed and described. Fixing neotypes will probably permit us to describe new species belonging to these two genera, as it has been done for *Terebellides* genus after designation of a neotype of *T. stroemii* (Parapar & Hutchings, 2014). With *T. demontaudouini* **n. sp.**, we describe a new species of *Trichobranthus* for European waters, but there are probably many cryptic species in this area as *T. glacialis* is recorded widely from all European waters. Our study also suggests the absence of the so-called “cosmopolitan” species *T. stroemi* from French waters, despite numerous specimens observed. Before this study, this species was the only representative of the genus *Terebellides* reported in France. With this new study a high diversity is revealed, represented by eight *Terebellides* species new for science, bringing the number of species in this genus in Europe to 14. This number of species is clearly an underestimate, even in French waters, since this genus is almost certainly represented by other undescribed species. Indeed, molecular results highlight the presence of sequences which we cannot associate with any of the newly described species of this paper. These sequences corresponded to a damaged specimens (sequences associated to clade 9) or a single specimen (SMA_Ban_17) and we prefer not describe them as new for science, but await future sampling campaigns in order to obtain more materials. Finally, lack of specimens from several French geographical areas (like Eastern Mediterranean Sea or Corsica), and also from deep waters, strongly suggests the possibility of discovering many more new species of this family in the future.

To describe new species, especially for *Terebellides* genus, we strongly encourage taxonomists to observe important characteristics using different tools. Firstly, SEM reveal significant details of the external anatomy of *Terebellides* (Parapar *et al.* 2011). During this study, SEM also permitted us to obtain more informative plates revealing useful additional characters which are possible to see under the classical stereomicroscope (except for teeth of uncini). The only problem we have encountered with SEM was the observation of *capitium* of geniculate acicular chaetae. Actually, we did not observe these denticles in the upper part of the acicular hooks although they were for example present among all Icelandic species (Parapar *et al.* 2011). Either the capitium is never present among French species, or its absence could be linked to the model of microscope (benchtop microscope) or to the method of coating the specimens.

Secondly, as many cryptic species of trichobranchids occur at small geographic scale and a lot of species go under the radar, molecular analysis is an important tool to differentiate morphologically similar species and confirm presence of new species. Recently, Nygren *et al.* (2018) identified 27 species from Northern Europe, most of them undescribed, using molecular tools. One of the important results of this last study was the co-occurrence of several species in the same habitat. In order to compare French species to those present in northern Europe we tried to obtain sequences from our material. Among all the French species, *Trichobranthus demontaudouini* **n. sp.**, *Terebellides gentili* **n. sp.**, *Terebellides parapari* **n. sp.** and *Terebellides resomari* **n. sp.** were not “molecular friendly”, as they were fixed in formalin during sampling campaigns. Concerning other species, we managed to amplify 16S sequences for seven species (two undescribed species) and COI sequences for three species only (one undescribed), confirming the difficulties to obtain DNA sequences for Terebellidae. When describing new species of trichobranchids, the best way is to fix a few posterior parapodia in 96% alcohol in order to perform molecular analysis and to fix the remaining specimen in formalin for morphological observation and species description. The DNA sequences will be associated with the type specimen stored in a collection, with registration numbers linking them.

However, in this revision, we tried to provide species diagnosis and identification key which can be used by scientists without resorting either to SEM or molecular biology. Among useful characteristics of diagnosis, we have found the following very useful. The first one is the degree of development of first notochaetae. These chaetae are generally of the same length (or slightly smaller) than following ones but they can also be longer (as in *T. mediterranea* and *T. parapari* **n. sp.**) or absent (or much smaller) as for *T. ceneresi* **n. sp.** Shape of the branchiae is also very important, particularly concerning the presence of 5th lobe, the number and shape of lamellae, the degree of fusion of upper and lower lobes and presence of terminal filaments (as for *T. shetlandica* and *T. parapari* **n. sp.**). Another consistent character is the presence of papillae on margins of branchial lamellae, even if this character has not been described in some previous species descriptions. Among French species, these papillae are only present in *T. bonifi* **n. sp.**, *T. europaea* **n. sp.**, *T. gentili* **n. sp.**, *T. lilasae* **n. sp.**, and *T. resomari* **n. sp.** Moreover, these five species can be separated by the shape of these papillae and the presence of these papillae on most of the lamellae or only on the most anterior ones (as *T. bonifi* **n. sp.** and *T. europaea* **n. sp.**). Finally, methyl green pattern is crucial. Indeed, this colouration permits the separation of species according to compact/striped pattern across the ventrum and seems to be very stable in *Terebellides* species. Particularly, the presence or absence and the shape of glandular region on the 3rd thoracic chaetiger is very important and should be observed with precision in future taxonomic studies. Dur-

ing this study, we have found eight species with this feature: *T. bonifi* n. sp., *T. europaea* n. sp., *T. gentili* n. sp., *T. gralli* n. sp., *T. lilasae* n. sp., *T. parapari* n. sp., *T. resomari* n. sp. and *T. stroemii* and five different shapes of this glandular area. This character also needs to be studied in detail in future studies.

To conclude, this first part of the ‘Spaghetti project’ devoted to the revision of French Trichobranchidae permitted us to describe nine new species. Eight of these species were previously recorded as *T. stroemii* which appears to be absent from French waters. This study using both morphological and molecular insights should facilitate the description of new species of trichobranchids especially from European waters.

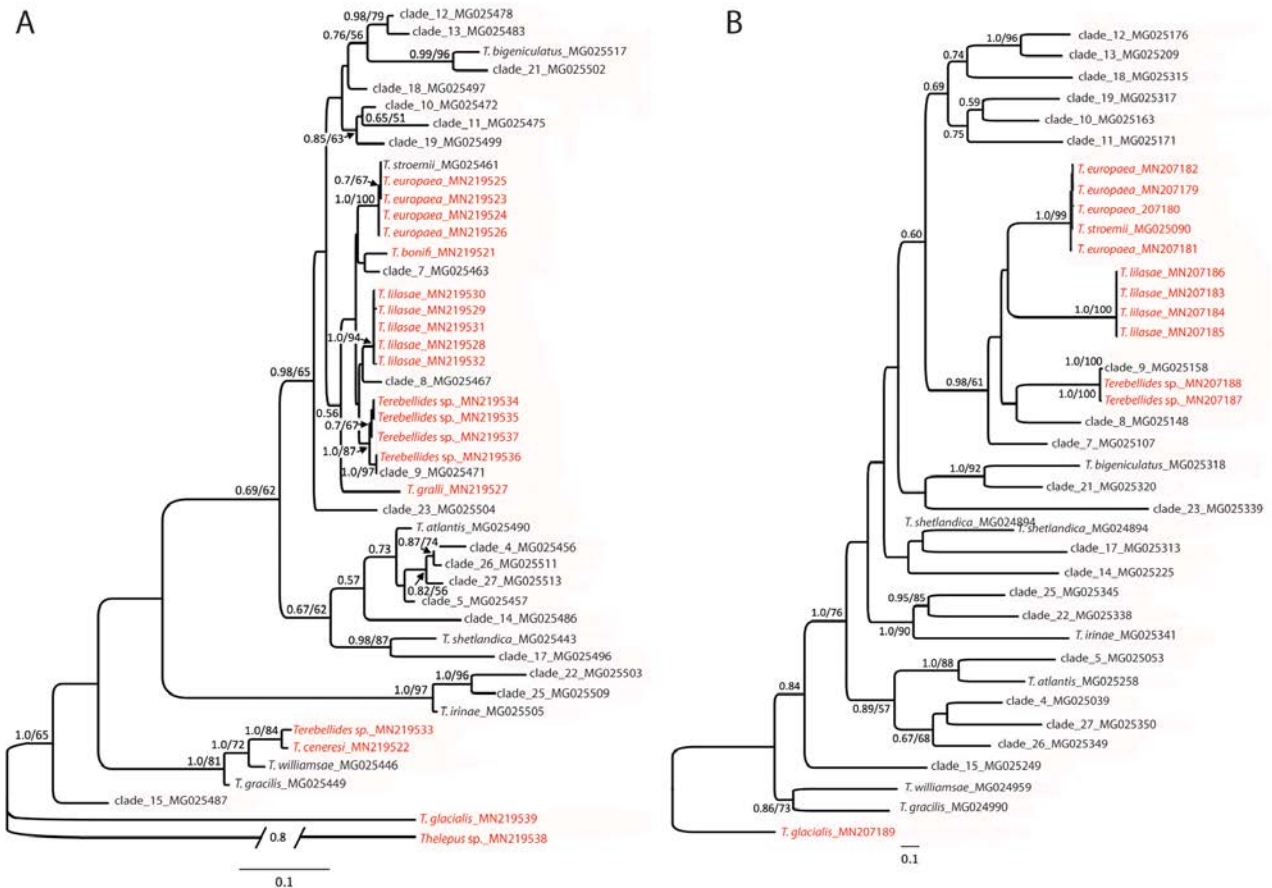


FIGURE 23. Maximum likelihood trees of valid European *Terebellides* species and available sequences of *Terebellides* species obtained in this study, based on **A.** 16S sequences; **b.** COI sequences. Values on nodes represent posterior probabilities > 0.5 (first values), or Maximum likelihood bootstrap support > 50 (second values). Sequence accession numbers refer to Table 1 and Nygren *et al.* (2018), text in red to specimens sequenced during this study.

Key to European species of Trichobranchidae

- 1A. One large branchia with transverse lamellae 2 (*Terebellides*)
- 1B. Two or three pairs of branchiae 14 (*Trichobranchus*)
- 1C. Four pairs of branchiae 16 (*Octobranchus*)
- 2A. Geniculate acicular chaetae on TC5 and TC6 *T. bigeniculatus*
- 2B. Geniculate acicular chaetae on TC6 only 3
- 3A. Branchial lamellae margins without papillae 4
- 3B. Branchial lamellae margins with papillae 11
- 4A. Lower branchial lobes with long filaments 5
- 4B. Lower branchial lobes without or with short projections 6
- 5A. Glandular region on TC3 present; branchial lamellae pointed; notochaetae from TC1 longer than following ones; dorsal papillae absent *T. parapari* n. sp.
- 5B. Glandular region on TC3 absent; branchial lamellae rounded; all notochaetae equal-sized; dorsal papillae present *T. shetlandica*
- 6A. Ventral white band on TC4 after MG staining present 7

6B.	No distinct pattern on TC4 after MG staining	8
7A.	Large species (>30 mm); 5 th branchial lobe present; notochaetae of TC1 similar than following ones; main fang of thoracic uncini straight	<i>T. gracilis</i>
7B.	Small species (<20 mm); 5 th branchial lobe absent; notochaetae of TC1 absent or shorter than following ones main fang of thoracic uncini ‘eagle head’ shaped	<i>T. ceneresi</i> n. sp.
8A.	First notopodia and notochaetae longer than following ones	<i>T. mediterranea</i>
8B.	First notopodia and notochaetae similar or shorter than following ones	9
9A.	Large species (>50 mm); dorsal rounded projections on TC1–TC5 conspicuous; main fang of thoracic uncini ‘eagle head’ shaped	<i>T. stroemii</i>
9B.	Small species (<20 mm); dorsal rounded projections on TC1–TC5 absent; main fang of thoracic uncini straight	10
10A.	Glandular region on TC3 and 5 th branchial lobe absent	<i>T. atlantis</i>
10B.	Glandular region on TC3 and 5 th lobe present	<i>T. gralli</i> n. sp.
11A.	Glandular region on TC3 round or oval	12
11B.	Glandular region on TC3 otherwise	13
12A.	Glandular region on TC3 stained white, branchial lamellae with rounded papillae, TC1–3 without conspicuous dorsal projection	<i>T. lilasae</i> n. sp.
12B.	Glandular region on TC3 stained blue, branchial lamellae with conical papillae, TC1–3 with conspicuous dorsal projection	<i>T. bonifi</i> n. sp.
13A.	Most of branchial lamellae with digitiform papillae, upper lip elongated	<i>T. resomari</i> n. sp.
13B.	Only first branchial lamellae with digitiform papillae, lamellae well packed, upper lip not elongated	<i>T. europaea</i> n. sp.
13C.	Branchial lamellae with widely spaced, small and elongated papillae, MG pattern with white stripes from CH1 to 12, fixed specimens whitish	<i>T. gentili</i> n. sp.
14A.	Two pairs of branchiae	15
14B.	Three pairs of branchiae	<i>T. glacialis</i>
15A.	Eyespots absent	<i>T. roseus</i>
15B.	Eyespots present	<i>T. demontaudouini</i> n. sp.
16A.	Pairs of branchiae of different shapes; abdominal uncini with three rows of secondary teeth above the main fang	<i>O. floriceps</i>
16B.	All pairs of branchiae similar; abdominal uncini with two rows of secondary teeth above the main fang	<i>O. lingulatus</i>

Acknowledgements

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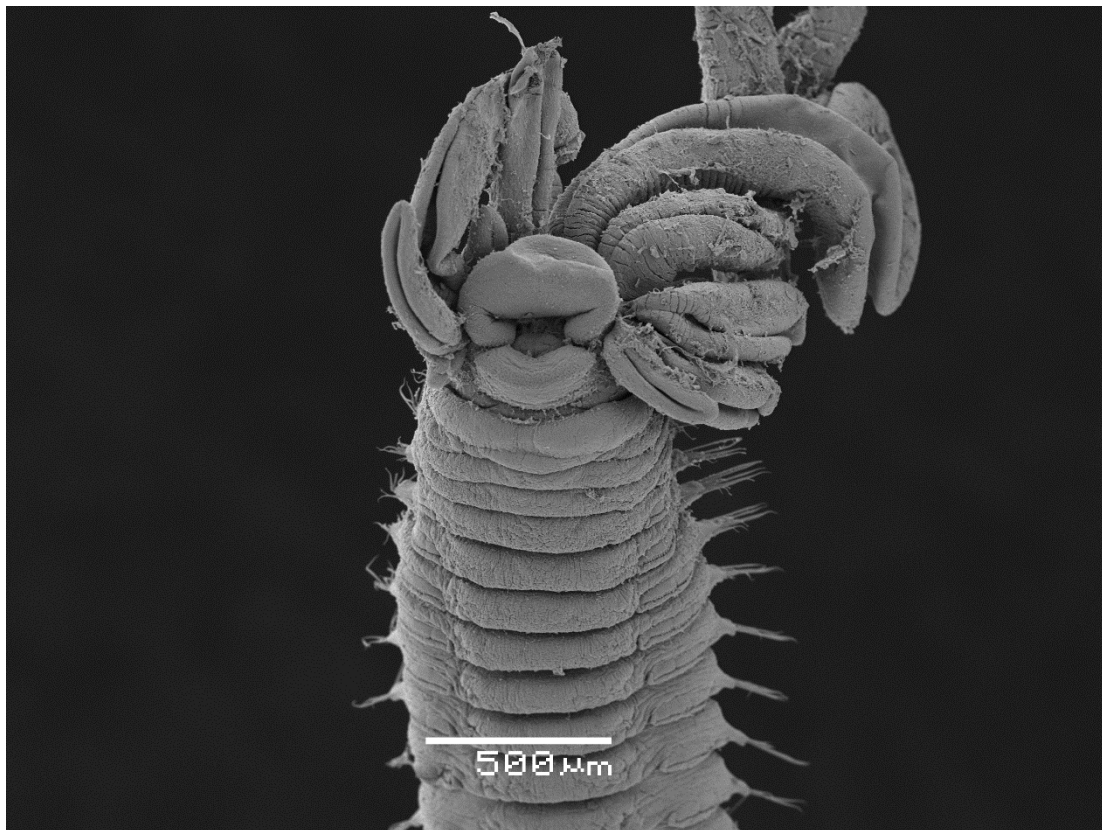
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CHAPITRE 2

Révision des Telothelepodidae et Thelepodidae

Lavesque N., Londoño-Mesa M.H., Daffe G., Hutchings P. (2020a). A revision of the French Telothelepodidae and Thelepodidae (Annelida, Terebelliformia), with descriptions of three species and first European record of a non-indigenous species. *Zootaxa* 4810 (2) 305-327*



Thelepus corsicanus Lavesque, Londoño-Mesa, Daffe & Hutchings 2020a

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A revision of the French Telothelepodidae and Thelepodidae (Annelida, Terebelliformia), with descriptions of three species and first European record of a non-indigenous species

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Abstract

Telothelepodidae and Thelepodidae from French waters are revised based on material available in French marine stations and newly collected specimens. This work is the second part of the Spaghetti Project aiming to revise French species of “Spaghetti” worms. It describes three new species using both morphological and molecular tools: *Streblosoma cabiochi* n. sp., *Streblosoma lindsayae* n. sp. and *Thelepus corsicanus* n. sp. This study also permitted us to detect the presence of an Asiatic species, *Thelepus japonicus*, in Arcachon Bay and Normandy, introduced via oysters transfers. An identification key for European species of both families is also provided.

Keywords: Polychaeta, Spaghetti Project, new species, molecular, morphology, taxonomy, exotic species

Introduction

This research is the second part of the “Spaghetti Project” aiming to revise French species of terebellids and trichobranchids. The first part, devoted to the Trichobranchidae, permitted us to describe nine new species along the French coasts (Lavesque *et al.* 2019). This collaborative project involves all benthic taxonomists of marine stations and includes newly collected material as well as material already available from the French marine stations (see Acknowledgements section). In this study, we undertook a comprehensive survey of both Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 and Thelepodidae Hessle, 1917, recently erected to family level after being considered as a single sub-family (Thelepodinae) of the family Terebellidae Johnston, 1846 (Nogueira *et al.* 2013).

Telothelepodidae is characterised by an upper lip narrow and expanded, distinctly longer than wide, by very poorly developed neuropodia throughout and anterior glandular ventral areas also poorly developed for most of the species (Nogueira *et al.* 2018; Hutchings *et al.* 2019). In European waters, this family is only represented by the genus: *Parathelepus* Caullery, 1915 (eight species) and the species *P. collaris* (Southern, 1914) (type locality: Ireland), recorded from French waters (Amoureux 1971; RESOMAR – French marine stations and observatories network – database, <http://resomar.cnrs.fr/bases/index.php>).

Thelepodidae is characterised by having short, hood-like upper lip, neuropodia as fleshy ridges and a distinctive uncinial morphology (short-handled avicular uncini, with terminal button, a reduced prow and strongly convex base) (Hutchings *et al.* 2019). This family is represented along the European coasts by three genera: *Euthelepus* McIntosh, 1885 (nine species), and the two speciose genera *Streblosoma* Sars, 1872 (40 species) and *Thelepus*

Leuckart, 1849 (52 species). In Europe, a single *Euthelepus* species is reported: *E. setubalensis* McIntosh, 1885 (type locality: off Portugal) (McIntosh 1885; Parapar & Moreira 2009) but never recorded from France. Five species belonging to the genus *Streblosoma* have been described or reported to date: *S. bairdi* (Malmgren, 1866) (type locality: Sweden), *S. intestinale* M. Sars in G.O. Sars, 1872 (type locality: Norway), and three species recently described from Mediterranean coasts (Italy): *S. hutchingsae* Lezzi & Giangrande, 2019, *S. nogueirai* Lezzi & Giangrande, 2019 and *S. pseudocomatus* Lezzi & Giangrande, 2019 (Gil 2011; Lezzi & Giangrande 2019). A single species was widely recorded from France: *S. bairdi* present from the North Sea to the Mediterranean Sea (Fauvel 1927; Amoureux 1971; de Montaudouin & Sauriau 2000; RESOMAR database). Concerning the genus *Thelepus*, seven species were recorded from European waters: *T. cincinnatus* (Fabricius, 1780) (type locality: West Greenland), *T. nucleolata* (Claparède, 1870) (type locality: Italy), *T. setosus* (Quatrefages, 1866) (type locality: France, English Channel), *T. triserialis* (Grube, 1855) (type locality: Mediterranean Sea) and the three species recently described: *T. davehalli* Jirkov, 2018 (type locality: NE Atlantic), *T. marthae* Jirkov, 2018 (type locality: Arctic Ocean), and *T. parapari* Jirkov, 2018 (type locality: Mediterranean Sea) (Gil 2011; Jirkov 2018). Only two species were recorded from French waters, from the North Sea to the Mediterranean Sea: *T. cincinnatus* and *T. setosus* (Quatrefages 1866; de Saint-Joseph, 1898; Fauvel 1927; Hirschberger *et al.* 1967; RESOMAR database).

During this study, we undertook a comprehensive survey of Telothelepodidae and Thelepodidae from French waters, based on both morphological and molecular analyses. We found three genera represented by five species, three of which are herein described as new. An Asian exotic species, *Thelepus japonicus* Marenzeller, 1884, originally described from Japan, is recorded for the first time in Europe. A taxonomic key for European species of Telothelepodidae and Thelepodidae is provided.

Material and methods

Morphological observations

Specimens were collected during different research programs or specific samplings (see Acknowledgements) along the French coasts (North Sea, English Channel, Bay of Biscay and Mediterranean Sea) (Fig. 1). For morphological analyses, specimens were fixed in 4% formaldehyde seawater solution; then, transferred to 70% ethanol. Methyl green, which can be washed out, was used to observe glandular areas. For molecular studies, a few parapodia were removed from several fresh specimens or from specimens fixed in 96% ethanol.

Preserved specimens were examined under a Nikon SMZ25 stereomicroscope and a Nikon Eclipse E400 microscope, and photographed with a Nikon DS-Ri 2 digital camera in Arcachon Marine Station, and under an Olympus S7X7 stereomicroscope and BX53 microscope, and photographed with an Olympus DP74 camera at the Australian Museum. Measurements were made using the NIS-Elements Analysis software, with width corresponding to the widest segments with parapodia, in the thoracic anterior region. Dehydrated specimens used for examination with scanning electron microscopy (SEM) were prepared by critical point drying, coated with gold and examined and photographed with a JEOL JSM 6480LA at Macquarie University, Sydney.

Description of new species is based on the holotype and morphological variations observed in the paratypes are given in brackets. The studied material is deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Australian Museum, Sydney (AM). Additional material is lodged in the collection housed at the Arcachon Marine Station, Arcachon, France (SMA).

Molecular data and analyses

Extraction of DNA was done with ISOLATE II Genomic DNA kit (BIOLINE) following protocol supplied by the manufacturers. The COI (cytochrome c oxidase subunit I) and 16S genes were amplified using different primers: 16SANNF (GCGGTATCCTGACCGTRCWAAGGTA) (Sjölin *et al.* 2005) with 16SBRH (CCGGTCTGAACT-CAGATCACGT) for 16S rDNA (Palumbi 1996); jgLCO1490 (TITCIACIAAYCAYAARGAYATTGG) and jgH-CO2198 (TAIACYTCIGGRTGICCRARAAYCA) (Geller *et al.* 2013) for COI. PCR (Polymerase Chain Reaction) occurred with Taq DNA Polymerase QIAGEN Kit in 20 µL mixtures containing: 2µL of 10X CoralLoad

PCR Buffer (final concentration of 1X), 1.5 μ L of MgCl₂ (25Mm) solution, 1.5 μ L of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 0.4 μ L of each primer (final concentration of 0.2 μ M), 0.1 μ L of Taq DNA Polymerase (5U/ μ l), 1 μ L template DNA and 13.1 μ L of nuclease-free water. The temperature profile was as follows for 16S: 94°C/60s - (94°C/40s-59°C/30s-72°C/90s) *40 cycles - 72°C/300s - 16°C, for COI: 94°C/300s - (94°C/30s-50°C/15s-72°C/60s)*35 cycles - 72°C/240s - 16°C. PCR success was verified by electrophoresis in a 1 % p/v agarose gel stained with Gelred. Amplified products were sent to Macrogen Company to complete double strain sequencing, using the same set of primers as used for PCR.

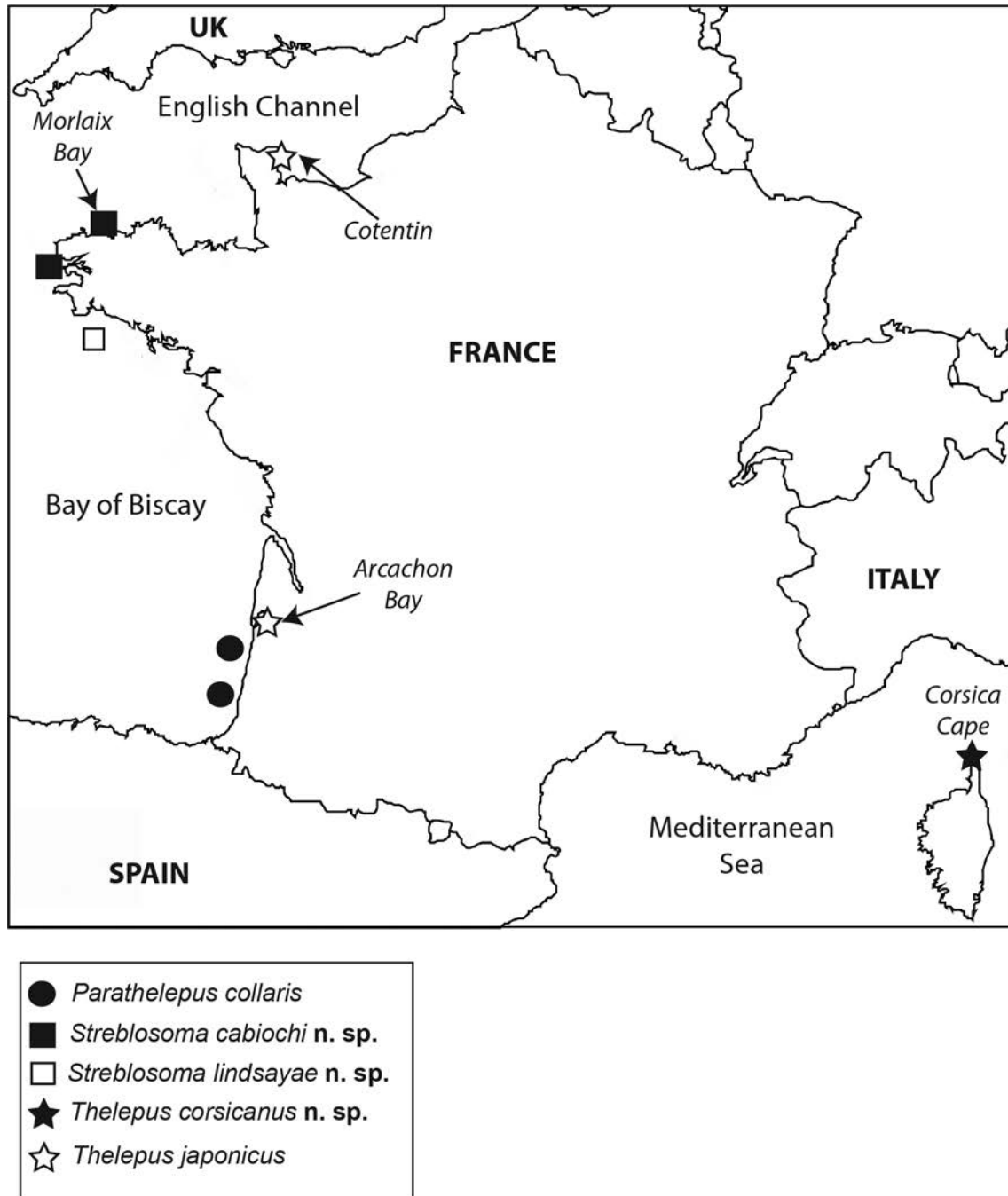


FIGURE 1. Schematic distribution of the different Telothelepodidae and Thelepodidae species along the French coasts.

Overlapping sequence (forward and reverse) fragments were merged into consensus sequences and aligned using Geneious Prime 2019.0.4. For COI, sequences were translated into amino acid alignment and checked for stop codons to avoid pseudogenes. All sequences obtained in this study were deposited in GenBank.

All COI and 16S sequences were aligned in Geneious Prime 2019.0.4 using the MUSCLE plugin and default settings. The AIC and BIC tests in jModeltest 2.2.10 (Darriba *et al.* 2012) were used to select the GTR + I + G model

of molecular evolution as the best evolutionary model for the COI gene alignment. The phylogenetic analysis was performed in MrBayes v3.2.6 (Ronquist & Huelsenbeck 2003). The analysis was run for 10 million generations (sampled every 1000), 25 % of the generations were discarded as burn-in and the standard deviation of split frequencies decreased below 0.01. FigTree v.1.4.4 (Rambaut 2007) was used to visualise the majority-rule consensus tree displaying all nodes with a posterior probability > 0.5.

Sequences of *Terebellides lilasae* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019 and *Loimia ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017 were used as outgroup (Table 1).

Finally, COI and 16S sequences were compared with Pairwise Kimura 2-parameter (K2P) genetic distances using MEGA version 7.0.26 (Kumar *et al.* 2016).

Tabl E 1: List of sequenced specimens with voucher specification, type and collection localities and Genbank accession numbers for 16S and COI genes.

Species	Voucher	Type locality	Collection locality	16S	COI
<i>Loimia ramzega</i>	MNHN-IA-TYPE 1790	France, English Channel	France, English Channel	KY555060	KY555063
<i>Terebellides lilasae</i>	SMA_VOG8C2-A	France, Bay of Biscay	France, Bay of Biscay	MN219528	MN207186
<i>Thelepus cincinnatus</i>	HUNTSPOL0361	Greenland	Canada, Casco Bay		MG423218
	HUNTSPOL0373	Greenland	Canada, Casco Bay		HQ024260
	HUNTSPOL0358	Greenland	Canada, Casco Bay		HQ024255
	SMNH 81625	Greenland	Norway, Trondheim	DQ779636	
<i>Thelepus corsicanus</i>	MNHN-IA-type 2003	France, Corsica	France, Corsica	MT566427	
<i>n. sp.</i>	MNHN-IA-type 2004	France, Corsica	France, Corsica	MT566429	
	SMA_COR_Thele_05	France, Corsica	France, Corsica	MT566428	
	AM W.53071	France, Corsica	France, Corsica	MT566430	
<i>Thelepus crispus</i>	BP2010-375	USA, California	Canada		HQ932691
	BP2010-215	USA, California	Canada		HQ932585
	BP2010-379	USA, California	Canada		HQ932694
<i>Thelepus hamatus</i>	BMBM-0882	USA, Alaska	USA, Lopez Island		MH242996
<i>Thelepus japonicus</i>	AM W.53072	Japan	France, Arcachon Bay	MT566422	MT556446
	SMA_ARC_Thele_08	Japan	France, Arcachon Bay		MT556447
	no voucher	Japan	Japan, Ago Bay		LC455932
	SMA_Thele_01	Japan	France, Arcachon Bay	MN219538	
	MNHN-IA- PNT 118	Japan	France, Cotentin	MT566423	
	AM W.53074	Japan	France, Cotentin	MT566424	
	SMA_ARC_Port02	Japan	France, Arcachon Bay	MT566425	
	SMA_ARC_Thele_09	Japan	France, Arcachon Bay	MT566426	
<i>Thelepus sp.*</i>	Tplag43		Chile, Patagonia		JF731023

* present in Genbank as *Thelepus plagiotoma* (Schmarda, 1861), an invalid taxon.

Abbreviations

AM	Australian Museum (Sydney, Australia)
CH	Chaetiger
COI	Cytochrome c Oxidase subunit I

MNHN	Muséum National d'Histoire Naturelle, (Paris, France)
MG	Methyl green
RESOMAR	French Marine Stations and Observatories Network
SEM	Scanning electron microscope
SG	Segment
SMA	Station Marine Arcachon (Arcachon, France)

Results

Taxonomic Account

Family Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013

Parathelepus Caullery, 1915

Type-species: *Thelepidides collaris* Southern, 1914, by original designation.

Parathelepus collaris (Southern, 1914)

Figures 2–3

Thelepidides collaris Southern, 1914: 125–126, pl. XIII, fig. 30A–E.

Parathelepus collaris (Southern, 1914) Nogueira *et al.* 2018, fig. 7.

Material examined: AM W.53063, one specimen, complete in two parts, Northeast Atlantic Ocean, Bay of Biscay, P12, 44°28'25"N 1°24'37"W, 51 m depth, May 2018, mounted for SEM. MNHN-IA- PNT 115, one specimen, complete, Northeast Atlantic Ocean, Bay of Biscay, P22, 44°03'03"N 1°28'05"W, 52 m depth, May 2018. AM W.53064, one specimen, anterior part, Northeast Atlantic Ocean, Bay of Biscay, P16, 44°23'00"N 1°23'51"W, 44 m depth, May 2018. MNHN-IA- PNT 116, one specimen, anterior part, Northeast Atlantic Ocean, Bay of Biscay, P18, 44°13'22"N 1°25'47"W, 50 m depth, May 2018. AM W.53065, one specimen, anterior part, Northeast Atlantic Ocean, Bay of Biscay, P22, 44°03'03"N 1°28'05"W, 52 m depth, May 2018.

Description. Specimens relatively small; complete entire specimen 31 mm long and 1.2 mm wide.

Transverse prostomium attached to dorsal surface of upper lip; eyespots in broad oblique row at each side, terminating dorso-laterally (Fig. 2A); distal part with poorly developed mid-dorsal process. Buccal tentacles of one type, very long, cylindrical and deeply grooved (Figs 2A; 3A–B). Peristomium forming lips, continuing dorsally as narrow annulation, upper lip much longer than wide, convoluted (Figs 2A–C; 3A–B); lower lip expanded, cushion-like (Fig. 2C), extending across entire venter and covering SG1 ventrally (Fig. 3B). Anterior body highly glandular ventrally, swollen, mid-ventral shields absent (Fig. 3B–C), mid-ventral groove extending from SG13; SG1 only conspicuous dorsally and laterally, terminating laterally to expanded lower lip; SG2 forming complete ring, SG3–10 progressively longer, anterior margins with ventral crests until SG8 (Figs 2B–C; 3A).

Two pairs of branchiae on SG2–3, each pair with few (up to 2–3 on either side) relatively thick filaments progressively tapering to tips (Figs 2A; 3A–B); branchial filaments originating in a line on anterior margin of SG2–3, those of SG2 extending laterally beyond level of notopodia; filaments from left and right sides within each pair separated by wide medial gap (Figs 2A; 3A–B).

Notopodia from SG3 to SG17; notopodia of SG3–7 inserted progressively more laterally, then aligned longitudinally; anterior notopodia with bulbous and hirsute bayonet-like chaetae in anterior row (Fig. 3D), and narrowly-winged hirsute notochaetae in posterior row, chaetae of posterior row longer. Posterior notochaetae narrowly-winged in both rows.

Neuropodia from SG11, as low ridges throughout; uncini as long as high, or slightly higher than long, with dorsal button at mid-length of base, short triangular heel and with 3 rows of teeth above the main fang (Figs 2D; 3E–F).

Lateral nephridial openings on SG5–7 (Fig. 3C). Pygidium crenulated.

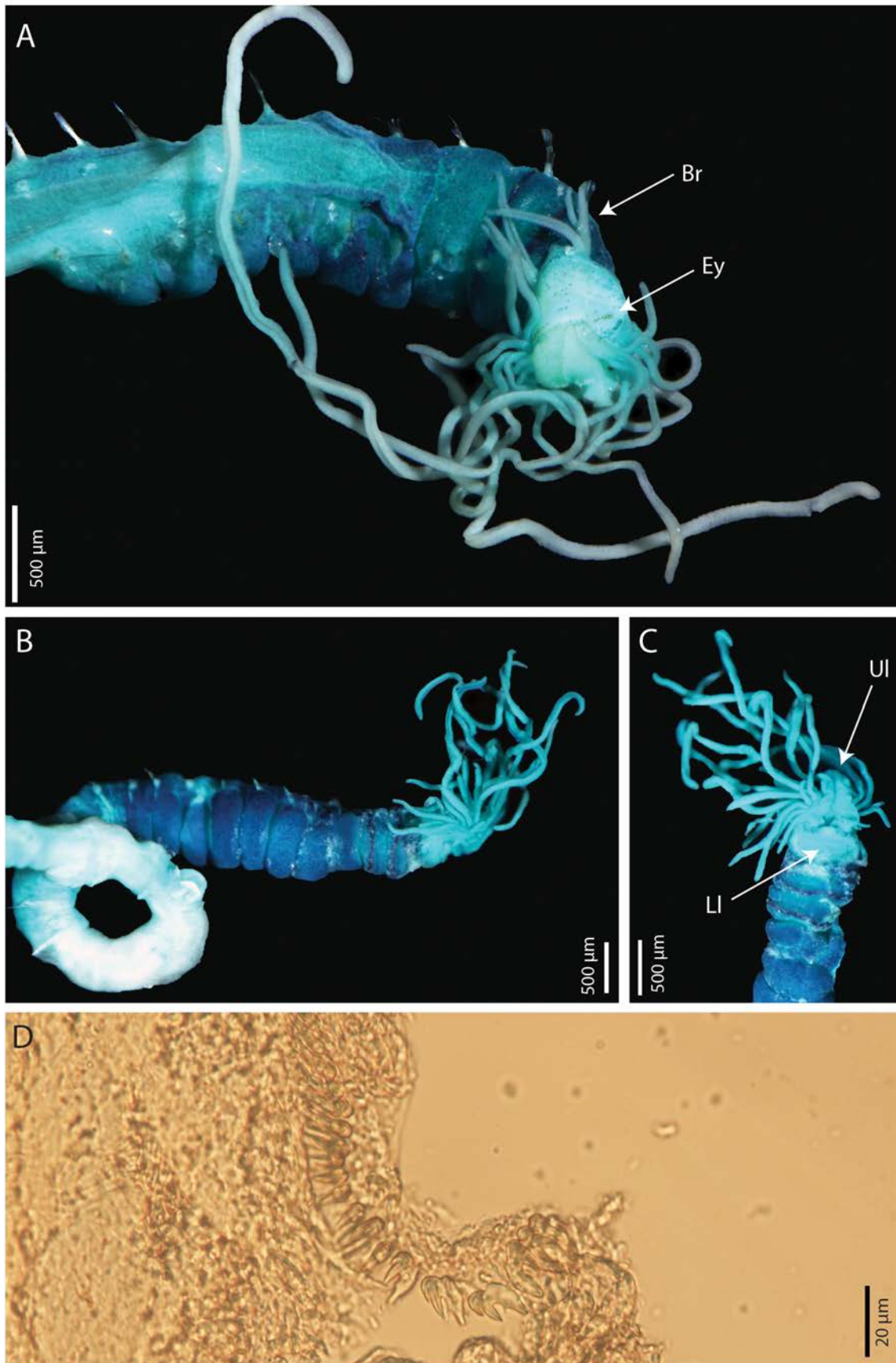


FIGURE 2. *Parathelepus collaris* (Southern, 1914) AM W.53063 (A), MNHN-IA- PNT 116 (B, C), AM W.53064 (D). A. Anterior end, fronto-lateral view, methyl green staining; B. Anterior end, lateral view, methyl green staining; C. Anterior end, ventral view, methyl green staining; D. Uncini, segment 28. Abbreviations: Br, branchiae; Ey, eyes; Ll, lower lip; Ul, upper lip.

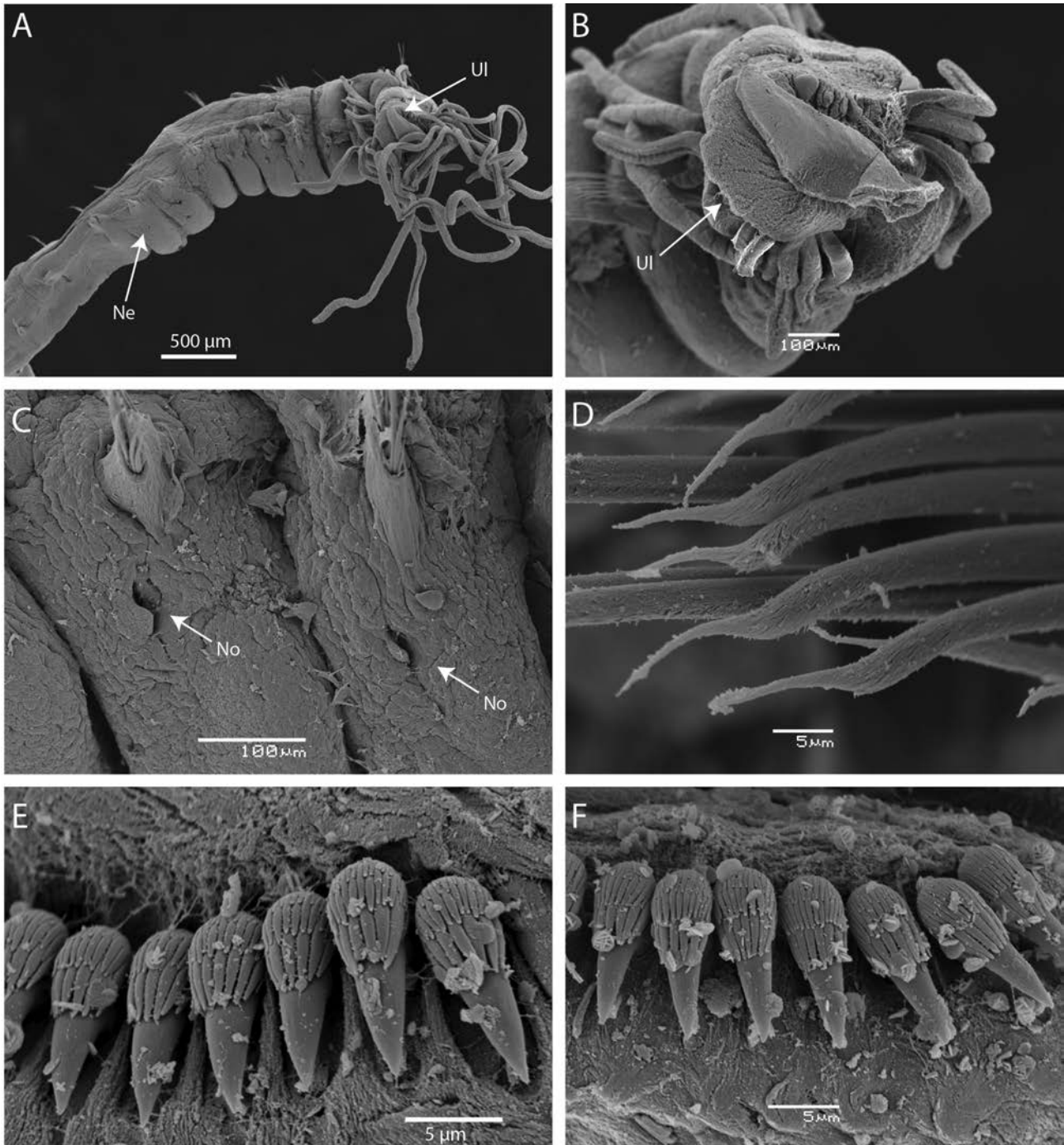


FIGURE 3. *Parathelepus collaris* (Southern, 1914) SEM, AM W.53063. A. Anterior end, lateral view; B. Anterior region, frontal view (most of the buccal tentacles removed); C. Anterior parapodia, lateral view (SG6–SG7); D. Tips of notochaetae of anterior row, CH4, antero-lateral view; E. Uncini, thoracic chaetiger; F. Uncini, abdominal chaetiger. Arrows indicate nephridial openings. Abbreviations: Ne, first neuropodia (SG11); No, nephridial openings; UI, upper lip.

Habitat. Rocky bottoms, 27 m depth (Southern 1914), mud to muddy sands, 80 to 120 m depth (Martinez *et al.* 2007), coarse sand, 40 to 50 m depth (this study).

Type locality. Clew Bay, County Mayo, Ireland.

Distribution. Azores (Gil 2011), Bay of Biscay (this study, Martinez *et al.* 2007), Ireland (Southern 1914), Egypt (Abd-Elnaby 2009), Italy (Giangrande 1988).

Remarks. Characteristics of the French material closely matches the description of the holotype recently published by Nogueira *et al.* (2018). Our specimens differ only by the presence of a third row of teeth above the main

fang of uncini (instead of two as described by Nogueira *et al.* 2018). However, this third row is only visible with SEM images. SEM images also permit us to observe for the first time the presence of nephridial openings on SG5 to 7.

Family Thelepodidae Hesse, 1917

Streblosoma Sars, 1872

Type-species. *Grymaea bairdi* Malmgren, 1866, by original designation.

Streblosoma cabiochi n. sp.

Figures 4–5

urn:lsid:zoobank.org:act:51245F7C-1561-4528-84E9-60E9CCA68E3F

Material examined: Holotype: MNHN-IA- type 2000, one specimen, incomplete, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N 3°51'58"W, 17 m depth, March 2019. **Paratypes:** AM W.53066, one specimen, incomplete, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N 3°51'58"W, 17 m depth, October 2014, mounted for SEM; MNHN-IA- type 2001, one specimen, incomplete, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N 3°51'58"W, 17 m depth, March 2019; MNHN-IA- type 2002, one specimen, incomplete, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N 3°51'58"W, 17 m depth, March 2019; AM W.53067, one specimen, incomplete, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N 3°51'58"W, 17 m depth, March 2019.

Additional material. SMA_ROS-Streblo-06, one specimen, incomplete, English Channel, Brittany, Morlaix Bay, Pierre Noire, 48°42'30"N 3°51'58"W, 17 m depth, October 2014. SMA_BR-Streblo-02, one specimen, incomplete, Northern Bay of Biscay, B3_APP1, 47°31'27"N 3°27'02"W, 52 m depth, May 2018.

Description. Large species, holotype incomplete (33 segments), 34.0 mm long (24.3–49.6), 1.3 mm wide (1.2–2.0).

Transverse prostomium attached to dorsal surface of upper lip; basal part with eyespots irregularly arranged in two separated lateral areas (Fig. 4C), distal part of prostomium strongly shelf-like. Short and thick grooved buccal tentacles (Fig. 4C). Peristomium forming lips; upper lip hood-like, slightly convoluted, broader than high (Figs 4B–C; 5A–B); lower lip short, hidden by expanded lobe derived from SG1, lobe broader than high (Figs 4B–C; 5A–C). SG1 short, visible dorsally and ventrally. Presence of a short lateral crest on SG2, covering SG1 laterally (Figs 4C; 5A).

Three pairs of branchiae, on SG2–4, SG2 with 5–8 filaments on either side, SG3 with 5–8 filaments on either side and SG4 with 5–7 filaments on either side (Figs 4A, C; 5C); branchial filaments thin, originating from body wall, dorsally to notopodia, not from cushion-like structure, with wide medial gap (Figs 4A; 5C); longest filaments about as long as body width at corresponding segment (Fig. 5C). Anterior ventral surface strongly glandular from SG2 to about SG12 (Fig. 4B), ventral shields absent, mid-ventral groove visible from about SG13 to end of specimen (Fig. 4B).

Notopodia from SG2 and extending until end of incomplete specimens (SG62 for paratype MNHN-IA- type 2002); first pair of notopodia shorter than following ones; first notopodia oriented dorsally (from CH1 to about CH8), moving progressively to lateral position (Figs 4C; 5A); notopodia large, roughly rectangular, distally rounded (Figs 4A; 5C), bilobed with notochaetae arising between lobes. Notochaetae in two rows, increasing in length from ventral to dorsal position. Notochaetae narrowly-winged, wings only present at tips, those of anterior row much shorter than those of posterior row (about 1/5 of the length) (Fig. 5D–E).

Neuropodia from SG5, first ones as fleshy ridges, progressively raised from surface of body. Uncini in straight rows until end of specimens (incomplete). Uncini with two rows of secondary teeth above the main fang, basal row with 2 teeth, second row with irregularly sized teeth, dorsal button relatively close to anterior margin, conspicuous prow, conspicuous heel, base strongly curved; uncini as long as high (Figs 4D & 5F).

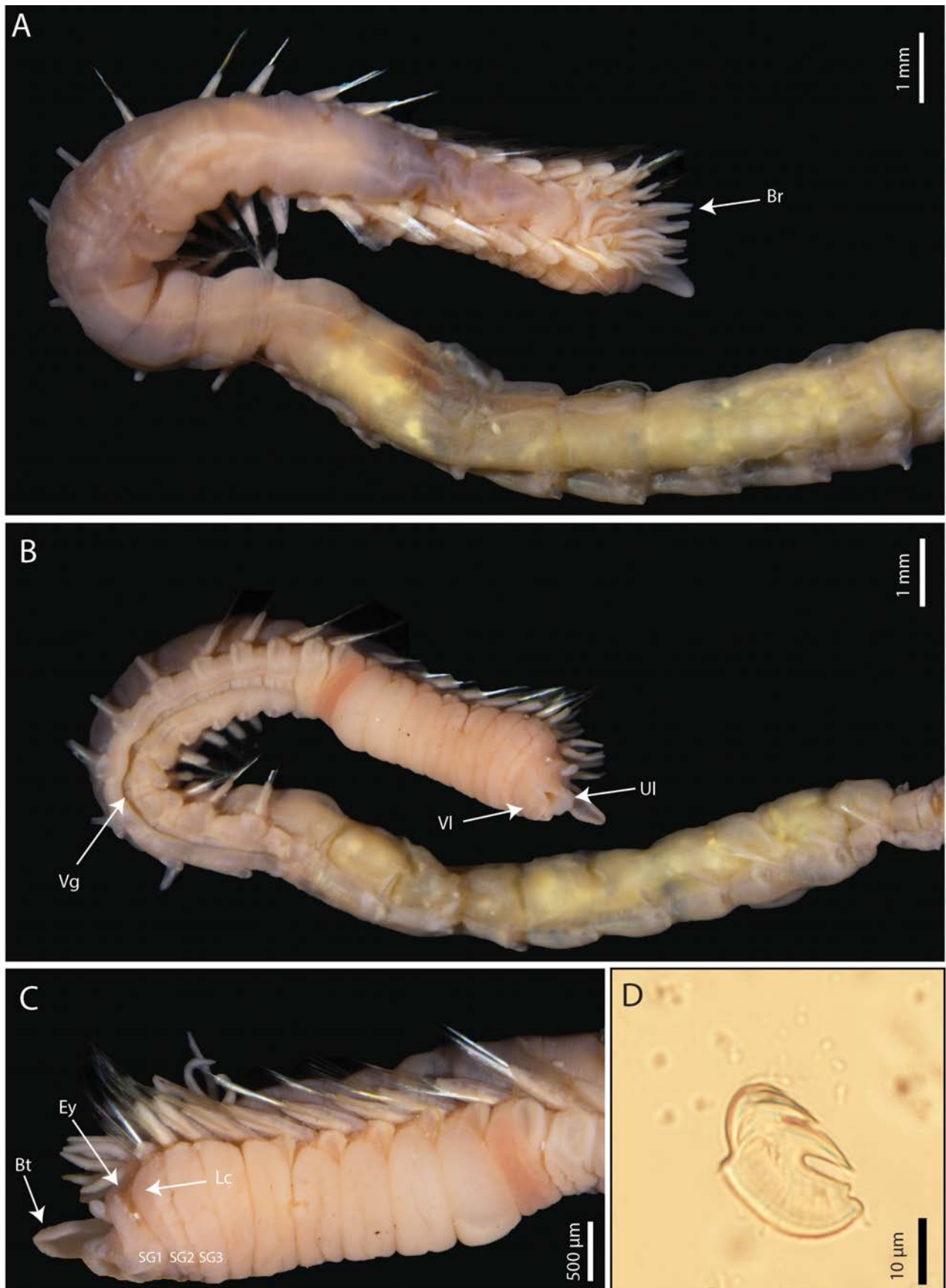


FIGURE 4. *Streblosoma cabiochi* n. sp., holotype MNHN-IA- type 2000. A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior end, lateral view; D. Uncinus, CH6. Arrow indicates lateral crest. Abbreviations: Br, branchiae; BT, buccal tentacle; Ey, eyes; Lc, lateral crest; Ul, upper lip; Vg, ventral groove; VI, ventral lobe derived from SG1.

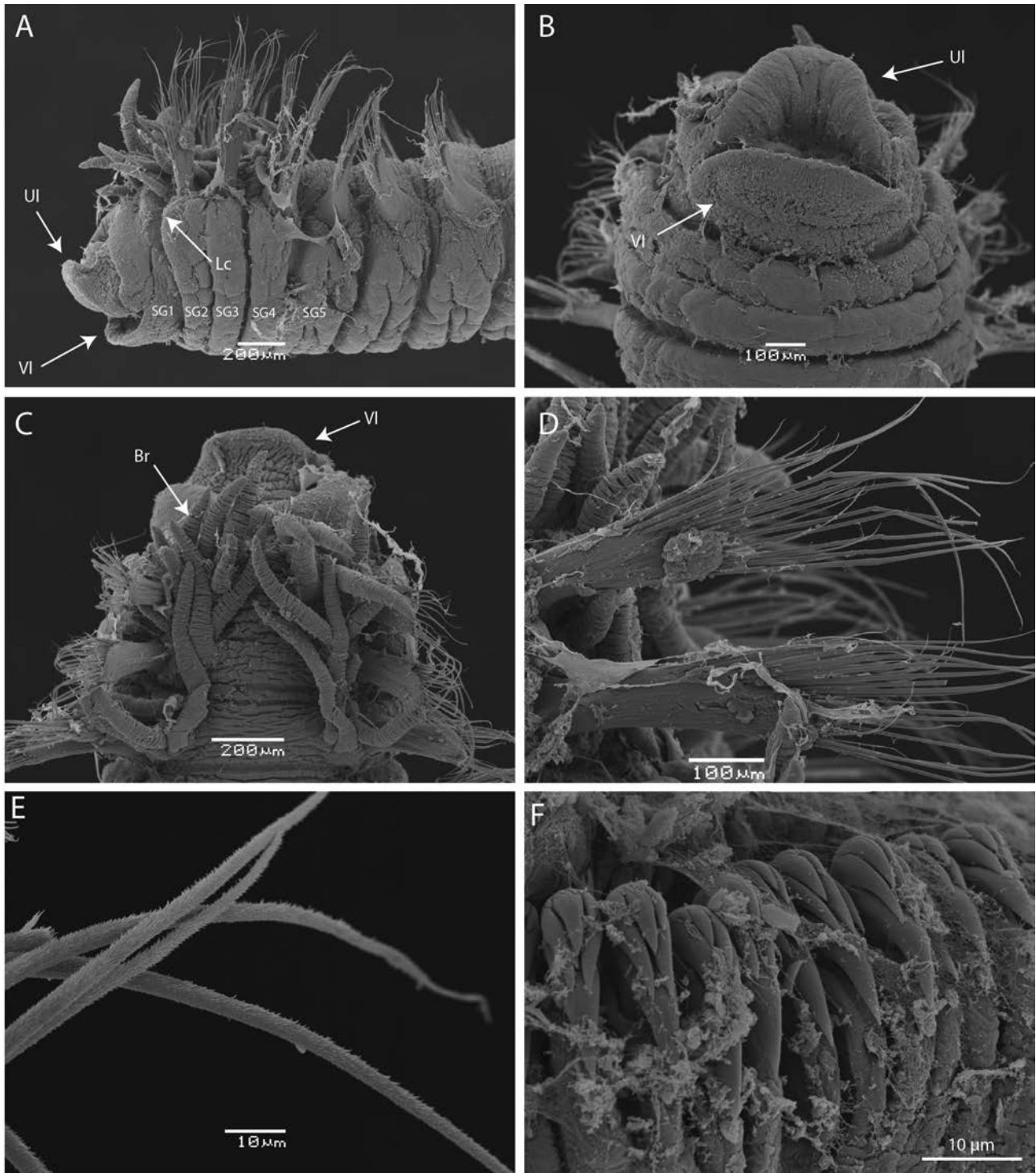


FIGURE 5. *Streblosoma cabiochi* n. sp., SEM, paratype AM W.53066. A. Anterior end, lateral view; B. Anterior end, ventral view; C. Anterior part, dorsal view; D. Notopodia, CH1–2, lateral view; E. Notochaetae, CH1; F. Uncini, CH9. Abbreviations: Br, branchiae; Lc, lateral crest; Ul, upper lip; Vl, ventral lobe derived from SG1.

Nephridial and genital papillae not visible. Pygidium unknown. Tubes made of coarse sand.

Etymology. The species is named after Dr. Louis Cabioch, for his many contributions to the benthic ecology and the exploration of the seabed of the English Channel. This species name was chosen in agreement with Céline Houbin and Eric Thiébaud, from the Station Biologique de Roscoff, who sent us the type material.

Habitat. Fine sands, 17 m depth; coastal maerl (rhodolith) beds, 1–5 m depth.

Type locality. Morlaix Bay, English Channel, France.

Distribution. Bay of Biscay (Bay of Brest), English Channel (Morlaix Bay).

Remarks. This new species is characterized by the presence of three pairs of branchiae and the absence of uncini in C-shaped loops from mid thorax. *S. cabiochi* n. sp. is similar to two European species: *S. bairdi* (Malmgren, 1866) and *S. intestinale* M. Sars in G.O Sars, 1872. However, *S. cabiochi* n. sp. differs from *S. intestinale* by the numbers of branchial filaments with 5–8 filaments on SG2, 5–8 on SG3 and 5–7 on SG4 (instead 3–5, 2–3 and 0–3 respectively for *S. intestinale*). *Streblosoma cabiochi* n. sp. also differs from *S. bairdi* by the shape of lateral crest on SG2 (small for *S. cabiochi* n. sp., protruding for *S. bairdi*), the absence of glandular pads where branchial filaments are inserted (present on *S. bairdi*) and the shape of uncini as long as high, with a strongly curved base and two rows of secondary teeth in *S. cabiochi* n. sp., longer than high, with slightly curved base and three well defined rows of secondary teeth in *S. bairdi*.

Streblosoma lindsayae n.sp.

Figure 6

urn:lsid:zoobank.org:act:2F59F1A9-86AA-4B26-AA64-08B546992236

Material examined: Holotype: MNHN-IA- type 1999, one specimen, incomplete, Northern Bay of Biscay, B3_APP1, 47°31'27"N 3°27'02"W, 52 m depth, May 2018, some parapodia mounted for SEM.

Description. Holotype incomplete (26 segments), 17 mm long, 3.1 mm wide.

Transverse prostomium attached to dorsal surface of upper lip; basal part with eyespots regularly arranged in a single continuous row all around the surface. All buccal tentacles lost. Peristomium forming lips; upper lip hood-like, convoluted, broader than high (Fig. 6C); lower lip short, rounded, covered by expanded lobe derived from SG1, lobe broader than high (Fig. 6C). SG1 large, visible dorsally and ventrally (Fig. 6C). Presence of a ventral crest on SG1 and short lateral crest on SG2–3 (Fig. 6C).

Two pairs of branchiae, on SG2–3, SG2 with 9–10 filaments on either side and SG3 with 7–9 filaments on either side (Fig. 6A–B); branchial filaments thin, originating dorsally to notopodia, arising directly from body wall, with wide medial gap (Fig. 6A–B); longest filaments about as long as width between left and right notopodia (Fig. 6–B). Anterior ventral surface strongly glandular from SG3 to about SG14, ventral shields absent (Fig. 6C), mid-ventral stripe visible from about SG16 to posterior end (SG26, incomplete).

Notopodia from SG2 (Fig. 6A–C) to posterior end; first pair of notopodia same size as following ones; first 12 notopodia oriented dorsally, moving progressively to a lateral position (Fig. 6A–C); notopodia small, roughly rectangular, distally rounded, bilobed with notochaetae arising between lobes. Notochaetae in two rows, increasing in length from ventral to dorsal position. Notopodia with bilimbate capillaries, those from posterior row longer, with well-developed wings, capillaries from anterior row shorter with fine tips (Fig. 6D).

Neuropodia from SG5, first pairs as fleshy ridges, slightly raised from posterior part of body. Uncini in straight rows until end of the body (SG26). Uncini with two rows of secondary teeth above the main fang, basal row with two teeth, second row with irregularly sized teeth; dorsal button close to anterior margin and longer than the prow, short triangular heel present, base curved; uncini longer than high (Fig. 6D–E).

Nephridial and genital papillae not visible. Pygidium unknown.

MG pattern. Ventral colouration until SG14, large blue dots on the dorsum, SG2–3 and ventral lobe of SG1 stained deeply. Anterior part of neuropodia blue (Fig. 6A–C).

Etymology. This species is named after Sue Lindsay from Macquarie University (Sydney), an amazing SEM technician who took hundreds of pictures for us and in recognition of her skills and her friendship.

Habitat. Muddy sands, 52 m depth.

Type locality. Northern Bay of Biscay, NE Atlantic.

Distribution. Only known from the type locality.

Remarks. The description of this new species is based on an incomplete holotype. However, as this specimen has only two pairs of branchiae, it differs from all other known European species. This character is sufficient to describe this species as new and most of the important diagnostic characters for the genus are present on this specimen.

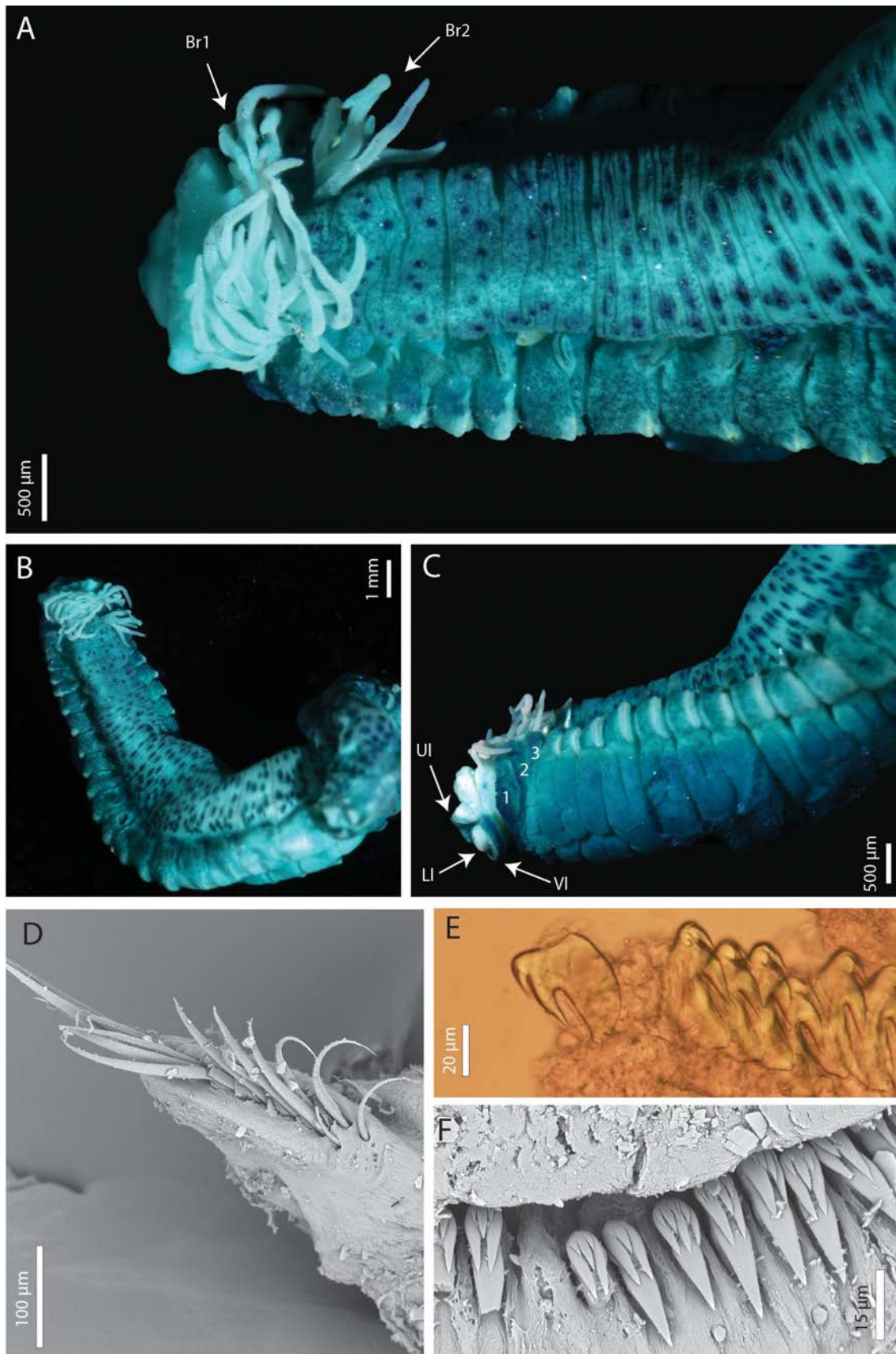


FIGURE 6. *Streblosoma lindsayae* n. sp., MNHN-IA- type 1999 A. Anterior end, dorso-lateral view, MG staining; B. Anterior end, dorsal view, MG staining; C. Anterior end, ventral view, MG staining; D. Notopodia, CH6, SEM. E. Uncini, CH23. F. Uncini, CH26, SEM. Abbreviations: Br1, first pair of branchiae; Br2, second pair of branchiae; UL, upper lip; LL, lower lip; VL, ventral lobe derived from SG1. Numbers referring to segments.

Thelepus lueckart, 1849

Type-species. *Thelepus cincinnatus* (Fabricius, 1780), by original designation.

Thelepus corsicanus n. sp.

Figures 7–8

urn:lsid:zoobank.org:act:AC447498-A085-4BF0-8DE4-49B0138E3930

Material examined: Holotype: MNHN-IA- type 2003, incomplete, Mediterranean Sea, Corsica Cape, CR37, 42°44'47"N 9°28'06"E, 21 m depth, May 2019, some parapodia used for molecular analyses and some parapodia mounted for SEM. **Paratypes:** MNHN-IA- type 2004, complete, Mediterranean Sea, Corsica Cape, CB03, 42°43'00"N 9°15'54"E, 29 m depth, May 2019, parapodia used for molecular analyses, AM W.53068, incomplete, Mediterranean Sea, Corsica Cape, CS16, 42°46'12"N 9°20'00"E, 22 m depth, May 2019, mounted for SEM. AM W.53069, incomplete, Mediterranean Sea, Corsica Cape, CB03, 42°43'00"N 9°15'54"E, 29 m depth, May 2019, mounted for SEM. AM W.53070, complete, Mediterranean Sea, Corsica Cape, CS25, 42°44'42"N 9°28'00"E, 16 m depth, May 2019.

Additional material: SMA_COR_Thele_05, incomplete, Mediterranean Sea, Corsica Cape, CS25, 42°44'42"N 9°28'00"E, 16 m depth, May 2019, parapodia used for molecular analyses. AM W.53071, incomplete, Mediterranean Sea, Corsica Cape, CS25, 42°44'42"N 9°28'00"E, 16 m depth, May 2019, mounted for SEM. SMA_COR_Thele_09, incomplete, Mediterranean Sea, Corsica Cape, CS25, 42°44'42"N 9°28'00"E, 16 m depth, May 2019.

Description. Holotype incomplete (51 segments) 37 mm long, 1.8 mm wide, paratypes very small (4.1–9.3 mm long, 0.6–1.01 mm wide).

Prostomium at base of upper lip; eyespots in thin and continuous discrete band (Fig. 7C); buccal tentacles very thick, deeply grooved, reaching ~SG16, leaving deep notches on prostomium (Figs 7A–D; 8A–B). Upper lip distinctly wider than long, not convoluted, thick, hood-like (Figs 7A–B, D; 8B); lower lip thick, surrounded by ventral crescent-shaped lobe originating from SG1 (Figs 7A–B, D; 8B). SG1 short, more visible dorsally, except for ventral lobe, SG2 with antero-lateral crest.

Two pairs of branchiae, on SG2–3, with 10 (2–3) filaments on SG2 and 6–7 (1) on SG3 (Figs 7A, C; 8A); filaments short, distally blunt, cylindrical, arising directly from body wall, with wide medial gap; branchial filaments arranged in two irregular rows (Fig. 8A).

Ventral surface of anterior segments strongly glandular, corrugated on anteriormost segments, ventral shields absent (Fig. 8B, D); mid-ventral stripe beginning from about SG22, discrete. Notopodia of incomplete holotype from SG3 to SG51, from SG3 to SG40 for complete paratype MNHN-IA- type 2004 (n=65 segments); notopodia short, roughly rectangular, distally rounded (Figs 7A, 8C), progressively shorter and more rounded from mid-body; notochoetae emerging between lobes. Few falcate notochoetae in both rows, anterior row with 8–10 (4–5) twisted winged chaetae (Fig. 8C–D), posterior row with about 7–8 (4–5) narrowly-winged notochoetae (Fig. 8C, E); well-marked difference in length between rows (Fig. 8C).

Neuropodia from SG5, as long fleshy ridges on anterior body, progressively shorter and more raised from mid-body segments onwards. Uncini with terminal dorsal button, short prow, much shorter than button, base curved; uncini longer than high (Fig. 7E–F). Crest of uncini with two rows of secondary teeth, basal row with 2–3 teeth, second row with irregularly sized teeth (Fig. 8F).

Nephridial and genital papillae not seen. Pygidium slightly crenulated (paratypes).

Etymology. The species name refers to the type locality and geographical distribution of this species.

Habitat. 16–29 m depth, among rocks (collected by scuba divers).

Type locality. Corsica Cape, Mediterranean Sea.

Distribution. Known only from type locality.

Remarks. Molecular analyses (Figs 11; 12) allowed us to confirm that all specimens from Corsica belong to a single species. Indeed, K2P distances for 16S were equal to 1% between holotype (MNHN-IA- type 2003) and other small type material. The number of branchial filaments is clearly size-dependent with 10 filaments on SG2 and 6–7 on SG3 for holotype, and only 2–3 and one, respectively for other small specimens. As holotype is incomplete and paratypes are all small individuals, it is not possible to state where notopodia terminate along the body (at least 49 segments on holotype, and on 60% of the body length for small specimens).

Among the European species, *T. corsicanus* n. sp. is similar to *T. davehalli* Jirkov, 2018, described from off the Faroe Islands, in having two pairs of branchiae and the absence of uncini forming a loop after SG14. However, these two species can be easily differentiated by the presence of eyespots in *T. corsicanus* n. sp. (absent in *T. davehalli*), the number of branchial filaments on SG2 (~10 for *T. corsicanus* n. sp., ~20 for *T. davehalli*), the absence of a convoluted upper lip for *T. corsicanus* n. sp. (*a priori* present for *T. davehalli*, but not reported in the description of this species, see Fig. 4B in Jirkov 2018), the shape of uncini (crest with three rows of teeth for *T. corsicanus* n. sp., crest with *a priori* only one row of teeth for *T. davehalli*, see Fig. 4G–H in Jirkov 2018) and the geographical distribution (Corsica, Mediterranean Sea for *T. corsicanus* n. sp., NE Atlantic shelf for *T. davehalli*).

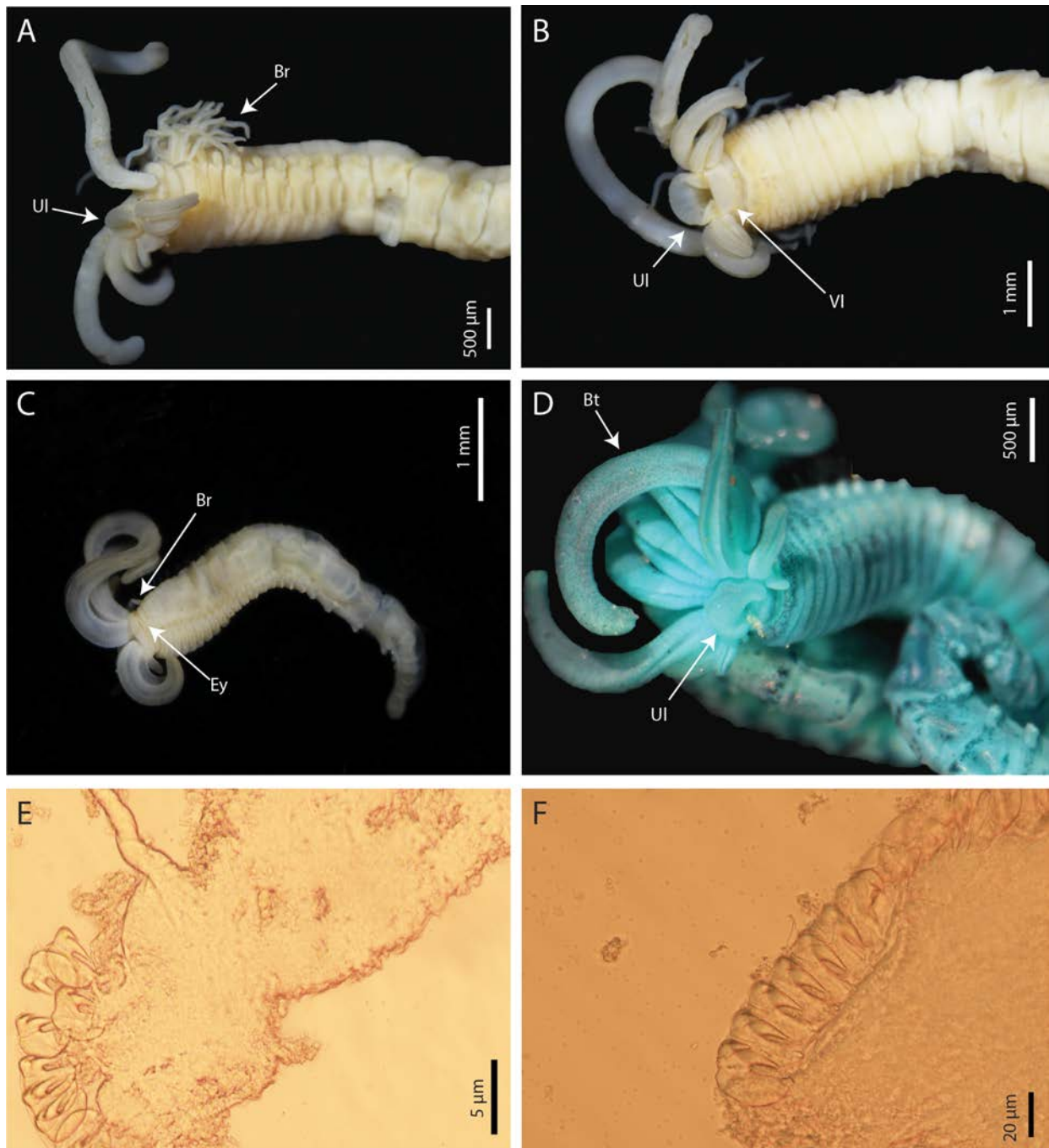


FIGURE 7. *Thelepus corsicanus* n. sp., holotype MNHN-IA-type 2003 (A–B, E–F), paratypes AM W.53069 (C), AM W.53068 (D). A. Anterior end, lateral view; B. Anterior end, ventral view; C. Entire worm, anterior end in lateral view; D. Anterior end, ventral view, MG staining; E–F. Uncini from CH9. Abbreviations: Br, branchiae; Bt, buccal tentacles; Ey, eyes; Ul, upper lip; Vl, ventral lobe.

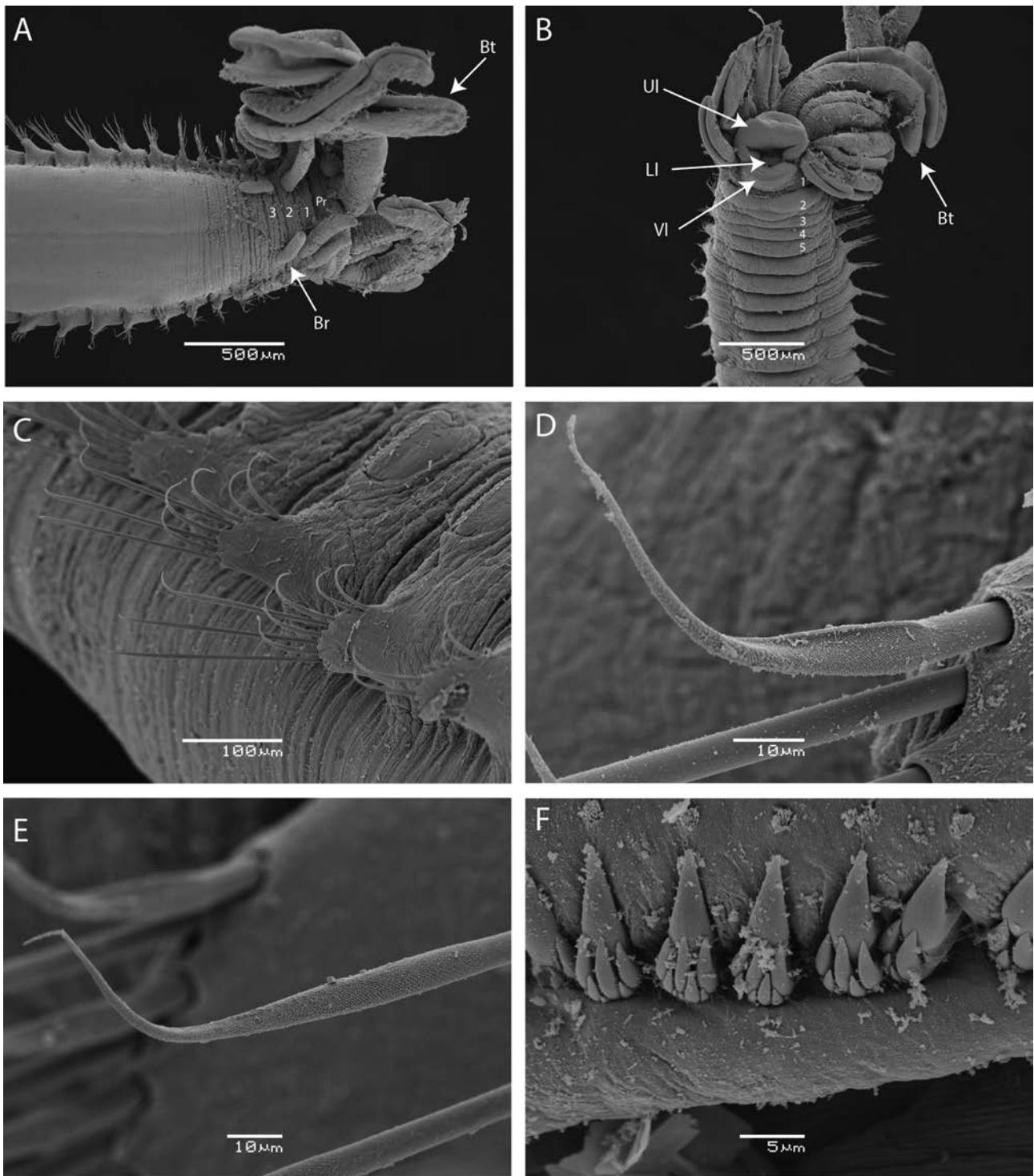


FIGURE 8. *Thelepus corsicanus* n. sp. SEM, paratypes AM W.53068 (A–E), AM W.53071 (F). A. Anterior end, dorsal view; B. Anterior end, ventral view; C. Anterior parapodia, antero-lateral view (from CH5 to CH8); D. Notochaeta from anterior row, CH6, anterior view; E. Tip of notochaeta from posterior row, CH6, anterior view, MG staining; F. Uncini, CH6. Abbreviations: Br, branchiae; Bt, buccal tentacles; Ll, lower lip; Pr, prostomium; Ul, upper lip; Vl, ventral lobe. Numbers referring to segments.

***Thelepus japonicus* Marenzeller, 1884**

Figures 9–10

Thelepus japonicus Marenzeller, 1884: 208–209, pl. II, fig.4.

Material examined: MNHN-IA- PNT 117, one specimen, complete, Northeast Atlantic Ocean, Arcachon Bay, Jacquets, 44°43'17"N 1°11'24"W, intertidal in oyster reefs, January 2018, some parapodia mounted for SEM. SMA_ARC_Thelepus_08, one specimen, complete, Northeast Atlantic Ocean, Arcachon Bay, Le Cla, 44°40'43"N 1°08'11"W, intertidal in oyster reefs, June 2017, some parapodia used for molecular analysis. AM W.53072, one specimen, complete, Northeast Atlantic Ocean, Arcachon Bay, Afrique Channel, 44°41'02"N 1°11'23"W, intertidal in oyster reefs, January 2019, some parapodia mounted for SEM and some used for molecular analysis. AM W.53073, one specimen, incomplete, Northeast Atlantic Ocean, Arcachon Bay, Jacquets, 44°43'17"N 1°11'24"W, intertidal in oyster reefs, January 2018. MNHN-IA- PNT 118, one specimen, complete, English Channel, Cotentin, Saint-Vaast-la-Hougue, 49°35'30"N 1°15'48"W, intertidal in oyster farms, April 2018, some parapodia mounted for SEM and some used for molecular analysis. AM W.53074, one specimen, complete, English Channel, Cotentin, Saint-Vaast-la-Hougue, 49°35'30"N 1°15'48"W, intertidal in oyster farms, April 2018, some parapodia used for molecular analysis. SMA-Arc-Thele-09, one specimen, incomplete, Northeast Atlantic Ocean, Arcachon Bay, Le Cla, 44°40'43"N 1°08'11"W, intertidal in oyster reefs, July 2017, some parapodia used for molecular analysis. SMA-Arc-Port02, one specimen, complete, Northeast Atlantic Ocean, Arcachon Bay, Harbour, 44°39'39"N 1°09'07"W, under pontoons, September 2017, some parapodia used for molecular analysis.

Comparative material: MNHN-IA- PNT 119, one specimen, complete, Northeast Pacific Ocean, Japan, Ago Bay, 34°18'00"N 136°50'44"E, November 2018. AM W.53075, one specimen, complete, Northeast Pacific Ocean, Japan, Ago Bay, 34°18'00"N 136°50'44"E, November 2018, some parapodia mounted for SEM. SMA_JAP-Thele-03, one specimen, complete, Northeast Pacific Ocean, Japan, Ago Bay, 34°18'00"N 136°50'44"E, November 2018.

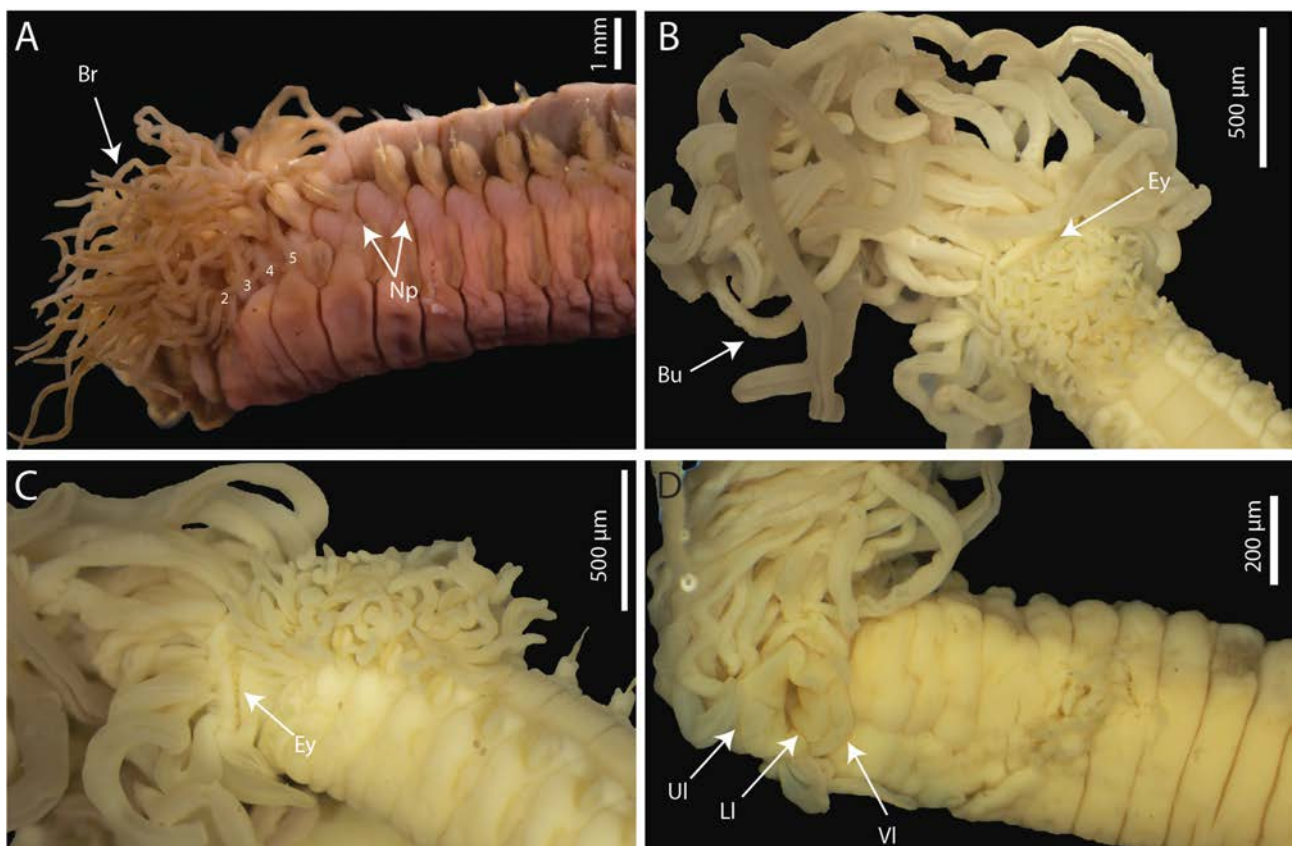


FIGURE 9. *Thelepus japonicus* AM W.53073 (A), SMA_Arc_Thele_08 (B–C), MNHN-IA- PNT 117 (D). A. Anterior end, lateral view; B. Anterior end, dorsal view; C. Anterior end, lateral view; D. Anterior part, ventral view. Br, branchiae; Bu, buccal tentacles; Ey, eyes; Np, nephridial papillae; Ll, lower lip; Ul, upper lip; Vl, ventral lobe. Numbers referring to segments.

Description. Specimens about 67–150 mm long, 5.0–6.5 mm wide.

Prostomium at base of upper lip; eyespots in thin and continuous dark band, with 2–3 irregular rows across posterior margin of basal part of prostomium (Fig. 9C); buccal tentacles long, reaching about SG24, deeply grooved (Fig. 9B–D). Peristomium continuing dorsally as narrow annulation; upper lip distinctly wider than long, not convoluted, hood-like (Fig. 9D); lower lip thick, surrounded by ventral crescent shape lobe originated from SG1 (Fig. 9D). SG1 short, more visible dorsally, except for ventral lobe.

Three pairs of branchiae, on SG2–4, with about 18–25 filaments on SG2, 11–13 on SG3 and 11–12 on SG4; filaments distally blunt, cylindrical, originating from glandular cushion-like structures, with large medial gap, the longest filaments about as long as body width at corresponding segments (Fig. 9A–C); branchial filaments arranged in two irregular rows; point of origin of filaments of SG2 and SG3 extending laterally beyond level of notopodia (Fig. 9A).

Ventral surface of anterior segments strongly glandular, corrugated on anteriormost segments, ventral shields absent (Fig. 9D); mid-ventral stripe beginning from about SG27, discrete. Notopodia from SG3, extending posteriorly to last segments; notopodia approximately rectangular, distally rounded, progressively shorter and more rounded from mid-body onwards; slightly bilobed, chaetae emerging between lobes (Figs 9A; 10A). Two rows of falcate notochaetae, anterior row with twisted winged chaetae (Fig. 10A), posterior row with narrowly-winged notochaetae, with tapering tips; well-marked difference in length between rows (Fig. 10A).

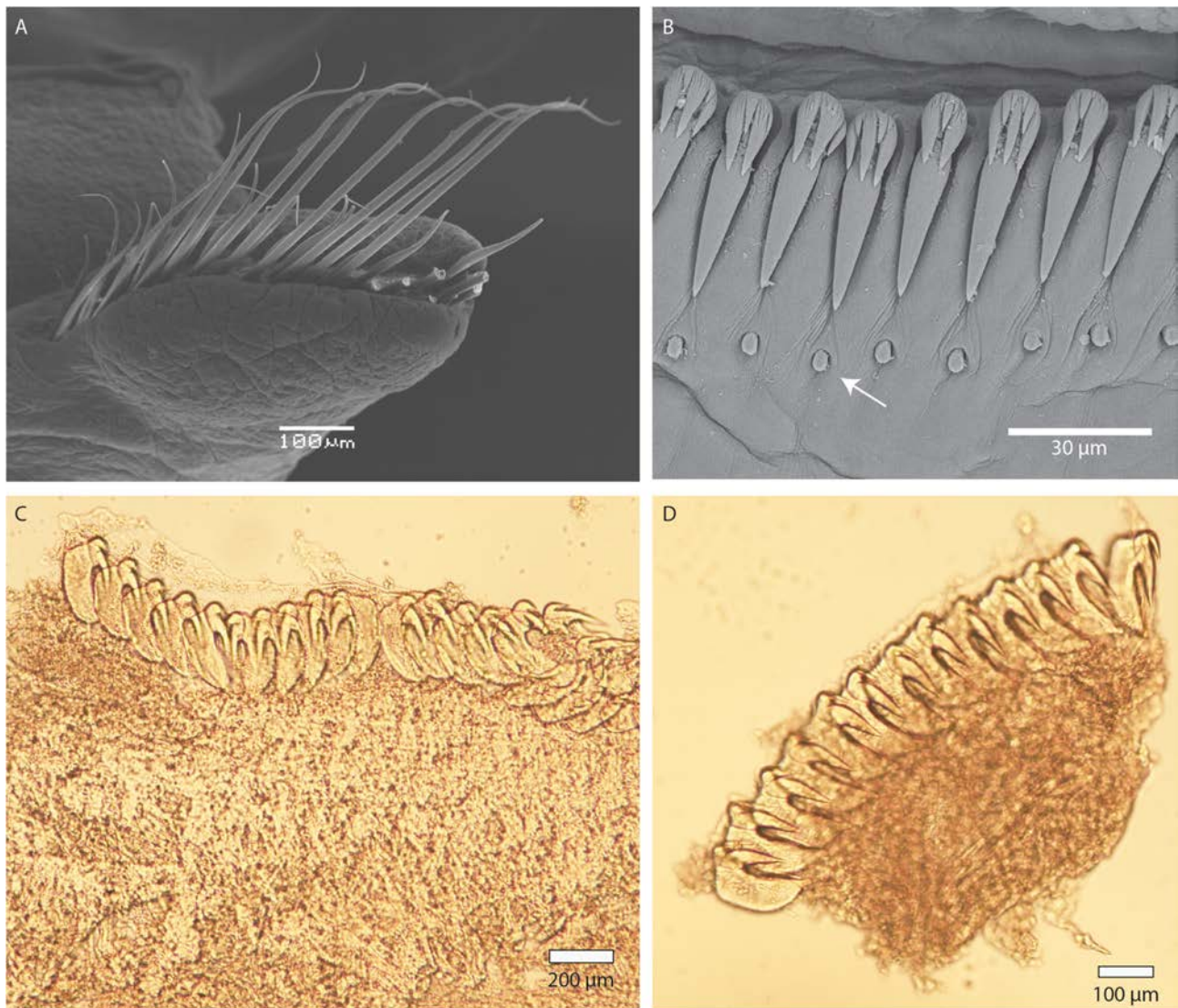


FIGURE 10. *Thelepus japonicus* AM W.53072 (A–B), MNHN-IA- PNT 119 (C), MNHN-IA- PNT 117 (D). A. Notochaetae, CH8, SEM; B. Uncini, CH37, SEM; C. Uncini, CH12; D. Uncini, CH15. Arrow indicates dorsal button.

Neuropodia from SG5, as long fleshy ridges on anterior body, progressively shorter and more raised from mid-body segments onwards. Uncini with terminal dorsal button, with triangular rounded heel and very short knob-like prow, crest with two rows of secondary teeth, basal row with 2–3 teeth, second row with 1–2 larger teeth in-between teeth of basal row and minute denticles inserted laterally to them (Fig. 10B–D).

Short, spherical nephridial and genital papillae on SG4–7 (Fig. 9A), between notopodia and neuropodia (or corresponding position, on SG4). Pygidium crenulated.

Habitat. Oyster reefs or in oyster farms (this study).

Type locality. Pacific Ocean, Japan.

Distribution (based on literature). British Columbia (Burd & Brinkhurst 1987), China (Treadwell, 1936), Japan (Marenzeller 1884; Kin *et al.* 2019), Korea (Paik *et al.* 2007), Kuwait (Al-Kandari *et al.* 2019), Bay of Biscay (Arcachon Bay), English Channel (Cotentin) (this study).

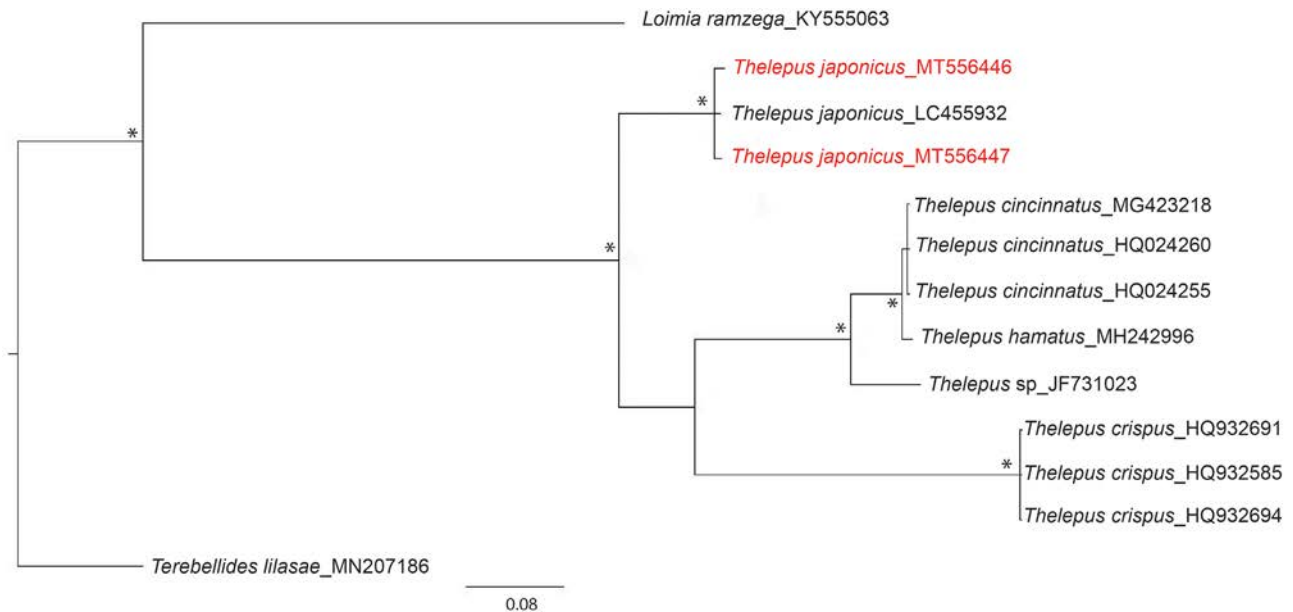


FIGURE 11. Majority-rule consensus tree of *Thelepus* species sequences obtained in this study and available on GenBank for COI gene. Asterisk indicates posterior probability > 80%. Sequence accession numbers refer to Table 1, text in red to specimens sequenced during this study.

Remarks. The morphology of the French specimens closely matches the Japanese material, except for the upper lip, which is crenulated in the Japanese material. This may be a preservation artifact, with muscular relaxation of the lip. Among the French specimens observed, MNHN-IA- PNT 117 shows an asymmetry of the notopodia, with notopodia starting from SG3 on the right side and from SG2 on left side. This asymmetry could be related to the animal regenerating anterior segments after sustaining damage.

Molecular analyses also confirm that French specimens are the same as Japanese ones (Figs 11; 12), with K2P distances comprised between 0.7% and 1.3% for COI. Sequence of *T. japonicus* deposited in Genbank (accession number: LC455932) was obtained from a specimen collected in Japan (type locality) exactly from the same place (Ago Bay) as specimens used for morphological comparison in this study (N. Jimi, *comm. pers.*)

DISCUSSION

Following the first part of the Spaghetti Project (Lavesque *et al.* 2019), this second one permits us to clarify identities of several species from French waters by describing three new species and identifying one non-indigenous species. As in European waters, the Telothelepodidae family is also poorly represented in French waters with the presence of only a single species *Parathelepus collaris*. Our specimens are similar to the holotype from Ireland recently redescribed by Nogueira *et al.* (2018) representing the first record of this species in French waters.

Among the Thelepodidae, several species show extensive geographical distributions and have been historically considered as cosmopolitan species. This includes *Streblosoma bairdi*, *Thelepus cincinnatus* and *T. setosus*, which

have been reported from many localities around the world (Carerrette *et al.* 2017; Hutchings & Kupriyanova 2018; Nogueira 2019). Recently, these three species were redescribed and have been shown to have restricted distributions (Carerrette *et al.* 2017; Nogueira 2019), although these authors did not examine all records but it is almost certain that they would represent mis-identifications. Our study suggests the absence of the previously so-called “cosmopolitan” species *T. cincinnatus* and *S. bairdi* from French waters, despite several earlier records from several localities in France. Instead, we describe one new species of *Thelepus*, *T. corsicanus* n. sp., and two new species of *Streblosoma*, *S. cabiochi* n. sp. and *S. lindsayae* n. sp. Surprisingly, we failed to obtain specimens of *Thelepus setosus*, which was originally described from Saint-Vaast-la-Hougue (Normandy) (Carerrette *et al.* 2017). From this locality, we have only found specimens of *Thelepus japonicus*, the type locality being Japan. As Carerrette *et al.* (2017) provided a very detailed redescription of the holotype of *T. setosus*, we had no need to re-examine the type lodged in Paris (NMHN type 464). During this study, we have also shown that dentition of uncini of this family is highly variable. Indeed, variation in the number of teeth of each row above the main fang is so consistently present, even within uncini of the same parapodia. Thus, we suggest that this character should be described in detail and not used as an important character to discriminate between species.

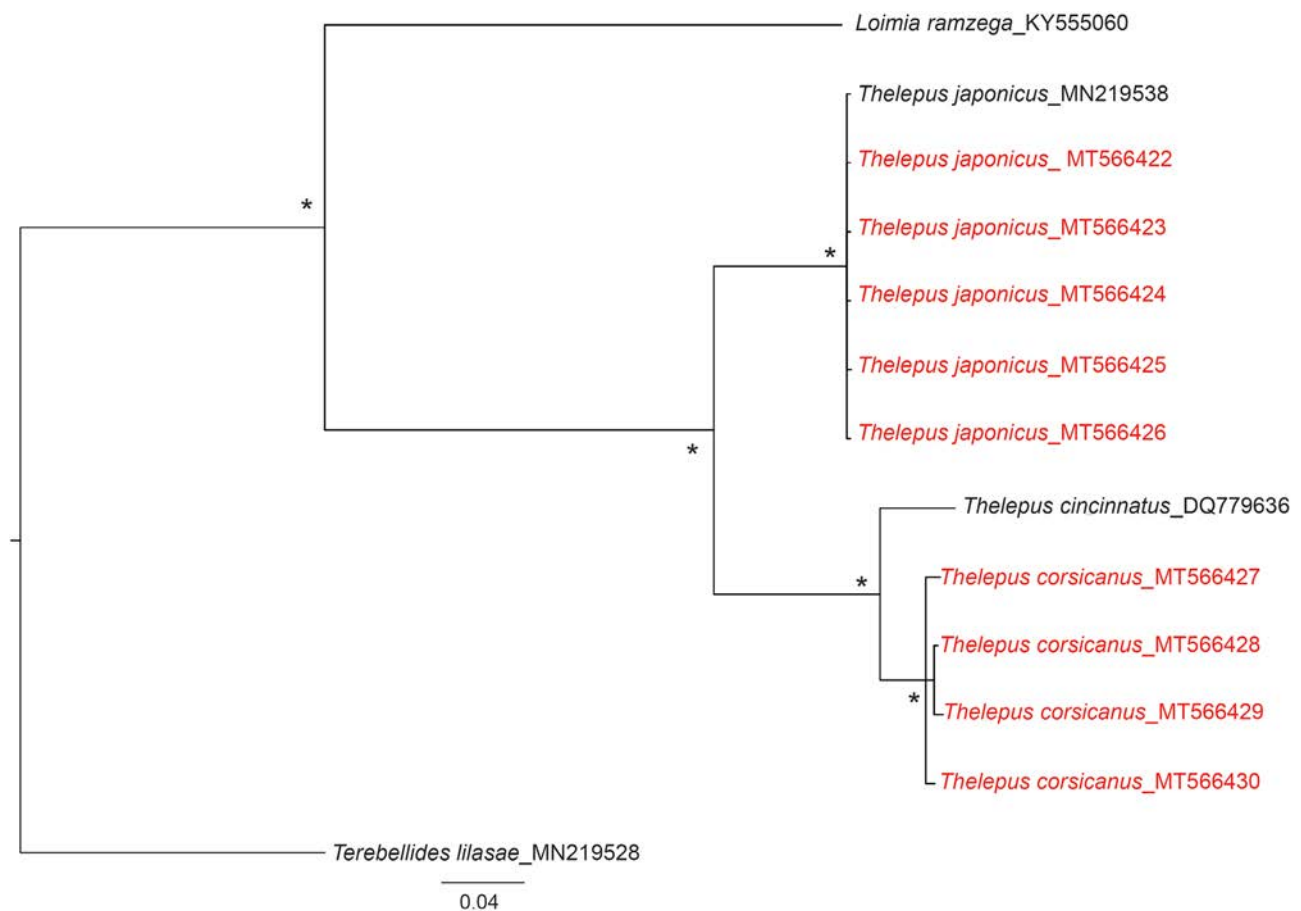


FIGURE 12. Majority-rule consensus tree of *Thelepus* species sequences obtained in this study and available on GenBank for 16S gene. Asterisk indicates posterior probability > 80%. Sequence accession numbers refer to Table 1, text in red refers to specimens sequenced during this study.

The presence of *Thelepus japonicus* is reported for the first time in European waters and confirmed by both morphological and molecular analyses. As for *Marphysa victori* Lavesque, Daffé, Bonifácio & Hutchings, 2017, an Asiatic species recently recorded in Arcachon Bay (Lavesque *et al.* 2020), the presence of *T. japonicus* in France is also linked to oyster transfers between Japan and France. Following the decimation of Portuguese cupped oysters *Crassostrea angulata* (Lamarck, 1819) in Arcachon Bay in the 1970s, more than 1200t of the exotic Pacific cupped oyster *Crassostrea gigas* (Thunberg, 1793) were imported. These oysters were introduced as spat from Sendai Bay (Japan) and as adults from British Columbia (Grizel & Héral 1991). Not surprisingly, *T. japonicus* is present both in Japan (type locality) and in British Columbia (Burd & Brinkhurst 1987) where it was probably introduced

before 1970s. In Arcachon Bay, this species is mainly present in oyster reefs or close to oyster farms, supporting this hypothesis. Its presence in oysters farms in Normandy (Cotentin) is also probably linked to imports from Arcachon Bay. Indeed, transfers of *C. gigas* among European regions occur daily and are responsible for introduction and spread of numerous alien species in northern Europe (Gouletquer *et al.* 2002). A study of population genetics would be interesting to understand (1) if specimens from Arcachon Bay were introduced directly from Japan or via a secondary transfer from British Columbia, and (2) if specimens from Normandy were introduced from Arcachon Bay.

Key to European species of Telothelepodidae and Thelepodidae

- 1A. Upper lip expanded; neuropodia poorly developed, beginning from S11..... *Parathelepus collaris* (Southern, 2014) (Telothelepodidae)
- 1B. Upper lip compact..... 2 (Thelepodidae)
- 2A. Notopodia from SG2..... 3 (*Streblosoma*)
- 2B. Notopodia from SG3.. 9
- 3A. Two pairs of branchiae..... *Streblosoma lindsayae* n. sp.
- 3B. Three pairs of branchiae..... 4
- 4A. Uncini arranged in C-shaped loops from mid thorax..... 5
- 4B. Uncini not arranged in C-shaped loops... 7
- 5A. Notopodia not extending until posterior body... 6
- 5B. Notopodia until posterior body. *Streblosoma pseudocomatus* Lezzi & Giangrande, 2019
- 6A. Eyespots absent... *Streblosoma hutchingsae* Lezzi & Giangrande, 2019
- 6B. Eyespots present..... *Streblosoma nogueirai* Lezzi & Giangrande, 2019
- 7A. Branchiae on SG3 and SG4 with 3 or less filaments *Streblosoma intestinale* M. Sars in G.O. Sars, 1872
- 7B. Branchiae on SG3 and SG4 with 5–10 filaments..... 8
- 8A. Small lateral crest on SG2, absence of branchial cushion, uncini with strongly curved base and two rows of secondary teeth. .
..... *Streblosoma cabiochi* n. sp.
- 8B. Protruding lateral crest on SG2, presence of branchial cushion, uncini with slightly curved base and three rows of secondary
teeth... *Streblosoma bairdi* (Malmgren, 1866)
- 9A. Lateral lobes on S2–S4..... *Euthelepus setubalensis* McIntosh, 1885
- 9B. Absence of lateral lobes... 10 (*Thelepus*)
- 10A. Two pairs of branchiae..... 11
- 10B. Three pairs of branchiae... 16
- 11A. Uncini in single rows throughout..... 12
- 11B. Uncini in loops from SG14..... *Thelepus nucleolata* (Claparède, 1870)
- 12A. Notopodia present on 50–66% of body length... 13
- 12B. Notopodia present on at least 90% of body length..... 14
- 13A. Eyespots absent... *Thelepus davehalli* Jirkov, 2018
- 13B. Eyespots present..... *Thelepus corsicanus* n. sp.
- 14A. Eyespots present..... 15
- 14B. Eyespots absent... *Thelepus marthae* Jirkov, 2018
- 15A. Branchiae separated by inconspicuous medial gap, notopodia present on 95% of body length
..... *Thelepus parapari* Jirkov, 2018
- 15B. Branchiae separated by wide gap, notopodia present on 70% of body length..... *Thelepus cincinnatus* (Fabricius, 1780)
- 16A. Prow of uncini well developed; notch between the prow and dorsal button of the uncini well marked...
..... *Thelepus triserialis* (Grube, 1855)

- 16B. Prow of uncini poorly developed; notch between the prow and dorsal button of the uncini poorly marked... 17
 17A. Notopodia present on about 60% of body length... *Thelepus setosus* (Quatrefages, 1866)
 17B. Notopodia present until end of body... *Thelepus japonicus* Marenzeller, 1884

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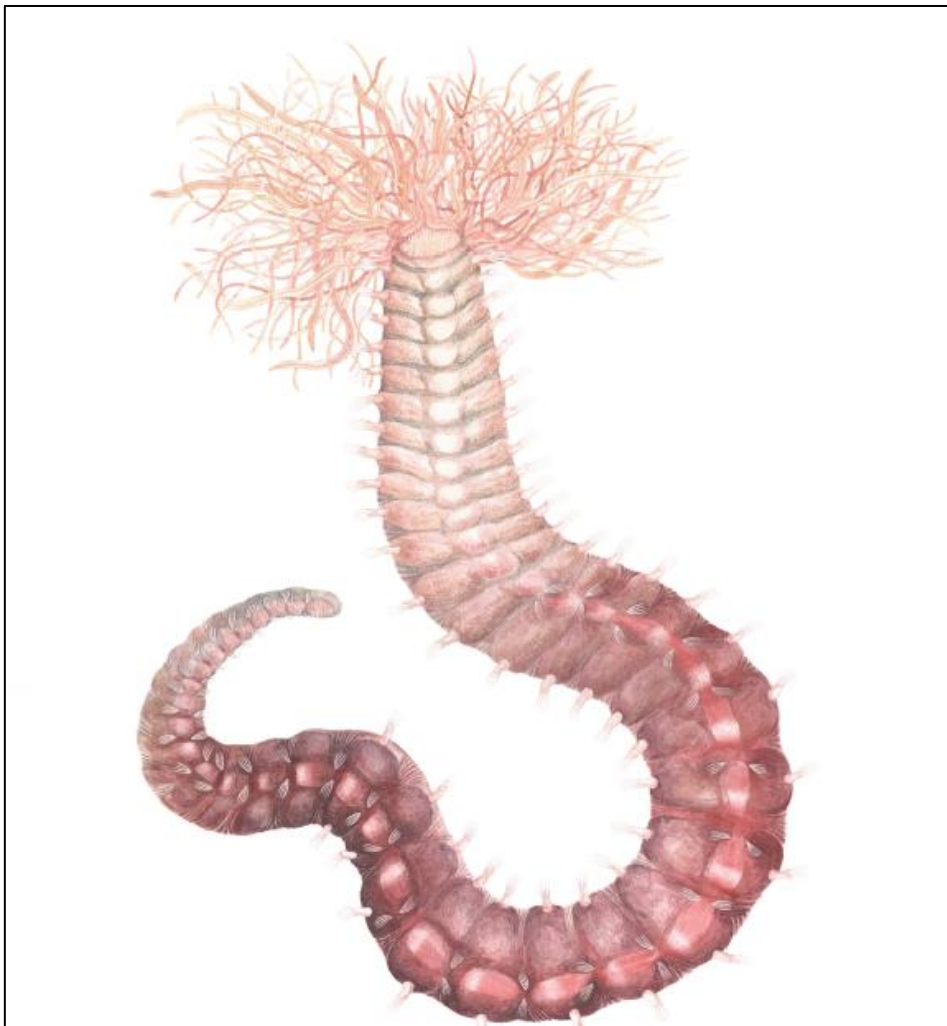
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CHAPITRE 3

Révision des Polycirridae

Lavesque N., Hutchings P., Daffe G., Londoño-Mesa M.H. (2020b) Revision of the French Polycirridae (Annelida, Terebelliformia), with descriptions of eight species. *Zootaxa* 4869 (2): 151-186*



Polycirrus gujanensis Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020b

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Revision of the French Polycirridae (Annelida, Terebelliformia), with descriptions of eight new species

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Abstract

Polycirridae from French waters are revised based on material available in French marine stations and newly collected specimens. This work is the third part of the Spaghetti Project aiming to revise French species of “Spaghetti” terebellid worms. It describes eight new species using both morphological (for all species) and molecular (for some species) tools: *Amaeana gremarei* n. sp., *Polycirrus catalanensis* n. sp., *P. glasbyi* n. sp., *P. gujanensis* n. sp., *P. idex* n. sp., *P. nogueirai* n. sp., *P. pennarbedae* n. sp. and *P. readi* n. sp., in addition to a previously described species. An identification key for European species of Polycirridae is also provided.

Keywords: Spaghetti Project, new species, molecular, morphology, taxonomy, systematics

Introduction

The “Spaghetti Project” aims to revise French species of Telothelepodidae, Thelepodidae, Polycirridae, Terebellidae and Trichobranchidae. This collaborative project involves all benthic taxonomists of marine stations and includes newly collected material as well as material already available from the French marine stations (see Acknowledgements section). The first part of the project, devoted to the Trichobranchidae, allowed us to describe nine new species along the French coasts (Lavesque *et al.* 2019). The second paper, focused on Telothelepodidae and Thelepodidae, described three new species (Lavesque *et al.* 2020). In this third study, we undertook a comprehensive survey of Polycirridae Malmgren, 1866 erected to family level after being considered as a sub-family (Polycirrinae) (Nogueira *et al.* 2013; Fitzhugh *et al.* 2015). Recently, Stiller *et al.* (2020) proposed to reinstate them as a sub-family within Terebellidae. However, in order to be consistent with other parts of the Spaghetti Project, we prefer following the classification of Nogueira *et al.* (2013) and we will discuss this proposed reinstatement of the subfamily status of Polycirridae in a subsequent paper (last chapter of the Spaghetti Project).

Most of the Polycirridae are non-tubicolous worms, although mucous sheaths are common (Glasby & Hutchings 2014). This family is characterized by the absence of branchiae and eyespots, the presence of a well-developed prostomium and upper lip, as well as the presence of at least two types of buccal tentacles (Nogueira *et al.* 2015a; Hutchings *et al.* 2019). Polycirridae is represented by six genera (*Amaeana* Hartman, 1959; *Biremis* Polloni, Rowe & Teal, 1973; *Enoplobranchus* Verrill, 1879; *Hauchiella* Levinsen, 1893; *Lysilla* Malmgren, 1866; and *Polycirrus* Grube, 1850), distinguished from each other by the presence/absence of noto- and neuropodia, and if present, the type of neurochaetae. In European waters, only *Amaeana*, *Hauchiella*, *Lysilla* and *Polycirrus* have been recorded to date.

The genus *Amaeana* comprises 12 valid species worldwide, seven of them recently described by Nogueira *et al.* (2015b). In Europe, this genus is represented by a single species: *Amaeana trilobata* (Sars, 1863) from Norway. *Amaeana colei* (McIntosh, 1926), described from the Isle of Man is considered as *species inquirenda* because this species was described based on an anterior fragment of only 5–6 segments and because material from the type locality is not available (Nogueira *et al.* 2015b). *Ameana trilobata*, wrongly considered as cosmopolitan (Hutchings & Kupriyanova 2018), was reported from several localities around the world (see references in Nogueira *et al.* 2015b). In Europe, *A. trilobata* was recorded from the Bay of Biscay (Glémarec 1969), the Mediterranean Sea (Fauvel 1927; Çinar 2005), the North Sea and the Norwegian Sea (Holthe 1986).

The genus *Hauchiella* comprises three species (Hutchings *et al.* 2019), with *Hauchiella tribullata* (McIntosh, 1869) described from Europe (type locality: Shetland Islands), but the genus has never been reported from French waters.

The genus *Lysilla* comprises 14 valid species (Hutchings *et al.* 2019) with two species described from European waters: *Lysilla nivea* Langerhans 1884 (type locality: Madeira) (Mackie & Garwood 1995) and *Lysilla loveni* Malmgren, 1866 (type locality: Sweden). The latter is the only species reported from French waters (RESOMAR – French marine stations and observatories network – database).

Finally, the most diverse genus of the family is *Polycirrus* with 74 valid species (Hutchings *et al.* 2019), represented by nine species in European waters: *Polycirrus arenivorus* (Caullery, 1915) (type locality: France), *Polycirrus asturiensis* Cepeda & Lattig, 2016 (type locality: Spain), *Polycirrus aurantiacus* Grube, 1860 (type locality: Croatia), *Polycirrus denticulatus* Saint-Joseph, 1894 (type locality: France), *Polycirrus elisabethae* McIntosh, 1915 (type locality: Scotland), *Polycirrus latidens* Eliason, 1962 (type locality: Skagerrak), *Polycirrus medusa* Grube, 1850 (type locality: France), *Polycirrus norvegicus* Wollebaek, 1912 (type locality: Norway), *Polycirrus plumosus* (Wollebaek, 1912) (type locality: Norway) (Glasby & Hutchings 2014, Cepeda & Lattig 2016). Four species have been reported from French waters: *P. arenivorus*, *P. aurantiacus*, *P. denticulatus* and *P. medusa* (Fauvel 1927). Additionally, the four following species, widely reported in European and French waters, have been considered *species inquirenda* as no type materials exist and the original descriptions are very brief (Glasby & Hutchings 2014): *P. caliendrum* Claparède, 1869, *P. haematodes* (Claparède, 1864), *P. pallidus* (Claparède, 1864), and *P. tenuisetis* Langerhans, 1881.

During this study, we undertook a comprehensive survey of this family from French waters, based on morphological analysis, supplemented by 16S gene analysis. We found two genera represented by nine species, of which eight are herein described as new. A taxonomic key for European species of Polycirridae is also provided.

Material and methods

Morphological observations

Specimens were collected during different research programs or specific samplings (see Acknowledgements) along the French coasts (Fig. 1). For morphological analyses, specimens were fixed in 4% formaldehyde seawater solution; then, transferred to 70% ethanol for preservation. Methyl green, which can be washed out, was used to reveal the abundant glandular areas and to highlight the ornamentation of these areas, which are difficult to observe otherwise. For molecular studies, a few parapodia or posterior parts were removed from several fresh specimens or from specimens fixed in 96% ethanol.

Preserved specimens were examined under a Nikon SMZ25 stereomicroscope and a Nikon Eclipse E400 microscope (objectives x40 and x100), and photographed with a Nikon DS-Ri 2 digital camera. Measurements were made using the NIS-Elements Analysis software, with width corresponding to the widest segments with parapodia, in the thoracic anterior region. Dehydrated specimens used for examination with scanning electron microscopy (SEM) were prepared by critical point drying, coated with gold and examined and photographed with a JEOL JSM 6480LA at Macquarie University, Sydney.

Morphological terminology for notochaetae follows Nogueira *et al.* (2015a) and Hutchings *et al.* (2019): notochaetae winged, wings of variable width, usually conspicuous under light microscopy, or pinnate, sometimes both types present on same parapodium. Under the SEM (or 100x objective in light microscopy), the wings are always hirsute. For uncini, terminology follows Glasby & Hutchings (2014) with two types of uncini: Type 1 with a short occipitum and a straight to slightly convex base; and Type 2 with a long occipitum and a concave base.

Description of new species are based on the holotype, and paratypes variations are given in brackets. The studied material is deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Australian Museum, Sydney (AM). Additional material is lodged in the collection housed at the Arcachon Marine Station (SMA).

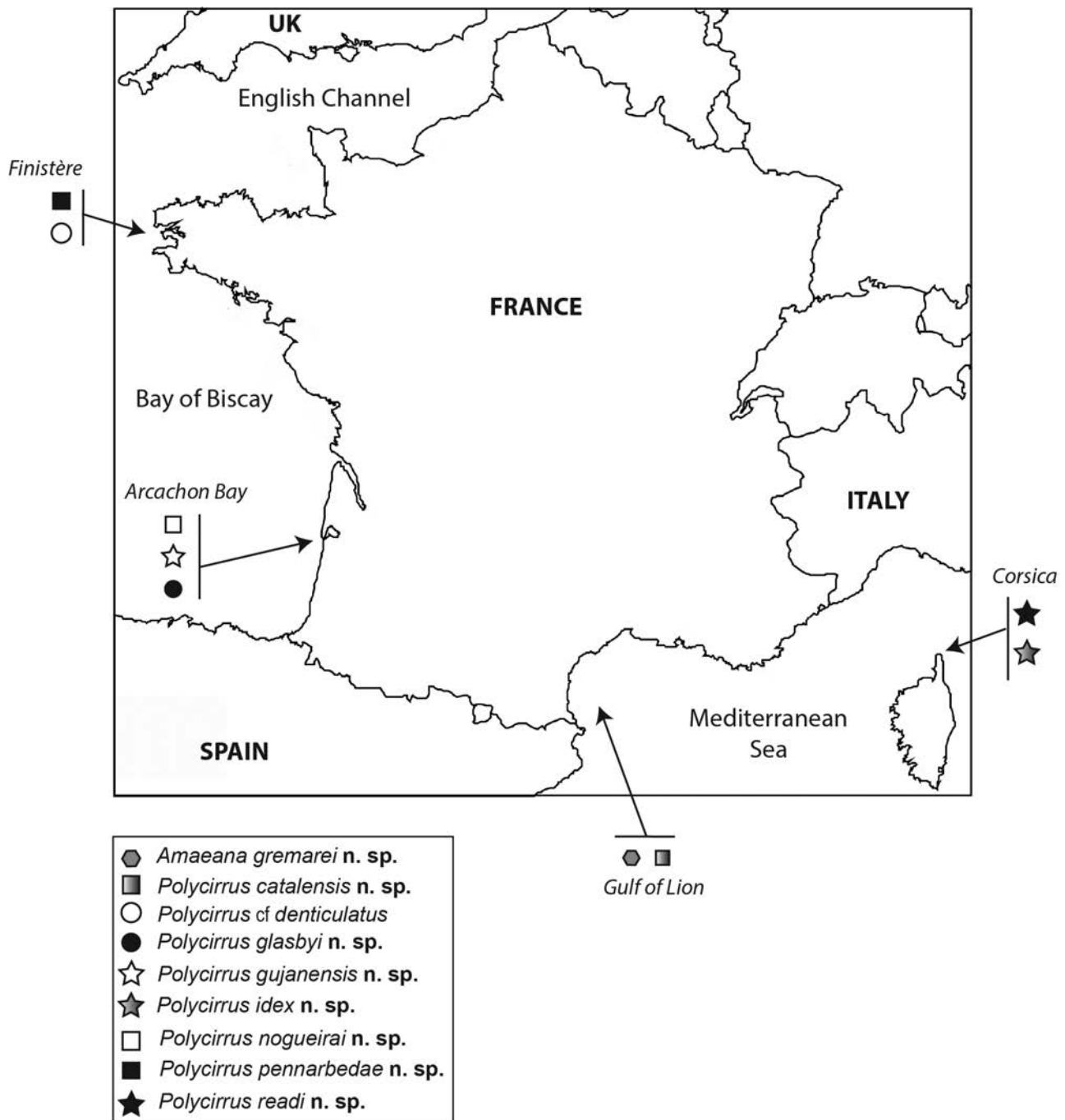


FIGURE 1. Schematic distribution of the different Polycirridae species along the French coasts.

Molecular data and analyses

Extraction of DNA was done with ISOLATE II Genomic DNA kit (BIOLINE) following protocol supplied by the manufacturers. The 16S genes were amplified using different primers: 16SANNF (GCGGTATCCTGACCGTRC-WAAGGTA) (Sjölin *et al.* 2005) with 16SBRH (CCGGTCTGAAGTCAAGATCACGT) (Palumbi 1996). Despite several tests with different primers or cocktails of primers, we failed to amplify COI genes. PCR (Polymerase Chain Reaction) occurred with Taq DNA Polymerase QIAGEN Kit in 20 µL mixtures containing: 2µL of 10X

CoralLoad PCR Buffer (final concentration of 1X), 1.5 µL of MgCl₂ (25Mm) solution, 1.5 µL of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 0.4 µL of each primer (final concentration of 0.2µM), 0.1 µL of Taq DNA Polymerase (5U/µl), 1 µL template DNA and 13.1 µL of nuclease-free water. The temperature profile was as follows for 16S: 94°C/60s - (94°C/40s-59°C/30s-72°C/90s) *40 cycles - 72°C/300s - 16°C, for COI: 94°C/300s - (94°C/30s-50°C/15s-72°C/60s)*35 cycles - 72°C/240s - 16°C. PCR success was verified by electrophoresis in a 1 % p/v agarose gel stained with Gelred. Amplified products were sent to Macrogen Company to complete double strain sequencing, using same set of primers as used for PCR.

Overlapping sequence (forward and reverse) fragments were merged into consensus sequences and aligned using Geneious Prime 2019.0.4. All sequences obtained in this study were deposited in GenBank (Table 1).

Sequences were aligned in Geneious Prime 2019.0.4 using the MUSCLE plugin and default settings. The phylogenetic analysis was performed in MrBayes v3.2.6 (Ronquist and Huelsenbeck 2003) with the GTR + I + G model molecular evolution. The analysis was run for 1 million generations (sampled every 1000), 25 % of the generations were discarded as burn-in and the standard deviation of split frequencies decreased below 0.01. FigTree v.1.4.4 (Rambaut 2007) was used to visualise the majority-rule consensus tree displaying all nodes with a posterior probability > 0.5.

The 16S sequences of *terebellides lilasae* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019 and *Loimia ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017 were used as an outgroup (Table 1).

Tabl E 1. Terminal taxa used in molecular part of the study (16S gene), with collection localities, voucher specimens, GenBank accession numbers and references.

Species	Collection locality	Voucher specimen	GenBank Accession Number	References
<i>terebellides lilasae</i>	South Bay of Biscay	SMA_VOG8C-A	MN219528	Lavesque <i>et al.</i> 2019
<i>Loimia ramzega</i>	North Brittany, English Channel	MNHN-IA-Ty PE 1790	Ky 555060	Lavesque <i>et al.</i> 2017
<i>Amaeana gremarei</i> n. sp.	Gulf of Lion, Mediterranean Sea	AM W.53110	MW035790	This study
<i>Amaeana trilobata</i>	Norway, Trondheimsfjord	A9442	MT166795	Stiller <i>et al.</i> 2020
<i>Polycirrus</i> sp.	Arcachon Bay, Bay of Biscay	SMA_ARC_Poly_12	MW035784	This study
<i>Polycirrus glasbyi</i> n. sp.	Arcachon Bay, Bay of Biscay	SMA_Arc_Poly_09	MW035781	This study
<i>Polycirrus glasbyi</i> n. sp.	Arcachon Bay, Bay of Biscay	SMA_Arc_Poly_10	MW035782	This study
<i>Polycirrus glasbyi</i> n. sp.	Arcachon Bay, Bay of Biscay	SMA_Arc_Poly_11	MW035783	This study
<i>Polycirrus carolinensis</i>	Belize	SIO:BIC:A1101	JX423681	Stiller <i>et al.</i> 2013
<i>Polycirrus idex</i> n. sp.	Corsica, Mediterranean Sea	AM W.53127	MW035788	This study
<i>Polycirrus idex</i> n. sp.	Corsica, Mediterranean Sea	MNHN-IA-Ty PE 2015	MW035789	This study
<i>Polycirrus</i> cf. <i>denticulatus</i>	Bay of Brest, Bay of Biscay	AM W.53114	MW035785	This study
<i>Polycirrus</i> cf. <i>denticulatus</i>	Bay of Brest, Bay of Biscay	AM W.53115	MW035786	This study
<i>Polycirrus readi</i> n. sp.	Corsica, Mediterranean Sea	AM W.53126	MW035787	This study

Abbreviations

AM	Australian Museum (Sydney, Australia)
MNHN	Muséum National d'Histoire Naturelle, (Paris, France)
MG	Methyl green
MT	Main tooth
RESOMAR	French Marine Stations and Observatories Network
SEM	Scanning electron microscope
SG	Segment
SMA	Station Marine Arcachon (Arcachon, France)

Results

Taxonomic Account

Family Polycirridae Malmgren, 1866

Genus *Amaeana* Hartman, 1959

Type-species. *Polycirrus trilobatus* Sars, 1863, designated by Hartman (1959).

Amaeana gremareï n. sp.

Figures 2–3

Material examined: Holotype: MNHN-IA-Ty PE 2006, incomplete, Mediterranean Sea, Gulf of Lion, 42°31'36"N, 3°23'47"E, 110 m depth, June 2019, posterior parapodia mounted for SEM. **Paratypes:** AM W.53110, incomplete, Mediterranean Sea, Gulf of Lion, A90, 42°32'39"N, 3°16'03"E, 90 m depth, April 2018. AM W.53111, incomplete, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°29'01"N, 3°08'48"E, 31 m depth, 2017, mounted for SEM.

Description. Large species, holotype incomplete, 16.4 (8.0–22.2) mm long and 2.2 (2.0–2.8) mm wide.

Prostomium at base of upper lip (Fig. 2D), both basal and distal parts developed, basal part as thickened crest (Fig. 2C), distal part with large lateral lobes and also oval mid-dorsal process (Fig. 2C); prostomium covering SG1 laterally and terminating laterally to lower lip, near mouth (Fig. 2D). Only few buccal tentacles remaining, short ones thin, uniformly cylindrical, intermediate ones (only on paratype AM W.53110) distally broader, spatulate (Fig. 2C–D). Peristomium restricted to lips, upper lip almost circular, wider than long, single lobe only (Figs 2C–D; 3A); lower lip large, almost rounded, as long as wide (Figs 2C–D; 3A).

Body progressively broader until SG7–8, then gradually tapering to narrower uniformly cylindrical posterior body, beginning from SG13–14 (Fig. 2A); achaetous gap between termination of notopodia and beginning of neuropodia, corresponding to SG13–16, with poorly marked segmentation, longer than region with notopodia (Fig. 2A). Segments biannulated, SG1 short, visible dorsally and ventrally, laterally covered by expanded prostomium (Figs 2D; 3A); SG 2 narrower and shorter than following segments, with large pentagonal to hexagonal mid-ventral shield at beginning of mid-ventral groove (Figs 2D; 3A), extending anteriorly through segment 1 until near ventral edge of lower lip. Ventrum highly glandular, covered by small papillae on SG2–11, less conspicuous on S13, then smooth body wall, with paired longitudinal crests bordering mid-ventral groove through posterior body (Figs 2C–D; 3A). Ventro-lateral pads on SG3–13; with transverse ridges but without longitudinal groove (Figs 2D; 3A).

Notopodia from SG3, extending through 10 segments, until segment 12 (Fig. 2A); distinctly elongate, rectangular with rounded distal part, with equal lobes (Fig. 3C). Notochaetae in both rows with narrow limbs (light microscopy), with fine hairs under SEM, emerging from the ventral face of notopodia to distal part (Fig. 3C–D). Neuropodia present from SG17 (hard to see exactly), laterally to mid-ventral groove, on outer margins of longitudinal crests (Fig. 2A). Neurochaetae up to 8–9 thin, long spines, with all tips broken (Fig. 3B).

Nephridial and genital papillae at anterior bases of first nine notopodia (Fig. 2B).

Pygidium unknown.

Etymology. This species is dedicated to Antoine Grémare for his many contributions to benthic ecology and his important support to NL and Céline Labrune, who sent us type material.

Habitat. Coastal heterogeneous sands, 30–100 m depth.

Type locality. Gulf of Lion, Mediterranean Sea, France.

Distribution. Only known from type locality.

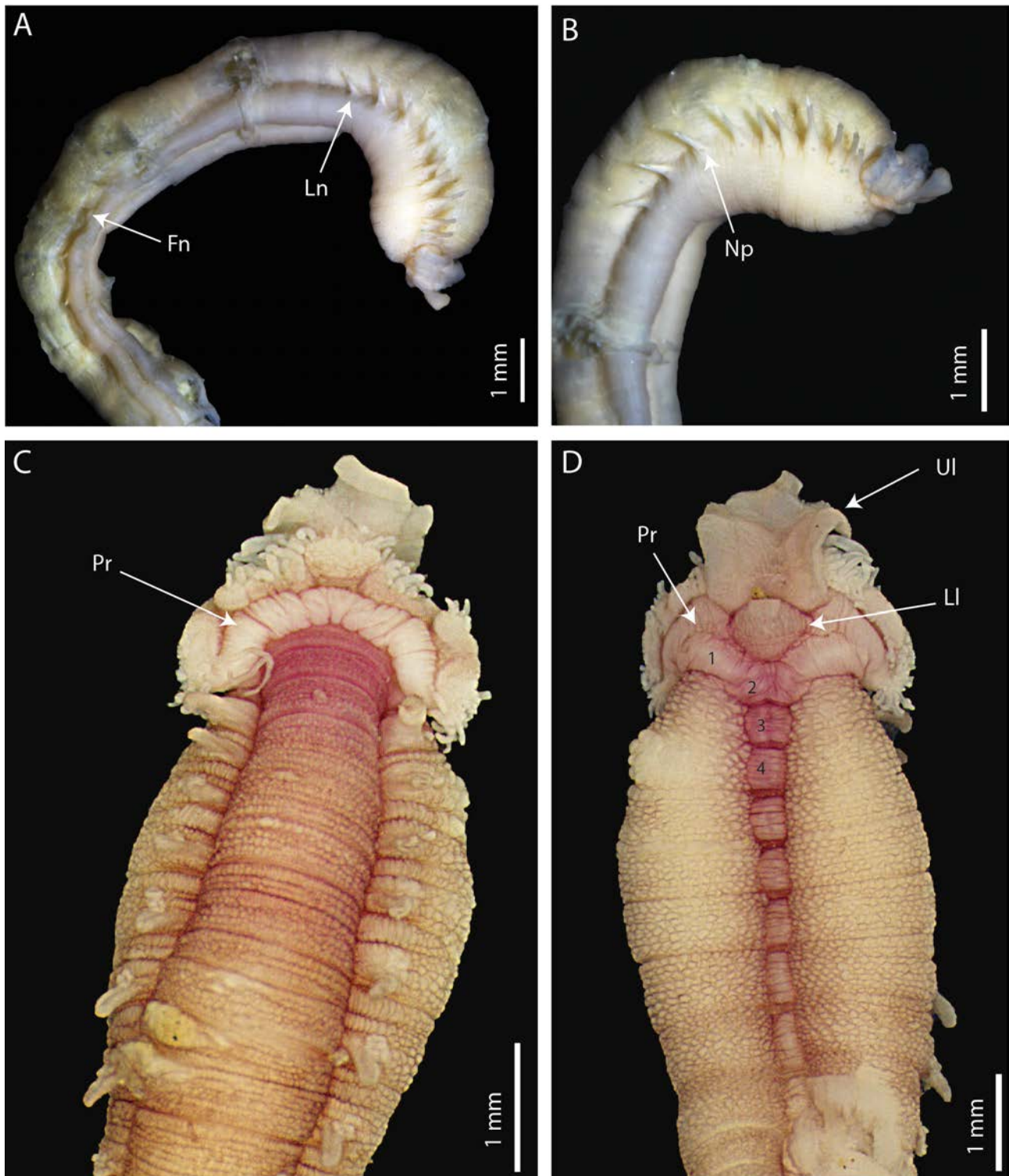


FIGURE 2. *Amaeana gremarei* n. sp., holotype MNHN-IA-Ty PE 2006 (A–B), paratype AM W.53110 (C–D). A. Entire specimen, lateral view; B. Anterior end, lateral view; C. Anterior end, dorsal view; D. Anterior end, ventral view. Abbreviations: Fn, first neuropodia, Ll, lower lip; Ln, last notopodia; Np, nephridial papilla, Pr, prostomium, Ul, upper lip. Numbers refer to segments.

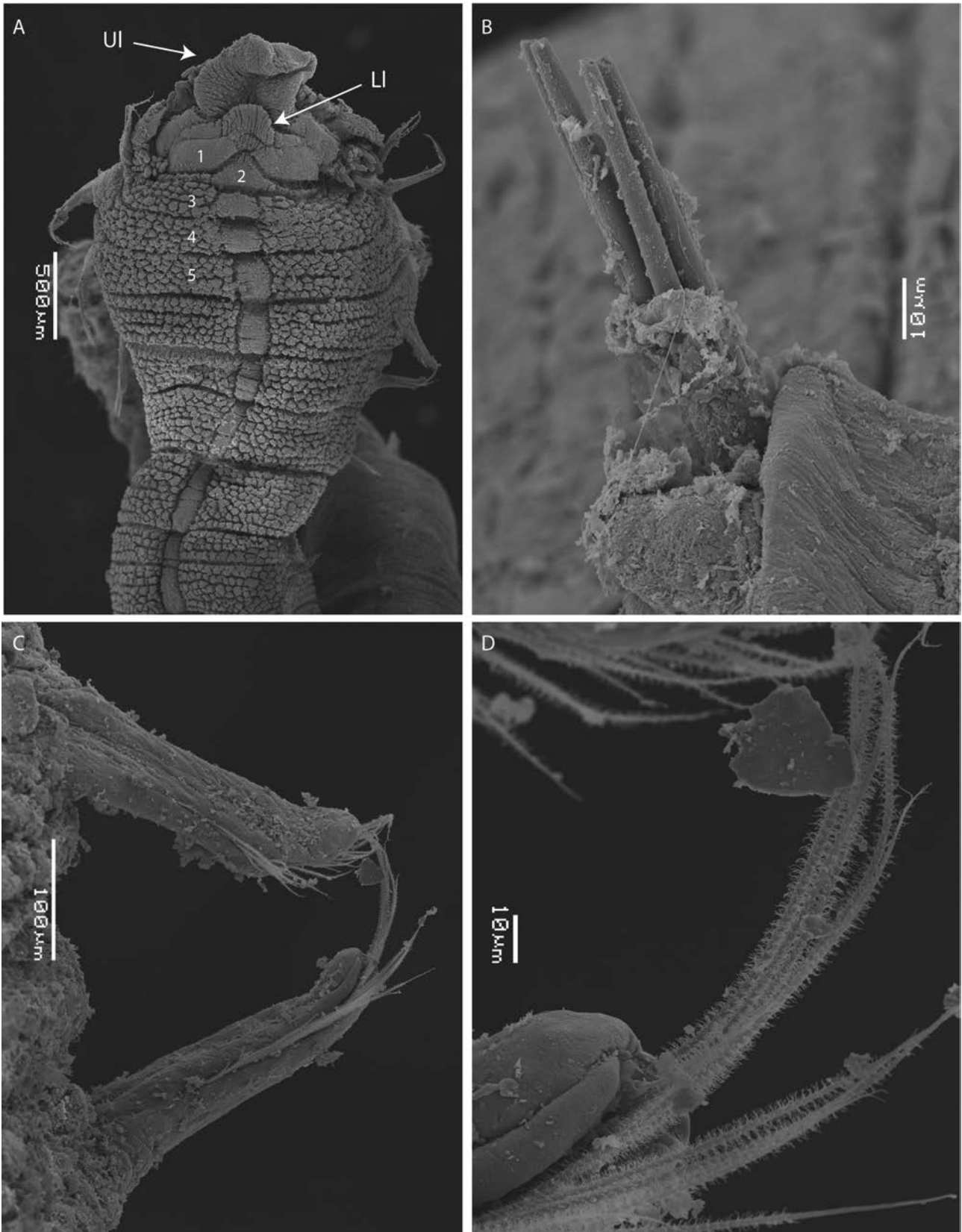


FIGURE 3. *Amaeana gremareii* n. sp., SEM, paratype AM W.53111 (A, C–D), holotype MNHN-IA-Ty PE 2006 (B) A. Anterior end, ventral view; B. Neuropodial abdominal spines; C. Segments 7–8, ventral view; D. Notochaetae, SG8, ventral view. Abbreviations: Ll, lower lip; Ul, upper lip. Numbers refer to segments.

Remarks. Among the valid species of this genus, a single species is known from European waters: *A. trilobata*. *Amaeana gremarei* **n. sp.** is similar to this species by both having 10 pairs of notopodia. However, *Amaeana gremarei* **n. sp.** differs in having a circular upper lip without distinct lobes (instead of upper lip with three lobes for *A. trilobata*), by a rounded lower lip, wider than long (instead of rectangular broad one as found in *A. trilobata*), by nephridial papillae on SG3–11 (instead of SG3–12 for *A. trilobata*), by a long achaetous region (instead of a short one as occurs in *A. trilobata*) and by ventro-lateral pads on SG3–13 (instead of on SG3–12 for *A. trilobata*).

Polycirrus Grube, 1850

Type-species. *Polycirrus medusa* Grube, 1850, by monotypy.

Polycirrus catalanensis **n. sp.**

Figures 4–5, Table 2.

Material examined: Holotype: MNHN-IA-Ty PE 2007, one complete specimen, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°29'01"N, 3°08'48"E, 31 m depth, 2017. **Paratypes:** AM W.53112, one complete specimen, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°29'01"N, 3°08'48"E, 31 m depth, 2017. MNHN-IA-Ty PE 2008, two complete specimens, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°29'01"N, 3°08'48"E, 31 m depth, 2017. AM W.53113, one complete specimen, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°29'01"N, 3°08'48"E, 31 m depth, 2017, mounted for SEM.

Description. Small species, holotype 11.5 (6.2–7.8) mm long and 0.5 (0.3–0.7) mm wide.

Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick crest across dorsum, extending laterally and dorsally, covering SG1 laterally and terminating lateral to lower lip. Buccal tentacles lost. Peristomium forming lips; upper lip, longer than wide, not elongated, with a single median and very thick convoluted lobe only (Figs 4A–D; 5A); lower lip rectangular with rounded corners, longer than wide, very glandular and ridged (Figs 4A–D; 5A).

SG1 and 2 reduced, SG1 visible dorsally, SG2 visible dorsally and laterally (Fig. 4C); body slightly broader until SG6, mid-body inflated, posterior part tapering (Fig. 4A–B, D). Ventro-lateral inflated pads present from SG3 to SG10, well-defined (Figs 4A–D; 5A). Anterior mid-ventral groove present from SG3 (Figs 4D, 5A).

Notopodia from SG3, extending for 15 (13) segments, until SG17 (SG15); distinctly elongate, rectangular, first two pairs slightly shorter, bilobed, postchaetal lobe digitiform, larger than prechaetal one (Fig. 5A–B). Narrowly winged notochaetae in two rows, distal ends whip-like (Fig. 5B–C), with wings inconspicuous under light microscopy (Fig. 4E). Neuropodia from SG17 (SG15–16); uncini with short occipitum and slightly convex base (Type 1) (Fig. 4F), crest with single row of secondary teeth, with a sharp elongate central tooth almost reaching tip of main fang, and two small lateral teeth on each side (Fig. 5D), subrostral process present as low protuberance (Fig. 4F).

Nephridial and genital papillae not seen.

Pygidium rounded with pointed tip (Fig. 4D).

Etymology. Species name refers to the Catalan Sea (north-western Mediterranean), where the species was found.

Habitat. Coastal heterogeneous sands, 30 m depth.

Type locality. Banyuls-Cerbere natural reserve, Catalan Sea, Mediterranean Sea, France.

Distribution. Only known from type locality.

Remarks. *Polycirrus catalanensis* **n. sp.** is characterized by the presence of notopodia extending over 13–15 segments which is similar to *P. denticulatus* (12–13 segments), *P. pennarbedae* **n. sp.** (12–13 segments) and *P. norvegicus* (14–20 segments) (Table 2). Among these species, only *P. pennarbedae* **n. sp.** shows almost the same range in the first appearance of neuropodia (from SG15–16 for *P. pennarbedae* **n. sp.**, from SG15–17 for *P. catalanensis* **n. sp.**) (Table 2).

However, *P. catalanensis* **n. sp.** differs from *P. pennarbedae* **n. sp.** by the shape of uncini (two rows of teeth above the main tooth and the absence of subrostral process for *P. pennarbedae* **n. sp.**, a single row of secondary teeth above the main tooth and the presence of subrostral process for *P. catalanensis* **n. sp.**), the shape of upper lip (elongated triangular medial lobe for *P. pennarbedae* **n. sp.**, very thick single medial lobe for *P. catalanensis* **n. sp.**), the shape of lower lip (oval and wider than long for *P. pennarbedae* **n. sp.**, rectangular and longer than wide

P. catalanensis n. sp.) and the presence of a large mid-ventral groove on anterior segments for *P. catalanensis* n. sp. (not visible for *P. pennarbedae* n. sp.) (Table 2).

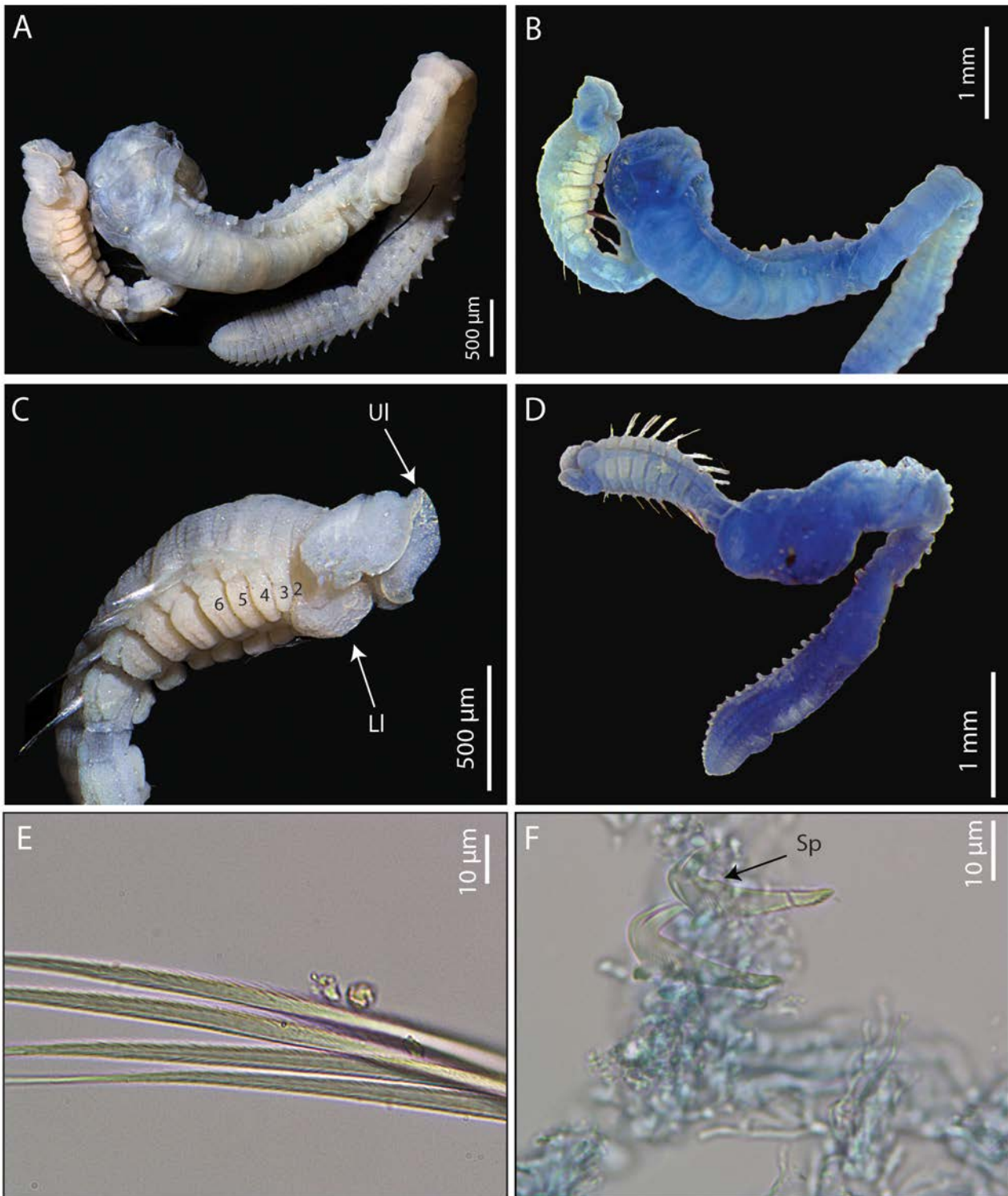


FIGURE 4. *Polycirrus catalanensis* n. sp., holotype MNHN-IA-Ty PE 2007 (A–C; E–F), paratype AM W.53112 (B) A. Entire specimen, lateral view; B. Anterior end, lateral view, methyl green staining; C. Anterior end, lateral view; D. Entire specimen, ventral view, methyl green; E. Notochaetae, SG8, 100x objective; F. Uncini, SG20, 100x objective. Abbreviations: LI, lower lip; UI, upper lip; Sp, subrostral process. Numbers refer to segments.

Polycirrus catalanensis n. sp. differs from *P. denticulatus* by the first appearance of neuropodia (from SG15–17 for *P. catalanensis* n. sp., from S12 for *P. denticulatus*), by the shape of lower lip (rectangular for *P. catalanensis* n. sp., subtriangular, pointing toward mouth for *P. denticulatus*), the shape of notochaetae (with wings inconspicuous

for *P. catalanensis* **n. sp.**, subdistally expanded for *P. denticulatus* following Glasby & Hutchings, 2014) and dental formula of uncini (MF:3 for *P. catalanensis* **n. sp.**, MF:1: α for *P. denticulatus*).

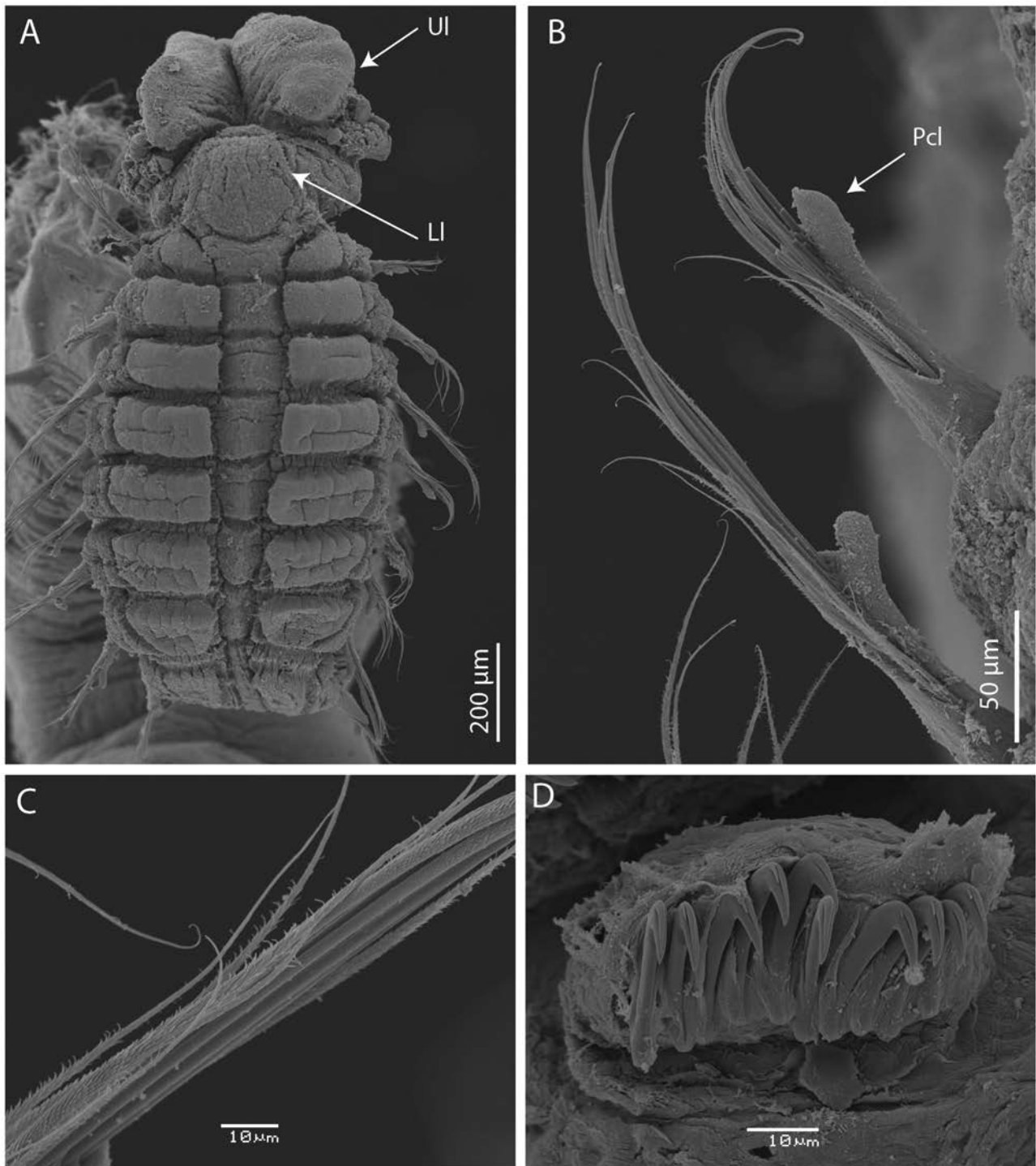


FIGURE 5. *Polycirrus catalanensis* **n. sp.**, SEM paratype AM W.53113 (C–E). A. Anterior end, ventral view; B. Notopodia, SG5–6, ventral view; C. Notochaetae, SG5; D. Abdominal uncini. Abbreviations: LI, lower lip; Pcl, postchaetal lobe; UP, upper lip.

Another species occurring in the French Mediterranean Sea, *P. medusa*, differs from *P. catalanensis* **n. sp.** by the presence of notopodia on 12 segments (instead of 13–15 for *P. catalanensis* **n. sp.**), by the type of notochaetae (absence of pinnate chaetae for *P. catalanensis* **n. sp.**, but present for *P. medusa*), by uncini with complete transverse series of secondary teeth above main tooth (instead of a crest with a very long tooth and two small lateral teeth for *P. catalanensis* **n. sp.**), by the presence of trefoiled upper lip with thin margin (instead of upper lip with single medial

lobe with thick margin for *P. catalanensis* n. sp.) and by the presence of a subtriangular lower lip, pointing towards the mouth (instead of a rectangular one for *P. catalanensis* n. sp.) (Table 2).

***Polycirrus* cf. *denticulatus* Saint-Joseph, 1894**

Figures 6–7, Table 2.

Material examined: AM W.53114, incomplete, NE Atlantic, Bay of Biscay, Bay of Brest, 48°21'28"N, 4°26'38"W, 7 m depth, May 2018, mounted for SEM, some parapodia used for molecular analysis. AM W.53115, incomplete, NE Atlantic, Bay of Biscay, Bay of Brest, 48°21'28"N, 4°26'38"W, 7 m depth, May 2018, mounted for SEM, some parapodia used for molecular analysis. MNHN-IA-PNT 121, incomplete, English Channel, Morlaix Bay, 48°41'04"N, 3°54'58"W, intertidal, February 2016. SMA_BR_Poly_17, incomplete, English Channel, 48°35'50"N, 4°37'27"W, intertidal, February 2015. SMA_BR_Poly_14, incomplete, English Channel, 48°35'50"N, 4°37'27"W, intertidal, February 2015.

Description. Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick semicircular crest across dorsum, extending lateral and posteriorly (Fig. 6B), covering SG1 laterally and terminating lateral to lower lip. Distal part extending along lip, terminating subdistally.

Few buccal tentacles remaining, short and thick, cylindrical (Figs 6A; 7A). Peristomium forming lips; upper lip comprising single medial lobe only, margin of lobe thickened and overturned (Figs 6A–C; 7A). Outer lower lip shield-like, subtriangular and pointing toward mouth, longer than wide, ridged and grooved, extending posteriorly to segment 3 (Figs 6A; 7A).

SG1 and 2 reduced, SG1 visible dorsally and laterally, SG2 visible dorsally, laterally and ventrally (Fig. 6A); body slightly broader until SG5, gently tapering until SG10, then of relatively uniform width, cylindrical (Fig. 6B). Vento-lateral inflated pads well-defined from SG3 to SG10, smooth and transversely ridged, subsequent ones less conspicuous until mid-body (Figs 6A, C; 7A). Deep mid-ventral groove from SG3 (Figs 6A; 7A).

Notopodia from SG3, extending for 12–13 segments, until SG14–15. Notopodia more-or-less rectangular, lobes slightly triangular (distally rounded) (Fig. 7B–C). Narrowly-winged notochaetae of two distinct lengths, slightly expanded subdistally, with fine tips (Figs 6D–E; 7B–C). Neuropodia beginning from SG12; type of uncini not seen (specimen used for SEM), crest with single elongate and sharp tooth on first row above main fang, with at least one additional row of shorter, irregularly sized teeth at base (exact number of additional rows not visible) (Fig. 7D).

Nephridial and genital papillae present on segments 3–8, ventral to bases of notopodia (Fig. 6C).

Pygidium unknown.

Habitat. Shallow waters, in maerl (rhodolith) beds, seagrass beds (this study) and among laminarians, algae, serpulids, and hydrozoa (Gil 2011).

Type locality. Brittany, France (exact locality problematic).

Distribution. NE Atlantic, English Channel, Mediterranean Sea (Fauvel 1927; Gil 2011), Adriatic Sea (Mikac 2015).

Remarks. French specimens, sampled close to the potential type locality, match almost completely with the recent redescription of type material by Glasby & Hutchings (2014). However, few minor variations were observed: mid-ventral groove appearing on segment 3 (instead of segment 4), notochaetigerous segments 12–13 (instead of 10, but type material is broken). Finally, we also document the first segment on which neuropodia begin.

As commented by Glasby & Hutchings (2014), doubts exist about the location of the type material. Indeed, the holotype seems to have been sampled in Concarneau (Brittany, Bay of Biscay) while in the original description Mr le Baron de St. Joseph (1894) reported the type locality in Dinard (Brittany, English Channel). Moreover, the redescription of the holotype does not fit exactly the type description (Glasby & Hutchings 2014). Consequently, until a neotype is collected and described, we prefer to identify these specimens as *Polycirrus* cf. *denticulatus*.

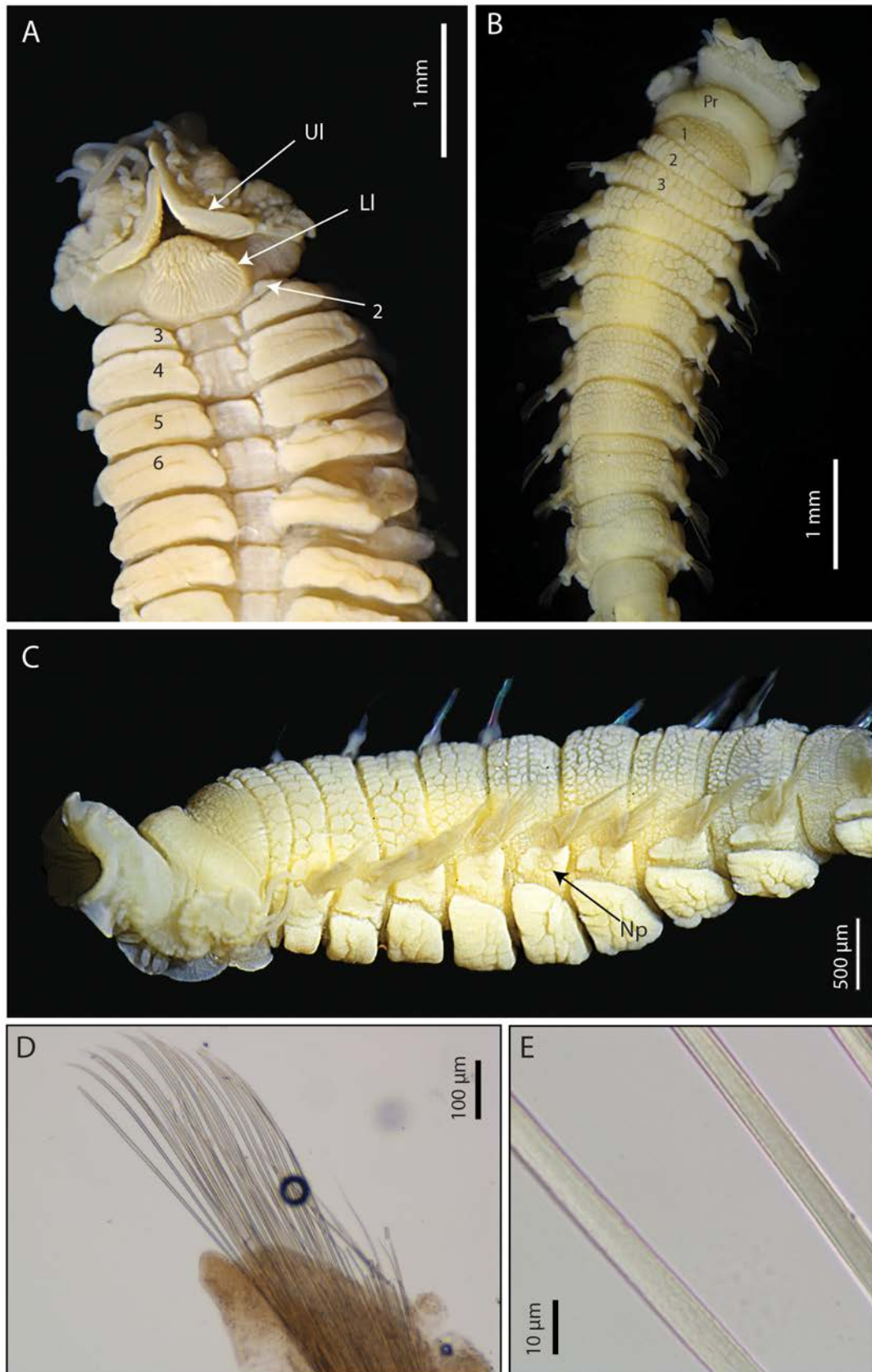


FIGURE 6. *Polycirrus cf. denticulatus*, material examined SMA_Br_Poly_17 (A), SMA_Br_Poly_14 (B–E). A. Anterior end, ventral view; B. Anterior end, dorsal view; C. Anterior end, lateral view; D. Notochaetae, SG6, 10x objective; E. Notochaetae, SG6, 100x objective. Abbreviations: Ll, lower lip; Pr, prostomium; Np, nephridial papilla; Ul, upper lip. Numbers refer to segments.

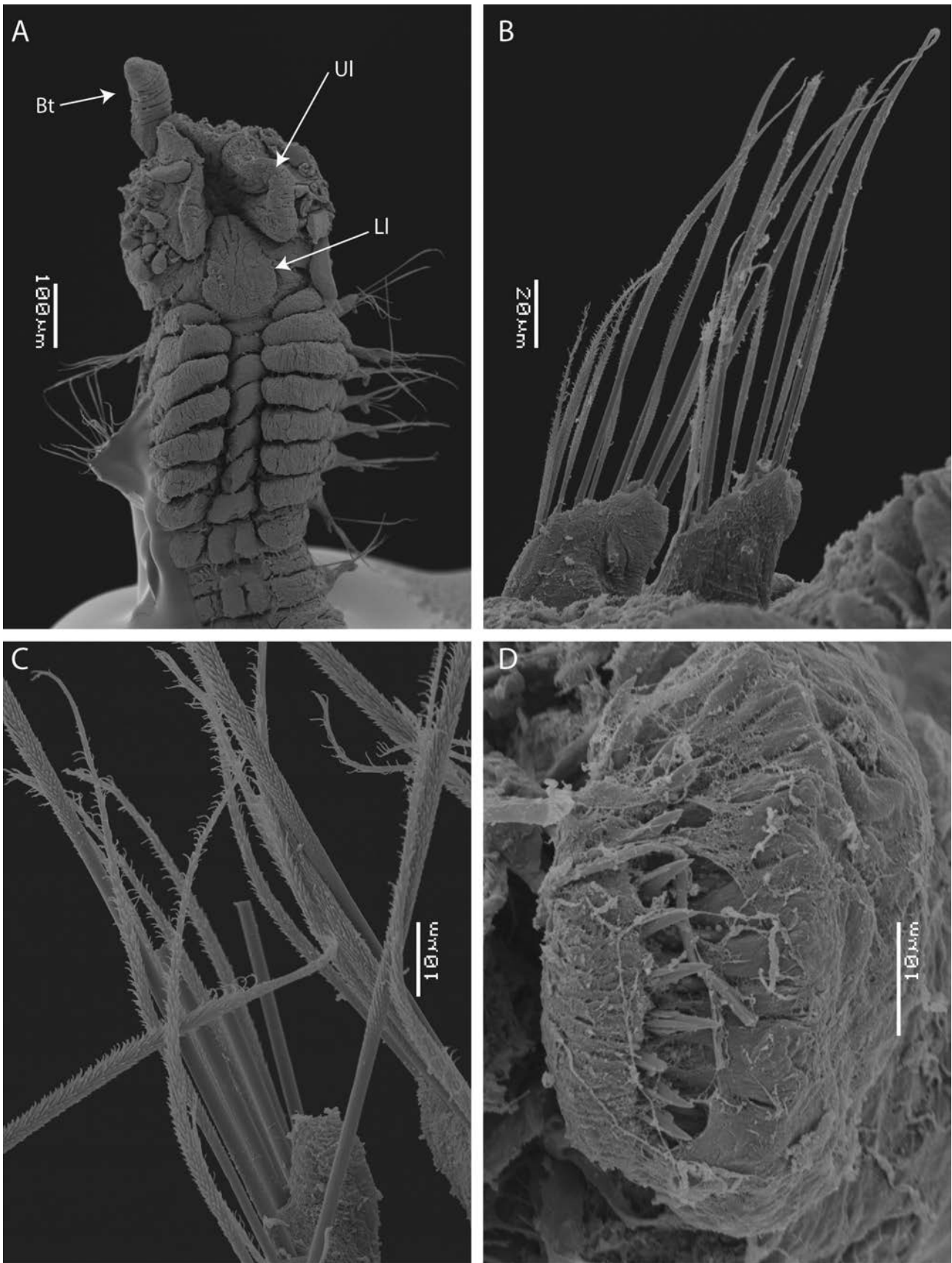


FIGURE 7. *Polycirrus* cf. *denticulatus*, SEM, material examined AM W.53114 (A, C), AM W.53115 (B, D). A. Anterior end, ventral view; B. Notopodia, SG3–4, ventral view; C. Notochaetae, SG4–5; D. Abdominal uncini. Abbreviations: Bt, buccal tentacle; LI, lower lip; UI, upper lip.

Polycirrus glasbyi n. sp.

Figures 8–9, Table 2.

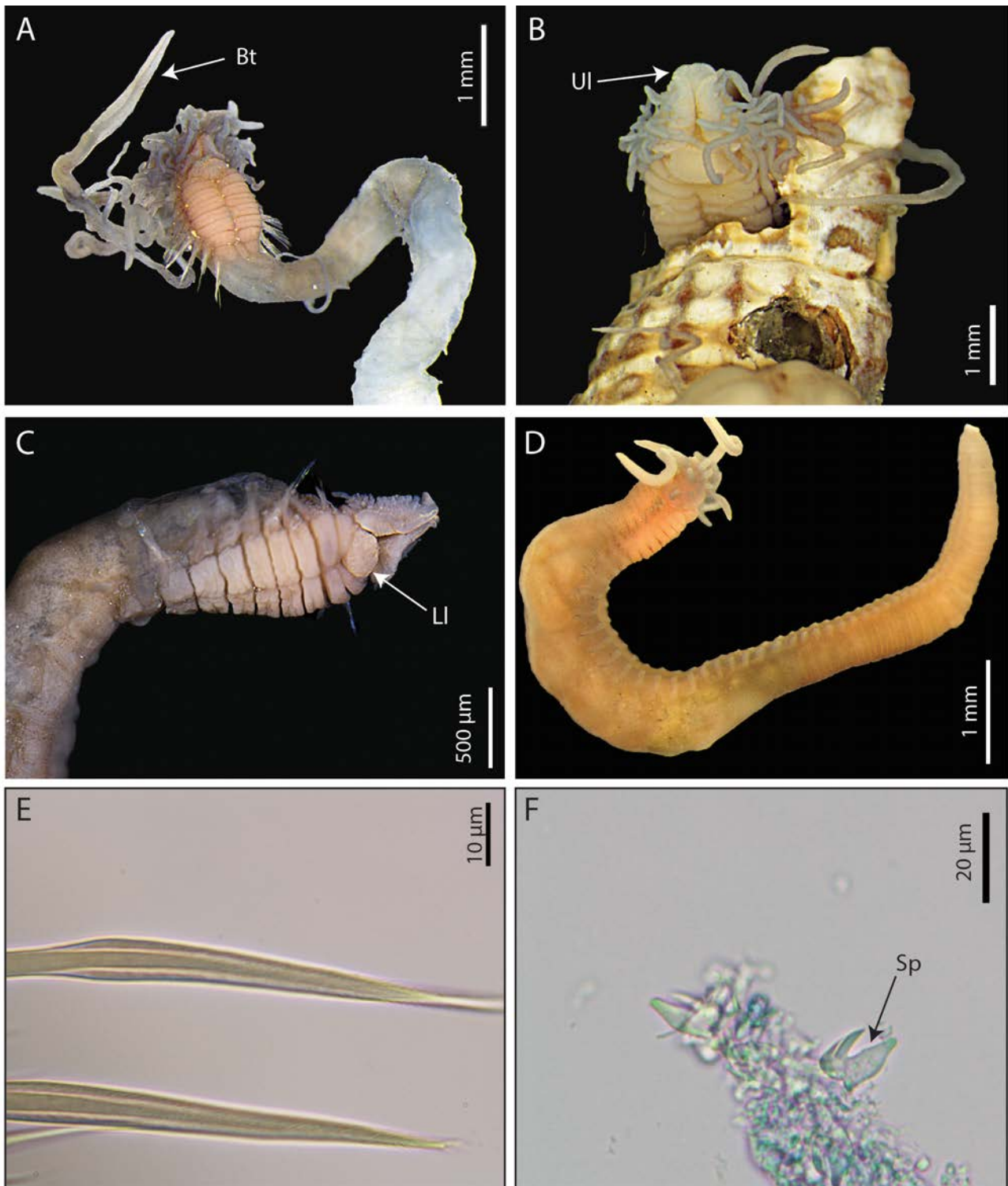


FIGURE 8. *Polycirrus glasbyi* n. sp., paratype MNHN-IA-Ty PE 2012 (A), additional material SMA-Arc-Poly-08 (B), holotype MNHN-IA-Ty PE 2010 (C), paratype AM W.53116 (D), paratype MNHN_Arc_Poly_29 (E), additional material SMA-Arc_Poly_09 (F). A. Anterior end, ventral view; B. Anterior end, in *Bittium reticulatum* shell, antero-frontal view; Anterior end, lateral view; D. Entire specimen, lateral view; E. Notochaetae, SG4, 100x objective; F. Uncini, SG13, 40x objective. Abbreviations: Bt, buccal tentacle; Ll, lower lip; Ul, upper lip; Sp, subrostral process.

Material examined: Holotype: MNHN-IA-Ty PE 2010, complete, NE Atlantic, Bay of Biscay, Arcachon Bay, Comprian, 44°40'33"N, 1°06'28"W, 9 m depth, April 2018. **Paratypes:** AM W.53116, one specimen, complete, NE

Atlantic, Bay of Biscay, Arcachon Bay, Comprian, 44°40'33"N, 1°06'28"W, 9 m depth, April 2018. AM W.53117, one specimen, incomplete, gravid, NE Atlantic, Bay of Biscay, Arcachon Bay, Comprian, 44°40'33"N, 1°06'28"W, 9 m depth, April 2018. MNHN-IA-Ty PE 2011, one specimen, incomplete, NE Atlantic, Bay of Biscay, Arcachon Bay, Comprian, 44°40'33"N, 1°06'28"W, 9 m depth, April 2018. MNHN-IA-Ty PE 2012, one specimen, incomplete, NE Atlantic, Bay of Biscay, Arcachon Bay, Comprian, 44°40'33"N, 1°06'28"W, 9 m depth, April 2018. AM W.53118, one specimen, complete, NE Atlantic, Bay of Biscay, Arcachon Bay, Jacquet, 44°43'08"N, 1°10'59"W, 9 m depth, December 2018, mounted for SEM.

Additional material. SMA_Arc_Poly_08, one incomplete specimen, NE Atlantic, Bay of Biscay, Arcachon Bay, Piraillan, 44°43'15"N, 1°10'45"W, 7 m depth, October 2017. SMA_Arc_Poly_09, one incomplete specimen, NE Atlantic, Bay of Biscay, Arcachon Bay, Piraillan, 44°42'17"N, 1°13'15"W, 9 m depth, October 2017, posterior part used for molecular analysis. SMA_Arc_Poly_10, one incomplete specimen, NE Atlantic, Bay of Biscay, Arcachon Bay, Piraillan, 44°42'17"N, 1°13'15"W, 9 m depth, October 2017, posterior part used for molecular analysis. SMA_Arc_Poly_11, one incomplete specimen, NE Atlantic, Bay of Biscay, Arcachon Bay, Piraillan, 44°42'17"N, 1°13'15"W, 9 m depth, October 2017, posterior part used for molecular analysis.

Description. Small species, holotype complete, 12.0 (0.7–12.2) mm long and 0.8 (0.6–1.1) mm wide.

Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick semicircular crest across dorsum, extending lateral and posteriorly, covering SG1 and 2 laterally and terminating lateral to lower lip. Buccal tentacles of two types, long and thin tentacles uniformly cylindrical, long and thick ones deeply grooved (Fig. 8A–B, D). Peristomium forming lips; upper lip elongate, longer than wide, folded into three lobes with a clear triangular shape (middle lobe very elongated) (Figs 8A–C; 9A); lower lip oval and inflated, wider than long, very glandular and ridged (Figs 8A–C; 9A).

SG1 and 2 reduced, only visible dorsally but hard to see; body with uniform width until mid-body, slightly tapering after (Fig. 8D). Vento-lateral inflated pads present from SG3 to SG9 (SG8), well-defined, smooth and transversely ridged, not separated by a gap (Figs 8A, C; 9A). Anterior midventral groove present until end of body as a stripe, narrow between anterior ventral shields (Figs 8A, C; 9A).

Notopodia from SG3, extending for 19 (18–22) segments, until SG21 (SG20–24); distinctly elongate, rectangular, first pair slightly shorter, bilobed, postchaetal lobe digitiform, larger than prechaetal one (Fig. 9B). Winged notochaetae of two distinct lengths, wings present at the distal half of notochaetae, tips whip-like (Figs 8E; 9B–C). Neuropodia beginning from SG10 (9–11); uncini with short occipitum and slightly convex base (Type 1) (Fig. 8F), crest with single elongate and sharp tooth on first row above main fang, with two additional rows of shorter, irregularly sized teeth at base (Fig. 9D), subrostral process present as low protuberance (Fig. 8F).

Nephridial and genital papillae not seen.

Pygidium rounded.

Etymology. This species is dedicated to Chris Glasby, for his friendship and for his great contributions to the knowledge of terebellids and *Polycirrus* species.

Habitat. Subtidal (5–9 m depth), muddy sands, sheltered waters. Many specimens found inside *Bittium reticulatum* (da Costa, 1778) shells (Fig. 8B).

Type locality. Arcachon Bay, Bay of Biscay, NE Atlantic Ocean, France.

Distribution. Only known from type locality.

Remarks. *Polycirrus glasbyi* n. sp. is characterized by the presence of notopodia extending for 18–22 segments which is similar to *P. plumosus* (17–19 segments) and *P. nogueirai* n. sp. (16–21 segments) (Table 2).

Polycirrus glasbyi n. sp. differs from *P. plumosus* by the first appearance of neuropodia (SG9–11 for *P. glasbyi* n. sp., SG18–20 for *P. plumosus*), by the shape of upper lip (triangular in *P. glasbyi* n. sp., with a single medial lobe only for *P. plumosus*), by the shape of lower lip (wider than long for *P. glasbyi* n. sp., longer than wide for *P. plumosus*), the type of notochaetae (absence of pinnate chaetae for *P. glasbyi* n. sp., present in *P. plumosus*) and by the shape of uncini (presence of a main tooth above the main fang for *P. glasbyi* n. sp., but absent in *P. plumosus*).

Polycirrus glasbyi n. sp. differs from *P. nogueirai* n. sp. by the first appearance of neuropodia (SG9–11 for *P. glasbyi* n. sp., SG14–16 for *P. nogueirai* n. sp.), by the shape of upper lip (triangular in *P. glasbyi* n. sp., whereas a single median elongated lobe present in *P. nogueirai* n. sp.), by the shape of lower lip (wider than long for *P. glasbyi* n. sp., rounded and as wide as long for *P. nogueirai* n. sp.), by the shape of notochaetae (with distal half enlarged for *P. glasbyi* n. sp., almost the same size for *P. nogueirai* n. sp.), by the presence of uncini with a subrostral process (absence in *P. nogueirai* n. sp.) and by a narrow gap between ventro-lateral pads (whereas a large gap present in *P. nogueirai* n. sp.).

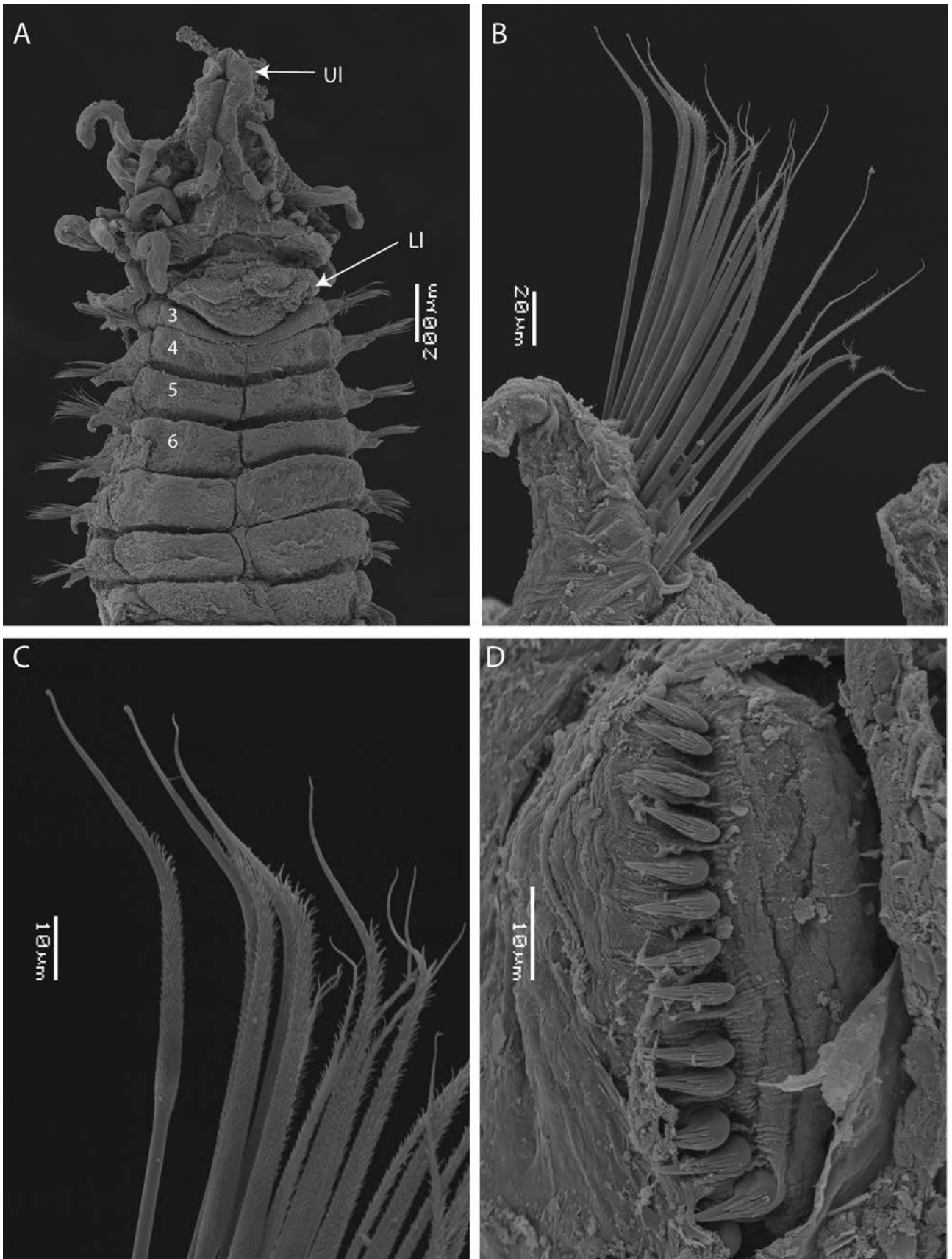


FIGURE 9. *Polycirrus glasbyi* n. sp., SEM, paratype AM W.53118. A. Anterior end, ventral view; B. Notopodia, SG5, ventral view; C. Notochaetae, SG5; D. Thoracic uncini. Abbreviations: LI, lower lip; UI, upper lip. Numbers refer to segments.

Polycirrus gujanensis n. sp.

Figures 10–11, Table 2.

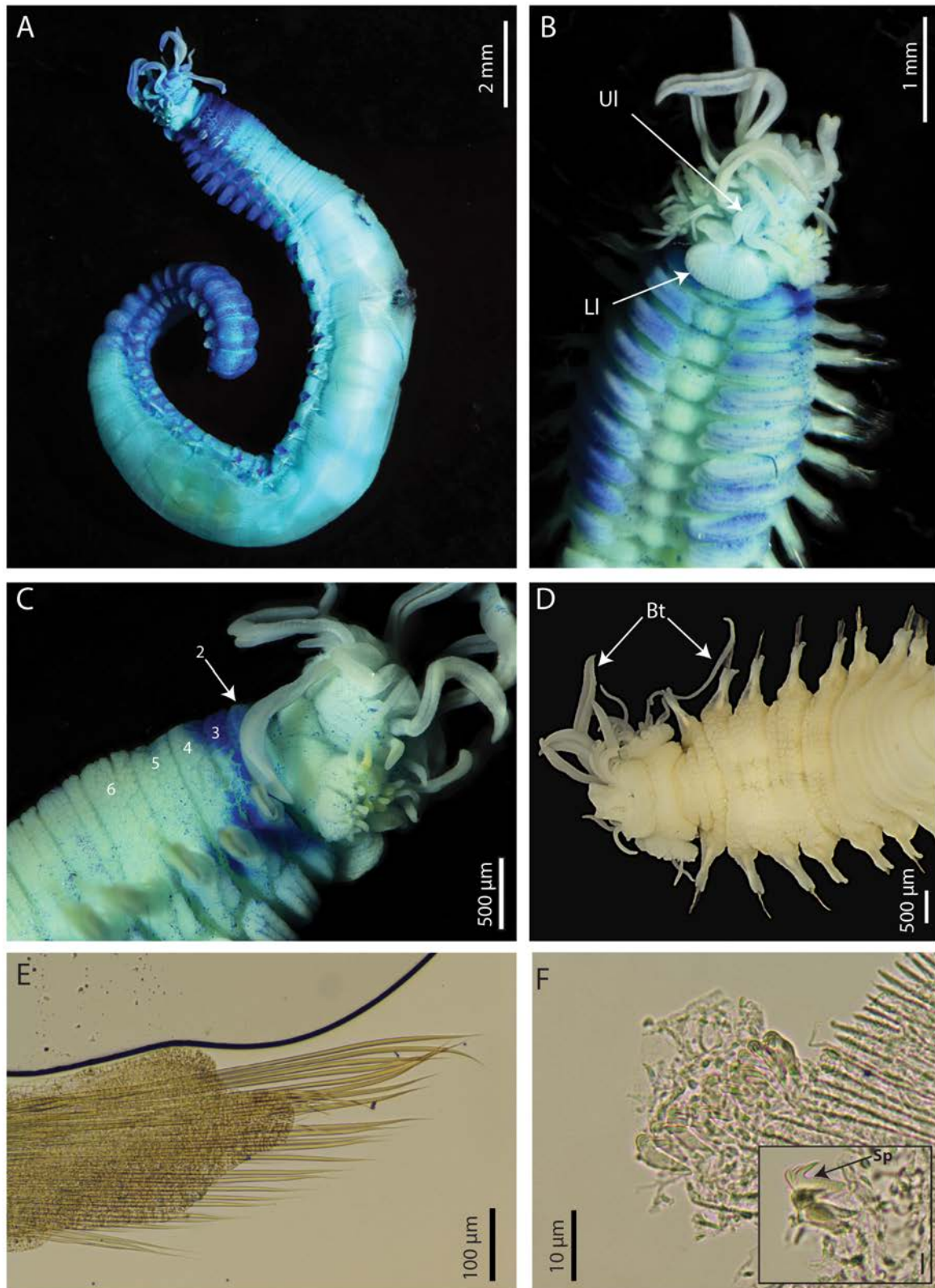


FIGURE 10. *Polycirrus gujanensis* n. sp., holotype MNHN-IA-Ty PE 2013 (A–C; E–F), paratype MNHN-IA-Ty PE 2014 (D). A. Anterior end, lateral view; B. Anterior end, ventral view; C. Anterior end, lateral view; D. Anterior part, dorsal view; E. Notochaetae, SG6, 10x objective; F. Uncini, SG17, 40x objective. Abbreviations: Bt, buccal tentacles; Ul, upper lip; Ll, lower lip; Sp, subrostral process. Numbers refer to segments.

Material examined: Holotype: MNHN-IA-Ty PE 2013, incomplete, NE Atlantic, Bay of Biscay, Arcachon Bay, Matelle, 44°39'51"N, 1°06'51"W, intertidal, May 2010, some parapodia mounted for SEM. **Paratypes:** MNHN-IA-Ty PE 2014, one specimen, incomplete, NE Atlantic, Bay of Biscay, Arcachon Bay, Matelle, 44°39'51"N, 1°06'51"W, intertidal, May 2010. AM W.53119, one specimen, incomplete, NE Atlantic, Bay of Biscay, Arcachon Bay, Dispute, 44°42'17"N, 1°06'48"W, intertidal, August 2016. AM W.53120, one specimen, incomplete, NE Atlantic, Bay of Biscay, Arcachon Bay, Matelle, 44°39'51"N, 1°06'51"W, intertidal, May 2010, mounted for SEM.

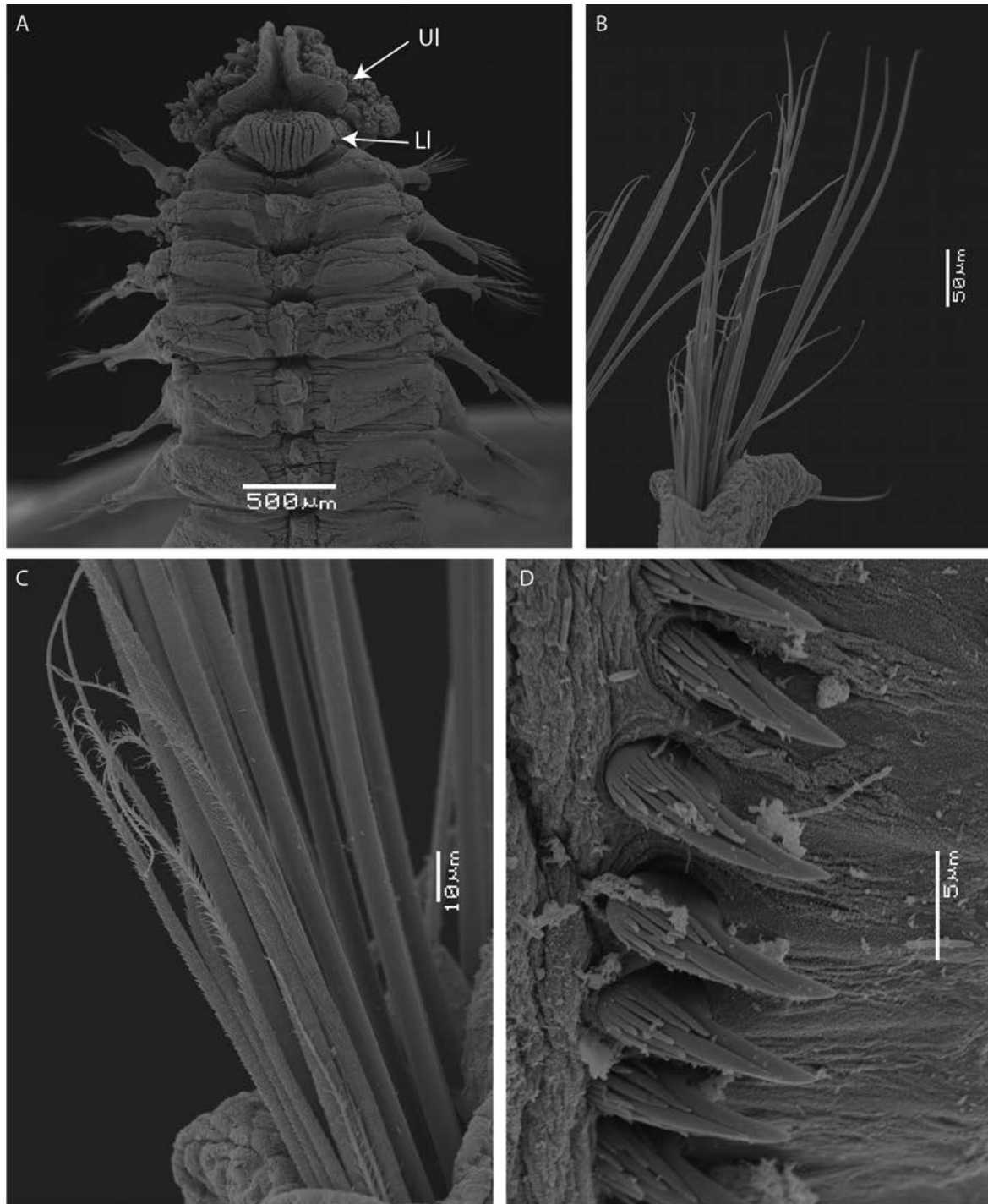


FIGURE 11. *Polycirrus gujanensis* n. sp., SEM, paratype AM W.53120 (A–C), holotype MNHN_Arc_Poly_15 (D). A. Anterior end, ventral view; B. Notopodia, SG5, ventral view; Notochaetae, SG5; D. uncini, posterior parapodia. Abbreviations: LL, lower lip; UL, upper lip.

Description. Large species, holotype incomplete (41 segments), 23.2 mm long and 2.2 mm wide.

Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick semicircular crest

across dorsum, extending lateral and posteriorly (Fig. 10D), covering SG1 laterally and terminating lateral to lower lip. Buccal tentacles of two types, short tentacles uniformly cylindrical, long ones deeply grooved, with pointed tips (Fig. 10A–D). Peristomium forming lips; upper lip elongate, longer than wide, highly convoluted, folded into three lobes, lateral ones well-developed (Figs 10B; 11A); lower lip oval and inflated, wider than long, very glandular and ridged (Figs 10B; 11A).

SG1 and 2 reduced, only visible dorsally (Fig. 10C–D); body slightly broader until SG8, gently tapering until SG10, then of relatively uniform width, cylindrical, tapering posteriorly (Fig. 10A). Ventro-lateral inflated pads well-defined from SG3 to SG12, smooth and transversely ridged, subsequent ones less conspicuous until mid-body (Figs 10A–C; 11A). Deep midventral groove from SG3 to end of the body, with small discrete shields from SG3 to midbody (Figs 10B; 11A).

Notopodia from SG3, extending for 28 segments, until SG30; distinctly elongate, rectangular, first two pairs slightly shorter, bilobed, postchaetal lobe larger than prechaetal one (Fig. 11B). Narrowly-winged notochaetae in two rows, with wings inconspicuous under light microscopy (Figs 10E; 11B–C). Neuropodia beginning from SG15; uncini with short occipitum and slightly convex base (Type 1) (Fig. 10F), crest with single elongate and sharp tooth on first row above main fang, with two additional rows of shorter, irregularly sized teeth at base (Fig. 11D), subrostral process present as small tooth (Fig. 10F).

Nephridial and genital papillae present on segments 3–8, anterior and ventral to bases of notopodia.

Pygidium unknown.

Etymology. The species name refers to the city of Gujan-Mestras, off where the species was sampled.

Habitat. Intertidal, medium sands, sheltered waters.

Type locality. Arcachon Bay, Bay of Biscay, NE Atlantic Ocean, France.

Distribution. Only known type locality.

Remarks. *Polycirrus gujanensis* **n. sp.** is characterized by the presence of 28 pairs of notopodia, and neuropodia from SG15, which is different from all European species, excepting *P. arenivorus* (29 pairs of notopodia, neuropodia from SG12) (Table 2). However, *P. gujanensis* **n. sp.** differs from this latter species by the shape of lower lip (oval and wider than long for *P. gujanensis* **n. sp.**, oblong and longer than wide for *P. arenivorus*), by the upper lip with three well-developed lobes (instead of medial lobe well developed only in *P. arenivorus*) and by uncini with an elongate tooth above the main fang (this tooth absent in *P. arenivorus*).

***Polycirrus idex* n. sp.**

Figure 12–13, Table 2.

Material examined: Holotype: MNHN-IA-Ty PE 2015, one complete specimen, Mediterranean Sea, Corsica Cape, 42°44'42"N, 9°28'00"E, 16 m depth, May 2019, posterior part used for molecular analysis. **Paratype:** AM W.53127, one complete specimen, Mediterranean Sea, Corsica Cape, 43°01'18"N, 9°24'30"E, 18 m depth, May 2019, mounted for SEM, posterior part used for molecular analysis.

Description. Small specimen 4.6 (4.3) mm long and 0.6 (0.7) mm wide.

Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick crest across dorsum, extending laterally and dorsally, covering SG1 laterally and terminating lateral to lower lip; distal part extending along upper lip, terminating subdistally. Buccal tentacles of two types, long grooved annulated and uniformly cylindrical ones, short thick grooved and distally enlarged ones (Figs 12A–B; 13A). Peristomium forming lips; upper lip elongate, longer than wide, with single median lobe only (Figs 12B–C; 13A); lower lip oblong, slightly longer than wide, very glandular, ridged (Figs 12C; 13A).

SG1 and 2 reduced, SG2 visible ventrally (Figs 12C; 13A); body slightly broader until SG7. Ventro-lateral inflated pads well-defined from SG3 to SG9 (SG8), less defined on SG10 (SG9), smooth (Figs 12C; 13A). Large anterior mid-ventral groove from S3, present until end of body as a stripe (Figs 12C; 13A).

Notopodia from SG3, extending for 13 (14) segments, until SG15 (SG16); not very elongate, rectangular, first pair slightly shorter, bilobed, postchaetal lobe conical with rounded tip, larger than prechaetal one (Fig. 18B). Winged notochaetae in two rows (Figs 12D; 13B–C). Neuropodia beginning from SG8 (SG7); uncini with short occipitum and slightly convex base (Type 1), crest with single elongate and sharp tooth on first row above main fang, with one additional row of 4–5 short, irregularly sized teeth (Fig. 13D), subrostral process present as small tooth (Fig. 13D).

Nephridial and genital papillae not seen.

Pygidium rounded.

Etymology. This species is named after IDEX (Excellence Initiative of Bordeaux University), which funded two grants for NL and GD to spend 9 months at the Australian Museum (Sydney). “I dex” is an unmodifiable noun in apposition.

Habitat. 18 m depth, among rocks.

Type locality. Corsica Cape, Mediterranean Sea.

Distribution. Only known from type locality.

Remarks. With 14 segments with notopodia and neuropodia starting on SG7–8, *P. idex* n. sp. differs from all other European species (Table 2). The closest species is *P. asturiensis* (notopodia on 10 segments and neuropodia starting on SG6) but this last species has a trefoiled upper lip (instead of a single lobe only for *P. idex* n. sp.), a lower lip wider than long (instead of longer than wide for *P. idex* n. sp.) and uncini showing two rows of secondary teeth above the main tooth (instead of a single row of secondary teeth for *P. idex* n. sp.).

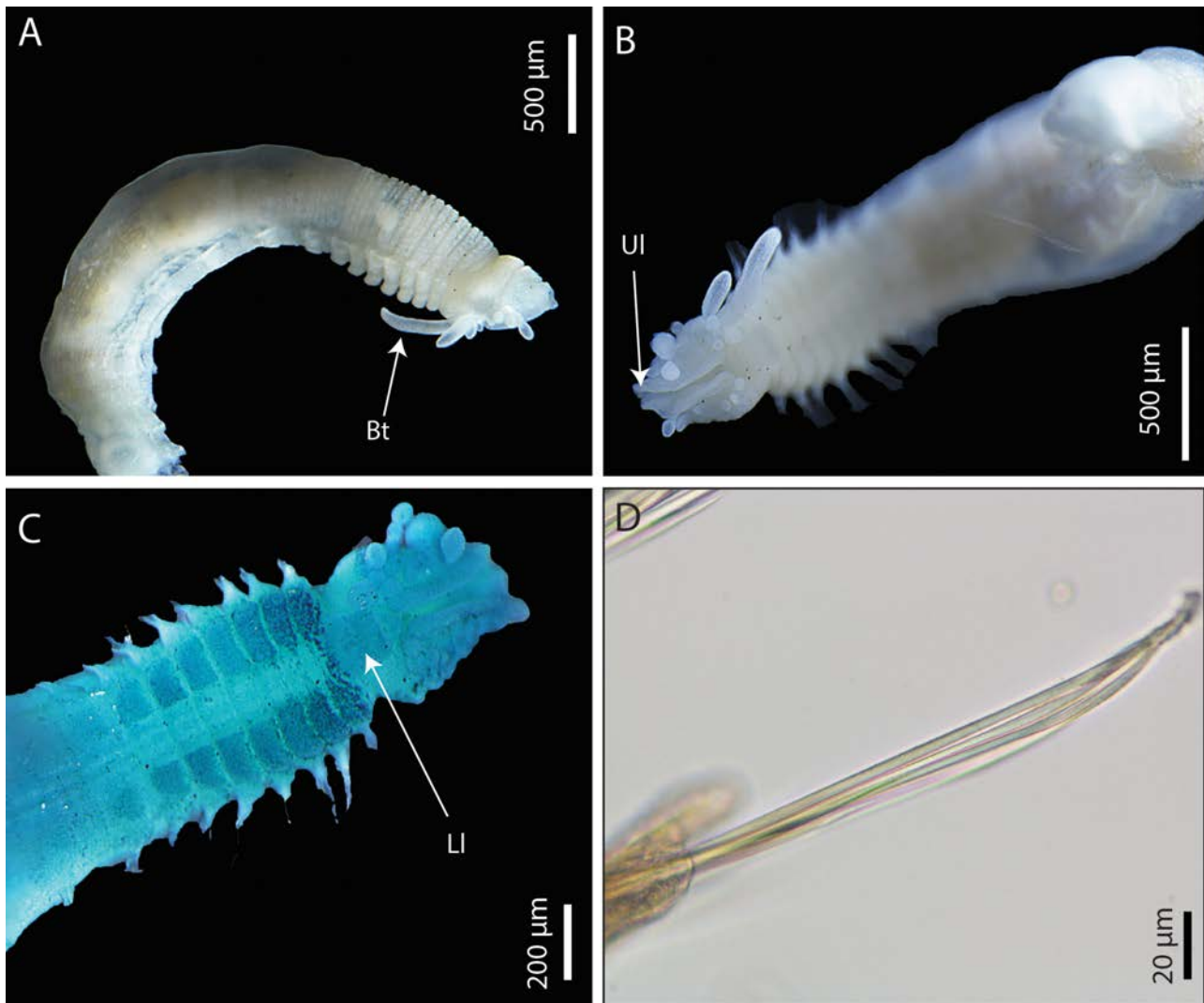


FIGURE 12. *Polycirrus idex* n. sp. holotype MNHN-IA-Ty PE 2015A. Anterior end, lateral view; B. Anterior end, ventral view; C. Anterior end, ventral view, methyl green staining; D. Notochaetae, SG7, 40x objective. Abbreviations: Bt, buccal tentacle; Ll, lower lip; Ul, upper lip.



FIGURE 13. *Polycirrus idex* n. sp., SEM paratype AM W.53127. A. Anterior end, ventral view; B. Notopodia, SG8, ventral view; C. Notochaetae, SG8; D. Abdominal uncini. Abbreviations: LI, lower lip; Ne, neuropodia, UI, upper lip. Numbers refer to segments.

Polycirrus nogueirai n. sp.

Figures 14–15, Table 2.

Material examined: **Holotype:** MNHN-IA-Ty PE 2016, incomplete, NE Atlantic, Bay of Biscay, Arcachon Bay, Jacquets, 44°43'21"N, 1°11'15"W, intertidal, December 2018. **Paratypes:** AM W.53121, one incomplete specimen, NE Atlantic, Bay of Biscay, Arcachon Bay, Jacquets, 44°43'21"N, 1°11'15"W, intertidal, December 2018, mounted for SEM. MNHN-IA-Ty PE 2017, one incomplete specimen, NE Atlantic, Bay of Biscay, Arcachon Bay, Jacquets, 44°43'21"N, 1°11'15"W, intertidal, December 2018. AM W.53122, one incomplete specimen, NE Atlantic, Bay of Biscay, Arcachon Bay, Jacquets, 44°43'21"N, 1°11'15"W, intertidal, December 2018.

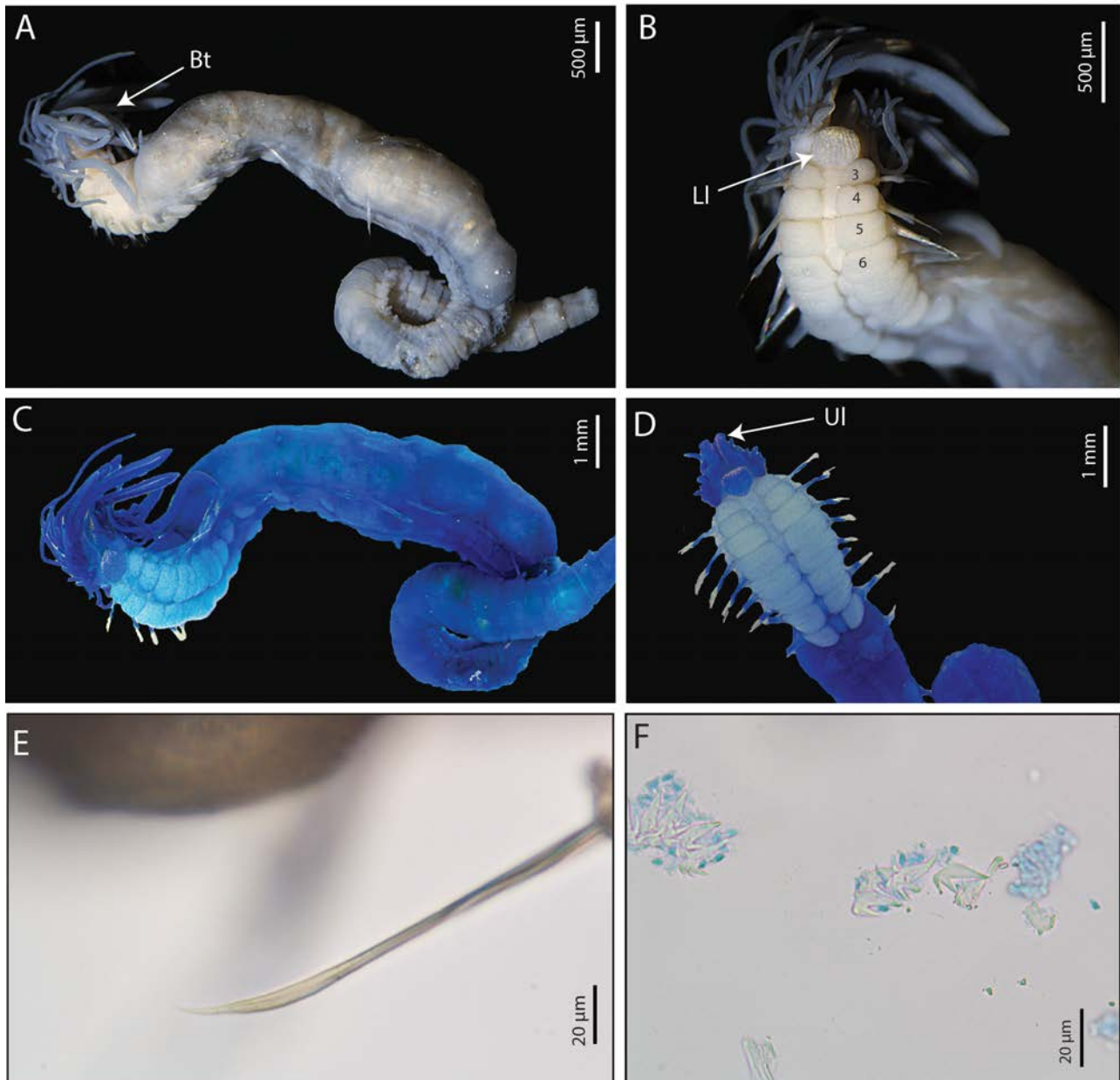


FIGURE 14. *Polycirrus nogueirai* n. sp., holotype MNHN-IA-Ty PE 2016 (A–C; F), paratype AM W.53121 (D), paratype MNHN-IA-Ty PE 2017 (E). A. Entire specimen, lateral view; B. Anterior end, ventral view; C. Entire specimen, lateral view, methyl green; D. Anterior end, ventral view, methyl green staining; E. Notochaetae, SG10, 40x objective; F. Uncini, SG16, 40x objective. Abbreviations: BT, buccal tentacle; LI, lower lip; UI, upper lip. Numbers refer to segments.

Description. Small species, holotype incomplete, 9.1 (4.5–11.0) mm long and 0.9 (0.6–0.8) mm wide.

Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick crest across dorsum, extending laterally, covering SG1 laterally and terminating lateral to lower lip. Buccal tentacles of two types, long

and thin tentacles uniformly cylindrical, long and thick ones deeply grooved, with pointed tips (Fig. 14A–C). Peristomium forming lips; upper lip elongate, longer than wide, with a single median lobe only (Figs 14B, D; 15A); lower lip rounded and inflated, as wide as long, very glandular and ridged (Figs 14B, D; 15A).

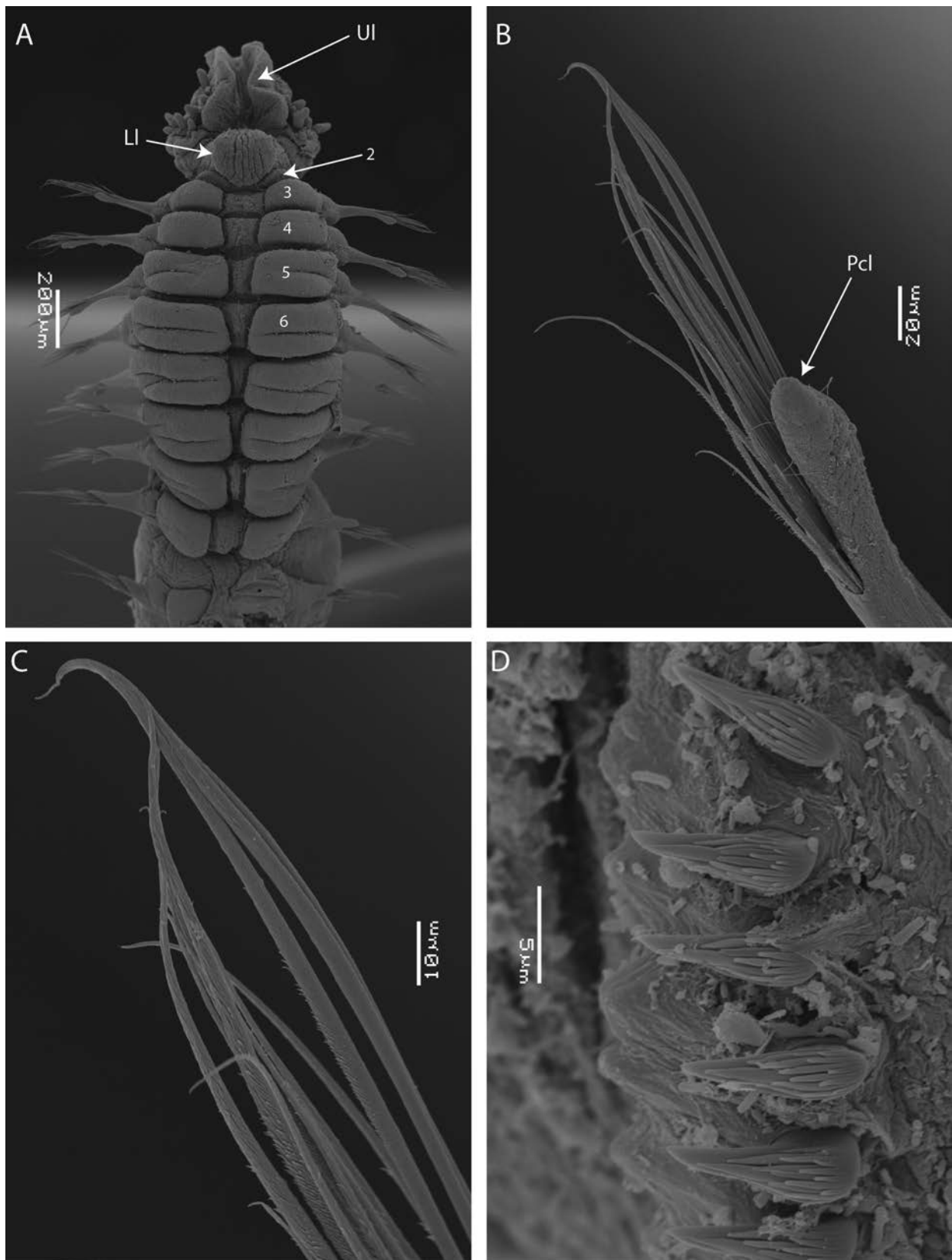


FIGURE 15. *Polycirrus nogueirai* n. sp., SEM, paratype AM W.53121. A. Anterior end, ventral view; B. Notopodia, SG3, ventral view; Notochaetae, SG3; D. Thoracic uncini. Abbreviations: Ll, lower lip; Pcl, postchaetal lobe; Ul, upper lip. Numbers refer to segments.

SG1 and 2 reduced, SG1 visible dorsally, SG2 dorsally, laterally and ventrally (Fig. 15A); body with relatively uniform width until SG20, gently tapering after (Fig. 14A, C). Ventro-lateral inflated pads present from SG3 to SG13 (SG14), well-defined, smooth and transversely ridged until SG10, subsequent ones less conspicuous (Figs 14 B–D; 15A). Midventral groove with small discrete shields from SG3 to SG10, continuing as a stripe until end of body (Figs 14B, D; 15A).

Notopodia from SG3, extending for 16 (19–21) segments, until SG18 (SG21–23); distinctly elongate, rectangular, first pair slightly shorter, bilobed, postchaetal lobe digitiform, larger than prechaetal one (Fig. 15B). Winged notochaetae of two lengths, distal ends whip-like (Figs 14E; 15 B–C). Neuropodia beginning from SG14 (SG16); uncini with short occipitum and slightly convex base (Type 1) (Fig. 14F), crest with single elongate and sharp tooth on first row above main fang, with two additional rows of shorter, irregularly sized teeth at base (Fig. 15D), absence of subrostral process (Fig. 14F).

Nephridial and genital papillae present on segments 3–8.

Pygidium unknown.

Etymology. This species is dedicated to João Nogueira for his great contribution to taxonomy of terebellids.

Habitat. Intertidal, muddy sands, sheltered waters.

Type locality. Arcachon Bay, Bay of Biscay, NE Atlantic Ocean, France.

Distribution. Only known from type locality.

Remarks. *Polycirrus nogueirai* n. sp. is characterized by the presence of notopodia on 16–21 segments, which is similar to *P. glasbyi* n. sp. (18–22 segments), *P. plumosus* (17–19 segments), *P. readi* n. sp. (13–17 segments), *P. elisabethae* (16 segments) and *P. norvegicus* (14–20 segments) (Table 2). Among these species, only *P. plumosus* shows almost the same range in appearance of neuropodia (from SG18–22 for *P. plumosus*, from SG14–16 for *P. nogueirai* n. sp.).

However, *P. nogueirai* n. sp. differs from *P. plumosus* by the presence of one type of notochaetae only (instead of two for *P. plumosus*), uncini with a median tooth in first row above main fang (absent for *P. plumosus*), the shape of lower lip (protruding above venter and longer than wide for *P. plumosus*, rounded and as wide as long for *P. nogueirai* n. sp.) and by the shape of ventro-lateral pads (poorly defined for *P. plumosus*, inflated for *P. nogueirai* n. sp.).

Polycirrus pennarbedae n. sp.

Figures 16–17, Table 2.

Material examined: Holotype: MNHN-IA-Ty PE 2018, one complete specimen, NE Atlantic, Bay of Biscay, Glenan, 47°44'06"N, 4°0'01"W, 7 m depth, March 2015. **Paratypes:** AM W.53123, one complete specimen, NE Atlantic, Bay of Biscay, Glenan, 47°43'43"N, 3°58'04"W, 5 m depth, March 2015. AM W.53124, one complete specimen, NE Atlantic, Bay of Biscay, Bay of Brest, 48°18'57"N, 4°22'40"W, 2 m depth, May 2017, mounted for SEM.

Additional material: MNHN-IA- PNT 122, one complete specimen, NE Atlantic, Bay of Biscay, Morlaix Bay, 48°42'44"N, 3°57'04"W, 4 m depth, February 2016. MNHN-IA- PNT 123, one complete specimen, NE Atlantic, Bay of Biscay, Morlaix Bay, 48°42'40"N, 3°57'03"W, 4 m depth, February 2016. AM W.53125, one complete specimen, NE Atlantic, Bay of Biscay, Morlaix Bay, 48°42'40"N, 3°57'03"W, 4 m depth, February 2016.

Description. Small species, holotype 11.5 (7.2–10.0) mm long and 0.7 (0.5–1.0) mm wide.

Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick crest across dorsum, extending laterally and dorsally, covering SG1 laterally and terminating lateral to lower lip. Buccal tentacles of two types, thin tentacles uniformly cylindrical, long and thick ones deeply grooved (Fig. 16C). Peristomium forming lips; upper lip elongate, longer than wide, triangular shape, comprising medial lobe only, very convoluted (Figs 16A–C; 17A); lower lip oval and inflated, wider than long, very glandular and ridged (Figs 16A–B; 17A).

SG1 and 2 reduced, SG1 visible dorsally, SG2 dorsally and laterally; body slightly broader until SG6, then of relatively uniform width until mid-body, posterior end tapering (Fig. 16A). Ventro-lateral inflated pads present from SG3 to SG10, smooth (Figs 16A–C; 17A). Anterior mid-ventral groove present until end of body as a stripe, shallow and narrow between anterior ventral shields (Figs 16A–C; 17A).

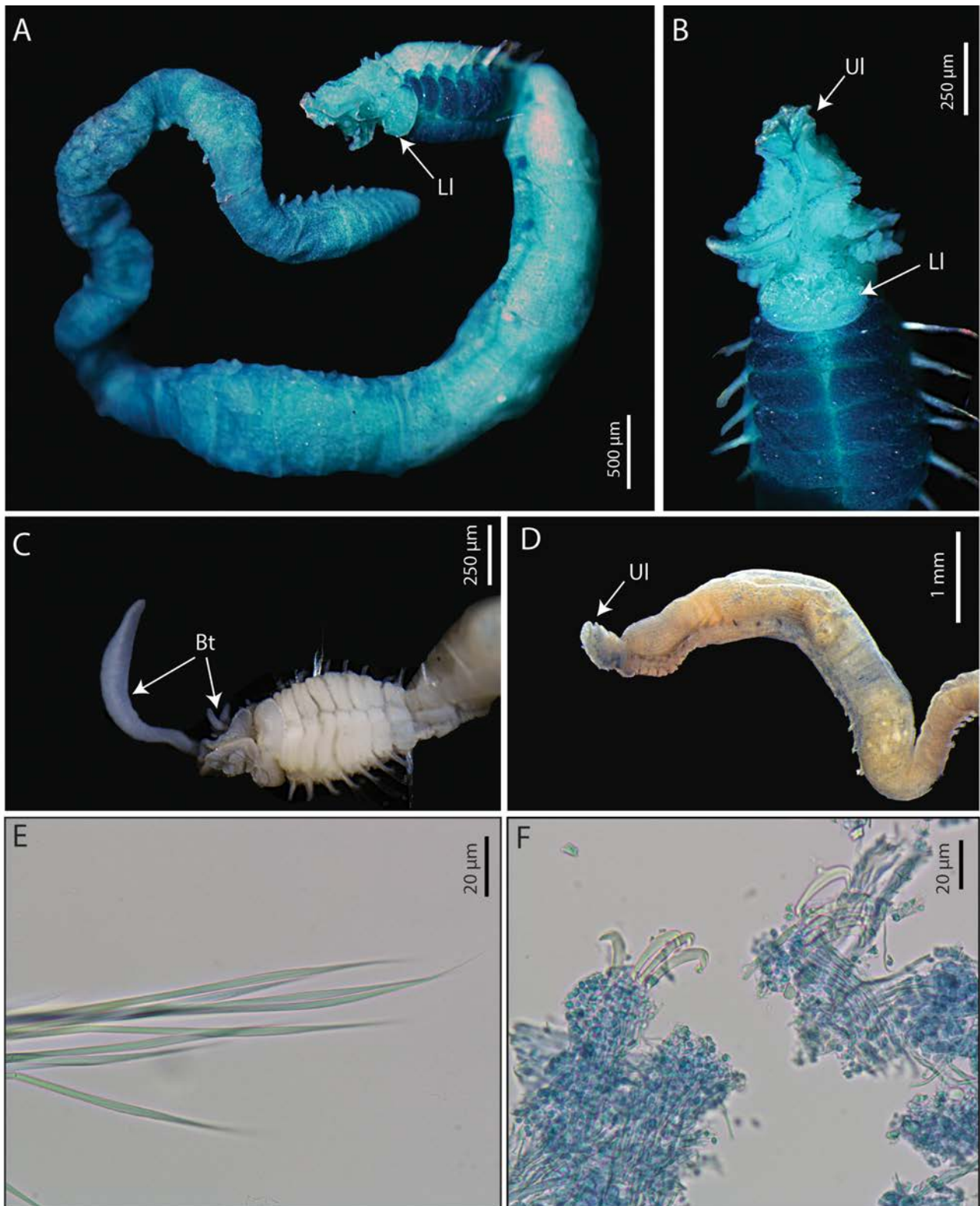


FIGURE 16. *Polycirrus pennarbedae* n. sp., holotype MNHN-IA-Ty PE 2018 (A–B), additional material MNHN-IA-PNT 122 (C) and MNHN-IA-PNT 122 (D–F). A. Entire specimen, ventro-lateral view, methyl green staining; B. Anterior end, ventral view, methyl green staining; C. Anterior end, ventral view; D. Anterior end, lateral view; E. Notochaetae, SG8, 40x objective; F. Uncini, posterior chaetiger, 40x objective. Abbreviations: Bt, buccal tentacles; LI, lower lip; UI, upper lip.

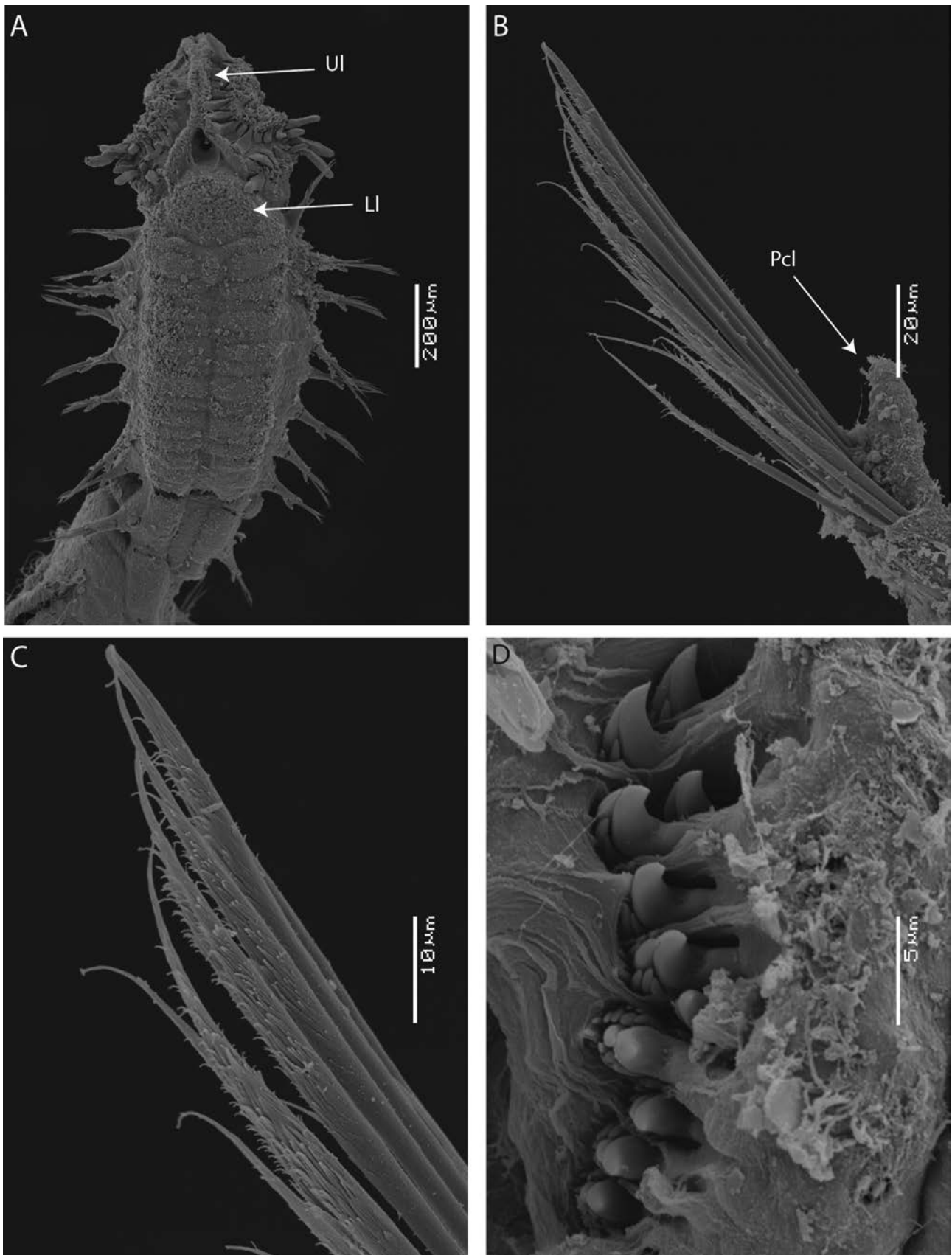


FIGURE 17. *Polycirrus pennarbedae* n. sp., SEM, paratype AM W.53124. A. Anterior part, ventral view; B. Notopodia from SG5, ventral view; C. Notochaetae from SG5; D. Abdominal uncini. Abbreviations: LI, lower lip; Pcl, postchaetal lobe; UI, upper lip.

Notopodia from SG3, extending for 12 (13) segments, until SG14 (SG15); distinctly elongate, rectangular, first two pairs slightly shorter, bilobed, postchaetal lobe digitiform, larger than prechaetal one (Fig. 17B). Narrowly winged notochaetae of two different lengths, with wings inconspicuous under light microscopy (Figs 16E; 17 B–C). Neuropodia beginning from SG15 (SG16); uncini with short occipitum and slightly convex base (Type 1) and with a very long prow (Fig. 16F), crest with single elongate and sharp tooth on first row above main fang, with two additional rows of shorter, irregularly sized teeth at base (Fig. 17D), absence of subrostral process (Fig. 16F).

Nephridial and genital papillae not seen.

Pygidium rounded with ventral pointed tip.

Etymology. The species name was chosen by V. Le Garrec who sent us the type material. It refers to Penn-Ar-Bed which is the Breton name for Finistère (Finis Terrae in latin), the French department situated on western part of Brittany. The term “*pennarbedae*” is the genitive of the noun “Penn-Ar-Bed”.

Habitat. Coastal maerl (rhodolith) beds in 2–7 m depth.

Type locality. Glenan archipelago, Bay of Biscay, NE Atlantic Ocean, France.

Distribution. Bay of Biscay (Glenan archipelago, Bay of Brest), English Channel (Morlaix Bay).

Remarks. *Polycirrus pennarbedae* n. sp. is characterized by 12–13 pairs of notopodia and neuropodia starting from SG14–15, which is similar to *P. medusa* (12 segments with notopodia, neuropodia from SG15), *P. latidens* (12 segments with notopodia, neuropodia from SG14) and *P. catalanensis* (13–15 segments with notopodia, neuropodia from SG15–17) (Table 2).

Polycirrus pennarbedae n. sp. differs from *P. medusa* by the presence of a triangular upper lip with elongated median lobe (instead of trefoiled upper lip for *P. medusa*), the presence of a lower lip oval, wider than long (instead of upper lip subtriangular and pointing towards the mouth), by the presence of one type of notochaetae (instead of two types for *P. medusa*) and the ventro-lateral pads not separated by a large mid-ventral groove (large mid-ventral groove on anterior segments for *P. medusa*) (Table 2).

Polycirrus pennarbedae n. sp. differs from *P. latidens* by having a narrow and shallow mid-ventral groove between ventro-laterals pads (instead of a well-defined mid-ventral groove present from SG4 for *P. latidens*), the presence of a lower lip oval (instead of oblong lower lip *P. latidens*). *Polycirrus latidens* is also characterized by uncini with teeth above main fang, arranged in single vertical series (instead of crests of teeth as present in *P. pennarbedae*) (Table 2).

Finally, *P. catalanensis* n. sp. differs from *P. pennarbedae* n. sp. by the shape of uncini (two rows of teeth above the main tooth for *P. pennarbedae* n. sp., a single row of secondary teeth above the main tooth for *P. catalanensis* n. sp.), the shape of upper lip (elongated triangular medial lobe for *P. pennarbedae* n. sp., in contrast a very thick single medial lobe present in *P. catalanensis* n. sp.), the shape of lower lip (oval and wider than long for *P. pennarbedae* n. sp., rectangular and longer than wide *P. catalanensis* n. sp.) and the presence of a large mid-ventral groove on anterior segments for *Polycirrus catalanensis* n. sp. (narrow and shallow for *P. pennarbedae* n. sp.) (Table 2).

***Polycirrus readi* n. sp.**

Figures 18–19, Table 2.

Material examined: Holotype: MNHN-IA-Ty PE 2019, one complete specimen, Mediterranean Sea, Corsica Cape, 42°44'23"N, 9°28'41"E, 60 m depth, May 2019. **Paratypes:** AM W.53126, one complete specimen, Mediterranean Sea, Corsica Cape, 43°01'18"N, 9°24'30"E, 18 m depth, May 2019, posterior part used for molecular analysis, mounted for SEM.

Additional material: MNHN-IA- PNT 124, one complete specimen, Mediterranean Sea, Calvi, 42°34'48"N, 8°43'45"E, 40 m depth, August 2011.

Description. Small specimens except MNHN-IA- PNT 124, holotype 8.3 (4.1–14.5) mm long and 0.6 (0.4–0.9) mm wide.

Transverse prostomium attached to dorsal surface of base of upper lip; basal part as thick crest across dorsum, extending laterally and dorsally, covering SG1 laterally and terminating lateral to lower lip. Buccal tentacles of two types, long and thin tentacles uniformly cylindrical, long and thick ones deeply grooved (Figs 18 A–D; 19A). Peristomium forming lips; upper lip elongate, longer than wide, with single median lobe only, triangular, convoluted (Figs 18B, D; 19A); lower lip oblong, longer than wide, very glandular, ridged (Figs 18B, D; 19A).

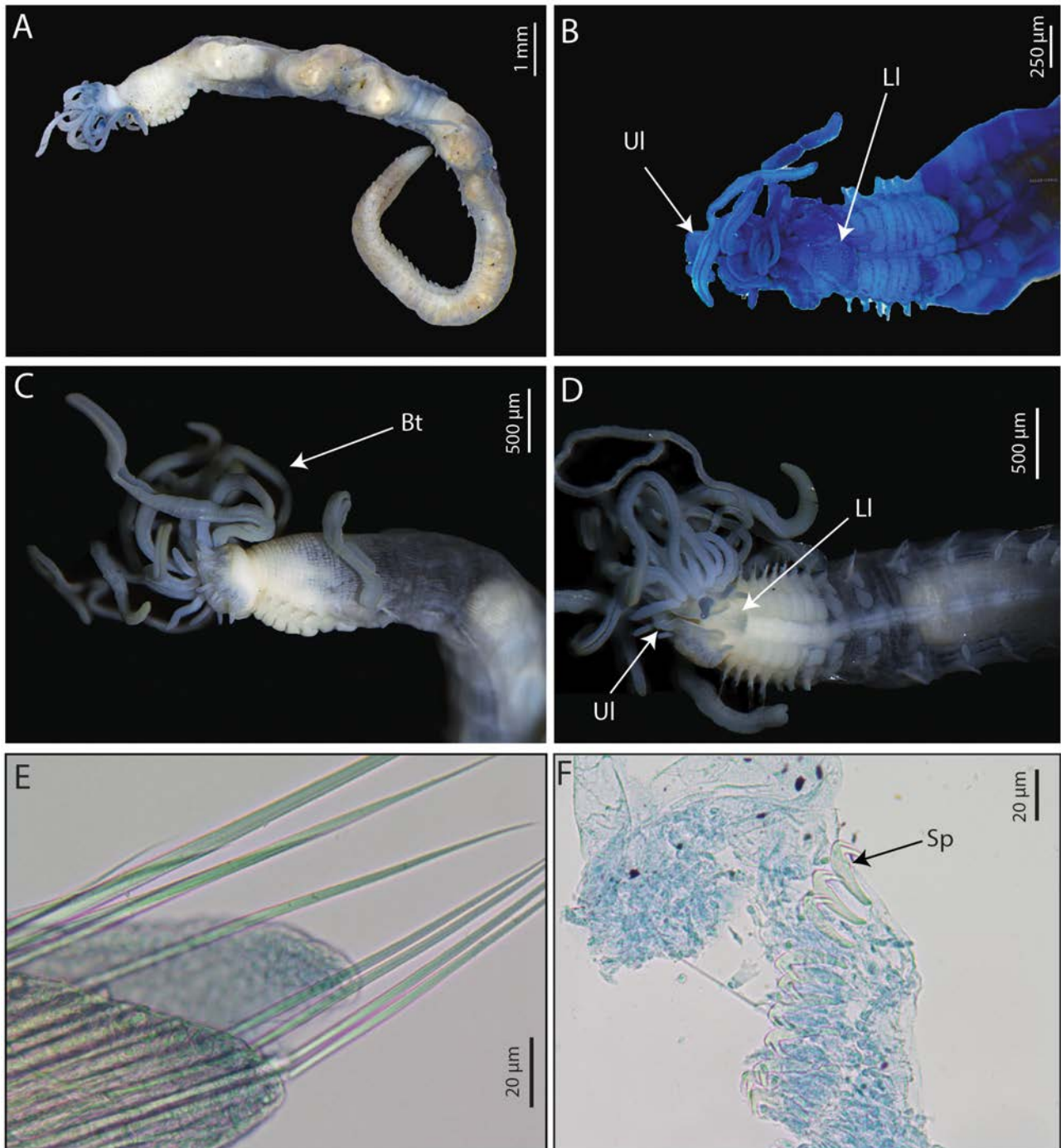


FIGURE 18. *Polycirrus readi* n. sp., additional material MNHN-IA-PNT 124 (A–B), holotype MNHN-IA-Ty PE 2019 (C–D). A. Entire specimen, lateral view; B. Anterior end, ventral view, methyl green staining; C. Anterior end, lateral view; D. Anterior end, ventral view. ; E. Notochaetae, SG8, 40x objective; F. Uncini, posterior chaetiger, 40x objective. Abbreviations: Bt, buccal tentacles; Ll, lower lip; Ul, upper lip; Sp, subrostral process.

SG1 and 2 reduced, SG1 visible dorsally, SG2 dorsally and laterally; body slightly broader until SG6, then tapering until SG10, then of relatively uniform width (larger than anterior part) until mid-body, posterior end tapering (Fig. 18A). Ventro-lateral inflated pads well-defined from SG3 to SG9 (SG10), smooth, with transverse ridges on largest specimen, subsequent ones less conspicuous until SG12 (SG15) (Figs 18 A–D; 19A). Large anterior mid-ventral groove from S3, present until end of body as a stripe (Figs 18B, D; 19A).

Notopodia from SG3, extending for 17 (13) segments, until SG19 (SG15); distinctly elongate, rectangular, first pair slightly shorter, bilobed, postchaetal lobe conical with rounded tip, larger than prechaetal one (Fig. 19B).

Winged notochaetae of two different lengths (Figs 18E; 19B–C). Neuropodia beginning from SG10 (SG9); uncini with short occipitum and slightly convex base (Type 1), crest with single elongate and sharp tooth on first row above main fang, with one additional rows of 4–5 short, irregularly sized teeth (Fig. 19D), subrostral process present as a protuberance (Fig. 18F).

Nephridial and genital papillae not seen.

Pygidium rounded with pointed tip.

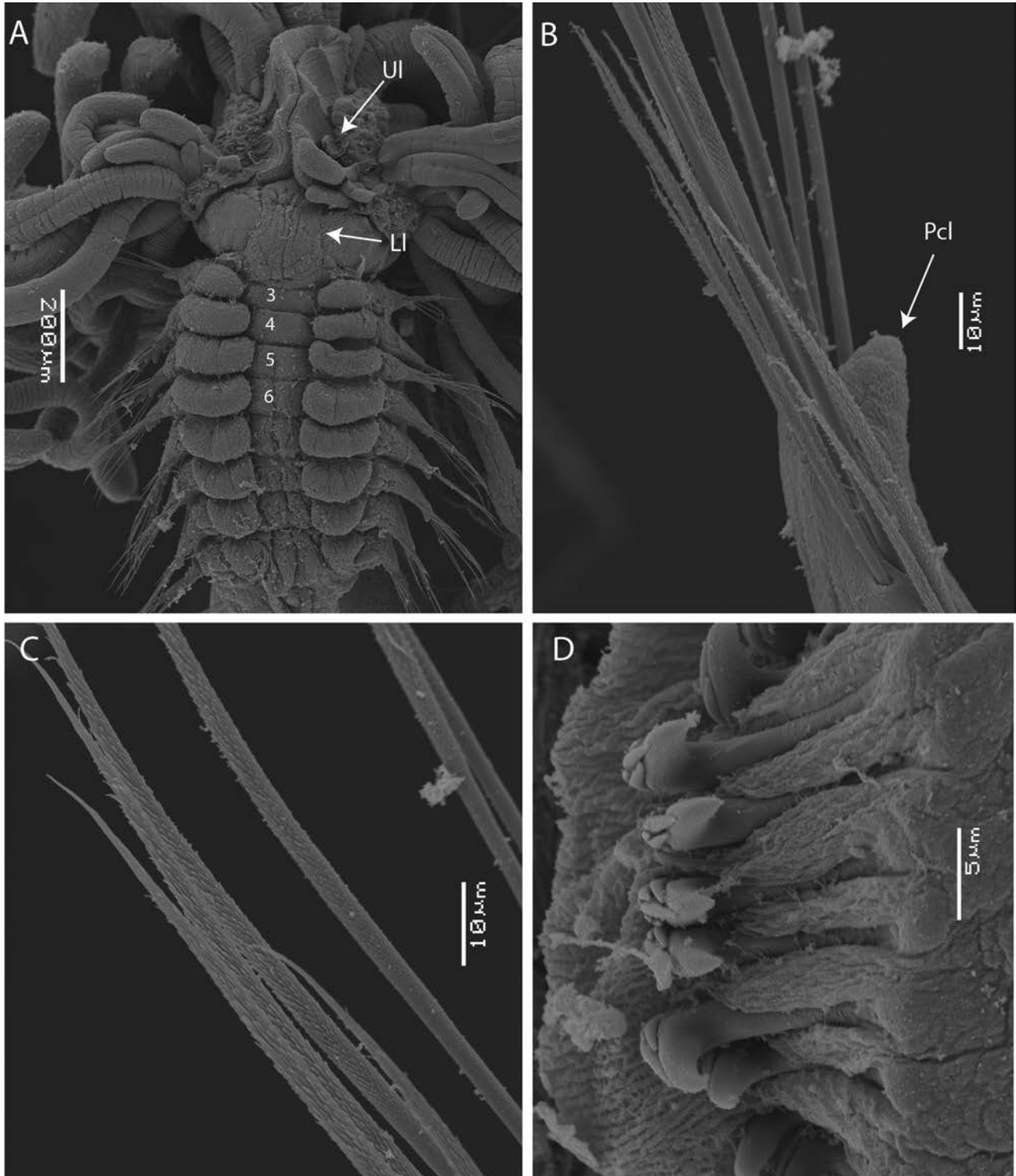


FIGURE 19. *Polycirrus readi* n. sp., SEM paratype AM W.53126. A. Anterior end, ventral view; B. Notopodia, SG5, ventral view; C. Notochaetae, SG5; D. Abdominal uncini. Abbreviations: LI, lower lip; Pcl, postchaetal lobe, UL, upper lip. Numbers refer to segments.

Tabl E 2. Distinguishing characters of European species of *Polycirrus* (Annelida: Polycirridae). MT: main tooth, SG: segment.

	Type locality	Number of pairs of notopodia	Start of neuropodia	Notochaetae	Uncini (type 1)	Upper lip	Lower lip	References
<i>P. arenivorus</i> (Caullery, 1915)	France (Normandy)	29	SG12	narrowly winged	MT absent, two rows above MF (MF:3:5)	medial lobe well developed only	oblong, longer than wide	Glasby & Hutchings, 2014
<i>P. asturiensis</i> Cepeda & Lattig, 2016	Spain (Cantabrian Sea)	10	SG6	broadly winged	MT present, with two rows above MT (MF:1:α:α)	trefoiled	cushion-shaped, wider than long	Cepeda & Lattig, 2016
<i>P. aurantiacus</i> Grube, 1860	Croatia (Adriatic Sea)	46	SG14	narrowly winged	MT present, with one row above MT (MF:1:0-6)	trefoiled (lateral parts blindly)	oblong, longer than wide	Glasby & Hutchings, 2014
<i>P. catalanensis</i> n. sp.	France (Mediterranean Sea)	13-15	SG15-17	narrowly winged	MT present, one crest with a very long tooth and two small lateral teeth (MF:3)	thick single medial lobe only	rectangular, longer than wide	This study
<i>P. denticulatus</i> Saint-Joseph, 1894	France (English Channel?)	12-13	SG12	narrowly winged, subdistally slightly expanded	MT present, at least on row of secondary teeth above MT (MF:1:α)	single medial lobe only	subtriangular, pointed toward mouth, longer than wide	Glasby & Hutchings, 2014; this study
<i>P. elisabethae</i> McIntosh, 1915	Scotland (North Sea)	16	SG11	winged, uniformly tapered	MT present, one row of 11-15 teeth above the MT (MF:1:11-15)	single medial lobe only	subtriangular, pointed toward mouth, wider than long	Glasby & Hutchings, 2014
<i>P. glasbyi</i> n. sp.	France (Bay of Biscay)	18-22	SG9-11	wings subdistally	MT present, two rows above MT (MF:1:α:α)	triangular (median lobe elongated)	oval, wider than long	This study
<i>P. gujanensis</i> n. sp.	France (Bay of Biscay)	28	SG15	narrowly winged	MT present, two rows above MT (MF:1:α:α)	trefoiled	oval, wider than long	This study
<i>P. idex</i> n. sp.	France (Mediterranean Sea)	14	SG8	winged	MT present, one row above MT (MF:1:α)	single medial lobe only	oblong, slightly longer than wide	This study
<i>P. latidens</i> Eliason, 1962	Skagerrak	12	SG14	winged, uniformly tapered	MT present, with 2-4 rows of one tooth above the main fang (MF:1:1:1 to MF:1:1:1:1:1)	medial only, triangular	oblong, wider than long	Glasby & Hutchings, 2014

...Continued on the next page

Tabl E 2. (Continued)

	Type locality	Number of pairs of notopodia	Start of neuropodia	Notochaetae	Uncini (type 1)	Upper lip	Lower lip	References
<i>P. medusa</i> Grube, 1850	France (Marseille)	12	SG15	two types, 1 st row winged, 2 nd row pinnate	MT present, with complete transverse series above MT (MF:1:α)	trefoiled	subtriangular pointed toward mouth	Glasby & Hutchings, 2014
<i>P. nogueirai</i> n. sp.	France (Bay of Biscay)	16–21	SG14–16	winged	MT present, two rows above MT (MF:1:α:α)	single elongated medial lobe	rounded, as wide as long	This study
<i>P. norvegicus</i> Wollebaek, 1912	Norway (North Sea)	14–20	SG10–12	winged, uniformly tapered	MT absent or present, one row of 1–4 above the main fang (MF:1–4)	single medial lobe only	shield-like, wider than long	Glasby & Hutchings, 2014
<i>P. pennarbedae</i> n. sp.	France (Bay of Biscay)	12–13	SG15–16	narrowly winged	MT present, two rows above MT (MF:1:α:α)	triangular (median lobe elongated)	oval, wider than long	This study
<i>P. plumosus</i> (Wollebaek, 1912)	Norway (North Sea)	17–19	SG18–20	two types, 1 st row winged, 2 nd row pinnate	Absence of MT, two rows above MF (MF:α:α)	single medial lobe only	subconical lobe protruding above venter, longer than wide	Glasby & Hutchings, 2014
<i>P. readi</i> n. sp.	France (Mediterranean Sea)	13–17	SG9–10	winged	MT present, two rows above MT (MF:1:α)	single medial lobe only, convoluted	oblong, as long as wide	This study

Etymology. This species is dedicated to Dr. Geoff Read for his outstanding contribution to WoRMS website and for sharing his immense knowledge on the annelida.net forum.

Habitat. 16–60 m depth, among rocks and dead leaves of *Posidonia* sp.

Type locality. Corsica Cape, Mediterranean Sea.

Distribution. Known from type locality only.

Remarks. *Polycirrus readi* n. sp. is characterized by the presence of notopodia extending on 13–17 segments and neuropodia from SG9–10, which is similar to *P. norvegicus* (notopodia on 14–20 segments neuropodia from SG10–12) and *P. elisabethae* (notopodia on 16 segments and neuropodia from SG11) (Table 2).

However, *P. readi* n. sp. differs from *P. norvegicus* by the presence of a mid-ventral groove from S3 (instead of S4 for *P. norvegicus*), of notopodia with conical postchaetal lobe (instead of digitiform lobe for *P. norvegicus*) and of uncini with a main tooth always present and secondary row of teeth above it (instead of teeth arranged in a single transverse row, with or without main tooth for *P. norvegicus*). Finally, the two species are described from very different geographical areas (North Sea for *P. norvegicus*, Mediterranean Sea for *P. readi* n. sp.).

Polycirrus readi n. sp. differs from *P. elisabethae* by the shape of lower lip (oblong and longer than wide for *P. readi* n. sp., subtriangular and wider than long for *P. elisabethae*), by the shape of ventro-lateral pads (very inflated for *P. readi* n. sp., discrete for *P. elisabethae*), by the appearance of the mid-ventral groove (from S3 for *P. readi* n. sp., from S4 *P. elisabethae*) and by the dental formula of uncini (secondary row with 4–5 teeth for *P. readi* n. sp., with 11–15 teeth for *P. elisabethae*).

Molecular data

Molecular analyses permitted to obtain 16S sequences for 10 specimens belonging to six species (Fig. 20). Until this work, only two sequences were stored in Genbank database: *Polycirrus carolinensis* Day, 1973 (Stiller *et al.* 2013) and *Amaeana trilobata* (Sars, 1863) (Stiller *et al.* 2020). Our molecular results show that *Amaeana* group is separated from all *Polycirrus* species. Moreover, *A. gremarei* n. sp. is clearly different from *A. trilobata* sampled from Norway, near to the type locality (Stiller *et al.* 2020).

Polycirrus species are well isolated from each other. *Polycirrus glasbyi* n. sp. is close to another species sampled in Arcachon Bay (*Polycirrus* sp.) but this specimen is unfortunately too damaged to permit a good identification (Fig. 20). Finally, the two Corsican species (*P. readi* n. sp. and *P. idex* n. sp.) are well separated and *P. idex* n. sp. is relatively close to *Polycirrus* cf. *denticulatus*. These sequences should facilitate the description of future new species of *Polycirrus*, especially from European waters.

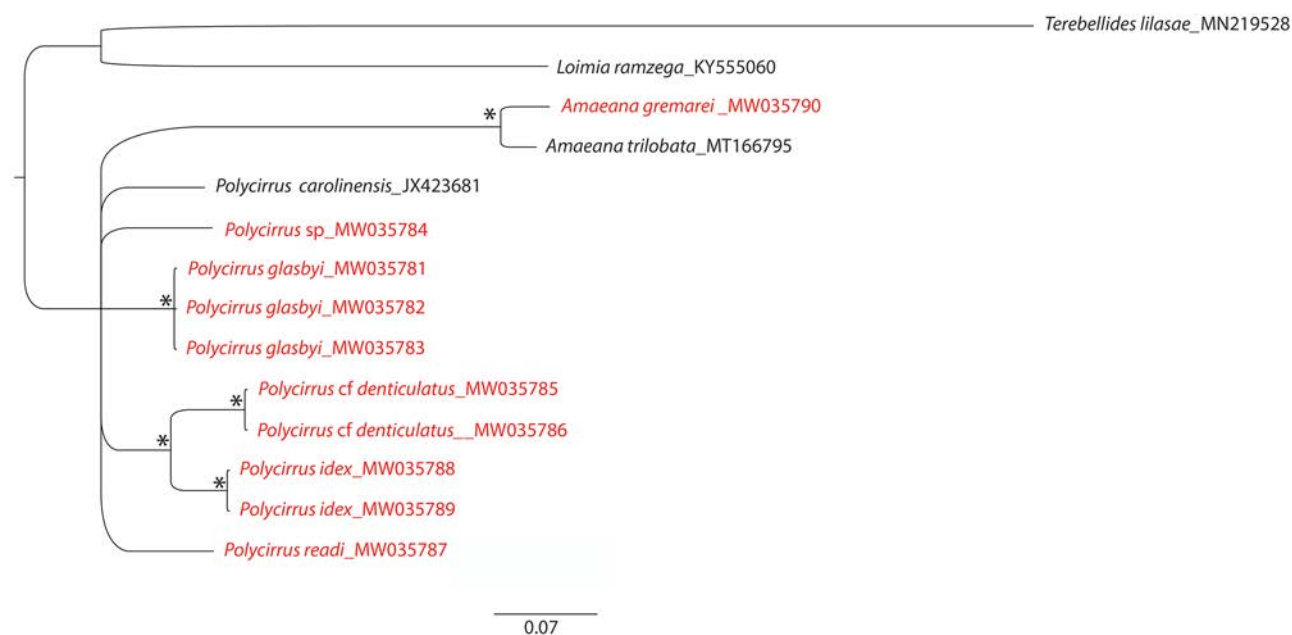


FIGURE 20. Majority-rule consensus tree from Bayesian analysis using 16S. Asterisks indicate posterior probability > 90 %. Text in red refers to specimens sequenced during this study.

Key to European species of Polycirridae

- 1A. Parapodia absent (no chaetae) *Hauchiella tribullata* (McIntosh, 1869)
 1B. Parapodia present 2
- 2A. Only notopodia present... 3 (*Lysilla*)
 2B. Notopodia and neuropodia present... 4
- 3A. Notochaetae with smooth tips, 6 pairs of thoracic nephridial papillae. *L. loveni* Malmgren, 1866
 3B. Notochaetae with plumose tips, 9 pairs of thoracic nephridial papillae *L. nivea* Langerhans, 1884
- 4A. Neuropodia with spines 5 (*Amaeana*)
 4B. Neuropodia with avicular uncini 6 (*Polycirrus*)
- 5A. Upper lip without lobe, lower lip rounded, long achaetous region *A. gremarei* n. sp.
 5B. Upper lip with three lobes, lower lip rectangular, short achaetous region *A. trilobata* (Sars, 1863)
- 6A. 28 or more segments with notochaetae 7
 6B. 22 or less segments with notochaetae. 8
- 7A. 29 segments with notopodia, neuropodia from S12, lower lip longer than wide, uncini without a main tooth above main fang *P. arenivorus* (Caulley, 1915)
 7B. 46 segments with notopodia, neuropodia from S14, lower lip longer than wide, uncini with a main tooth above the main fang *P. aurantiacus* Grube, 1860
 7C. 28 segments with notopodia, neuropodia from S15, lower lip wider than long, uncini with a main tooth above the main fang *P. gujanensis* n. sp.
- 8A. Neuropodia beginning before SG8. 9
 8B. Neuropodia beginning between SG9 and SG12. 10
 8C. Neuropodia beginning after SG13 14
- 9A. Upper lip trefoiled, lower lip wider than long, uncini with 2 rows of teeth above MT *P. asturiensis* Cepeda & Lattig, 2016
 9B. Upper lip with single medial lobe, lower lip longer than wide, uncini with 1 row of teeth above MT *Polycirrus idex* n. sp.
- 10A. Uncini without a main tooth about the main fang *P. norvegicus* Wollebaek, 1912
 10B. Uncini with a main tooth about the main fang 11
- 11A. Lower lip subtriangular, pointed toward mouth 12
 11B. Lower lip oval or oblong 13
- 12A. 12 or 13 segments with notopodia, lower lip longer than wide *P. denticulatus* Saint-Joseph, 1894
 12B. 16 segments with notopodia, lower lip wider than long. *P. elisabethae* McIntosh, 1915
- 13A. 18 or more segments with notopodia, lower lip oval, ventro-lateral pads not separated by a large mid-ventral groove. *P. glasbyi* n. sp.
 13B. Less than 18 segments with notopodia, lower lip oblong, ventro-lateral pads separated by a large midventral groove *P. readi* n. sp.
- 14A. 16 or more segments with notopodia 15
 14B. Less than 16 segments with notopodia. 16
- 15A. Neuropodia beginning from SG14–16, uncini with a main tooth above main fang. *P. nogueirai* n. sp.
 15B. Neuropodia beginning from SG18–20, uncini without a main tooth above main fang *P. plumosus* (Wollebaek, 1912)
- 16A. Neuropodia beginning from SG14, uncini with four rows of one tooth above the main fang. *P. latidens* Eliason, 1962
 16B. Neuropodia beginning from SG15 or after, secondary teeth of uncini not as above 17
- 17A. Upper lip trefoiled, lower lip subtriangular pointed toward mouth *P. medusa* Grube, 1850
 17B. Upper lip with a single median lobe, lower lip not subtriangular 18
- 18A. Upper lip with thick medial lobe, uncini with two small lateral teeth above the main tooth, lower lip rectangular longer than wide *P. catalanensis* n. sp.
 18B. Upper lip with elongated triangular medial lobe, uncini with two rows of teeth above the main tooth, lower lip oval and wider than long. *P. pennarbedae* n. sp.

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CHAPITRE 4

Révision des Terebellidae *sensu stricto*

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Revision of the French Terebellidae *sensu stricto* (Annelida, Terebelliformia), with descriptions of nine new species

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Abstract

This work is the last of four papers of the *Spaghetti Project*, aiming to revise the species of terebellids, a.k.a. “spaghetti” worms, present in the European French waters. In this last paper the Terebellidae, *sensu stricto*, from French waters are revised based, on material available in the French marine stations, type materials stored in the MNHN collection and newly collected specimens. Nine new species are described using both morphological and molecular tools: *Eupolymnia gili* n. sp., *E. lacazei* n. sp., *E. meissnerae* n. sp., *Lanice kellylateri* n. sp., *Paramphitrite dragovabeci* n. sp., *Pista labrunae* n. sp., *P. miosseci* n. sp., *P. sauriaui* n. sp., and *Terebella banksyi* n. sp. European species of *Eupolymnia* are distinguished mainly by the shape of the lateral lobes and the size of the branchial stems. The two species belonging to *Lanice* genus are distinguished by the fusion of the first ventral shields, the shape of both noto- and neuropodia, and the pigmentation of the upper lip. The two species of *Paramphitrite* are distinguished by the presence or absence of a medial dorsal gap between the pairs of branchiae, by the shape of the lateral lobes and the presence or absence of a nephridial papilla on segment 4. The different species of *Pista* are distinguished by the number of pairs of branchiae, the shape of the lateral lobes and uncini. Finally, the two species of *Terebella* are distinguished by the number of segments with nephridial and genital papillae and the segments on which the branchiae occur. An identification key for European species of Terebellidae *sensu stricto* is also provided.

Key words: *Spaghetti Project*, new species, molecular, morphology, taxonomy, systematics

Introduction

This study represents the last taxonomic paper of the “*Spaghetti Project*”, revising species of Polycirridae, Telothelepodidae, Thelepodidae, Terebellidae and Trichobranchidae present in French waters. This collaborative project has involved benthic taxonomists from all French marine stations (see Acknowledgement section), and has included newly collected material as well as material already available and deposited in the French marine stations and type materials stored in the MNHN collection. The first three papers of the project allowed us to describe nine new species of Trichobranchidae (Lavesque *et al.* 2019a), three new species of Telothelepodidae and Thelepodidae (Lavesque *et al.* 2020a), and eight new species of Polycirridae (Lavesque *et al.* 2020b). In this fourth paper, we have undertaken a comprehensive survey of the Terebellidae Johnston, 1846 *sensu stricto* (*s.s.*), as defined by recent studies (Nogueira *et al.* 2013; Hutchings *et al.* 2021a, b).

In European waters, and prior to this study, the Terebellidae *s.s.* were well represented with 18 genera and 43 species considered to be valid (Fauvel 1927; Holthe 1986; Gil 2011; Hutchings *et al.* 2021a, appendix). Among these genera, most of which were established by Malmgren (1866), seven genera are represented only by a single species in European waters: *Artacama* Malmgren, 1866; *Baffinia* Wesenberg-Lund, 1950; *Lanice* Malmgren, 1866; *Laphania* Malmgren, 1866; *Leaena* Malmgren, 1866; *Paramphitrite* Holthe, 1976 and *Terebella* Linnaeus, 1767. Nine of them are represented by two European species each: *Amphitritides* Augener, 1922; *Axionice* Malmgren, 1866; *Eupolymnia* Verrill, 1900; *Lanassa* Malmgren, 1866; *Loimia* Malmgren, 1866; *Nicolea* Malmgren, 1866; *Phisidia* Saint-Joseph, 1894; *Pistella* Hartmann-Schröder, 1996 and *Proclea* Saint-Joseph, 1894. Finally, the most diverse European genera are *Amphitrite* Müller, 1771, with ten species, and *Pista* Malmgren, 1866 with eight.

For several reasons, this last paper is definitively the most challenging of the series. Firstly, several species of Terebellidae, described by the earlier European naturalists, represent the type species of several genera, some of which present major taxonomic issues. Most of the type species of genera within Terebellidae *s.s.* were described before the 20th century (Hutchings *et al.* 2021a). These descriptions are often seen as inappropriate or incomplete in comparison to modern standards, lacking some important morphological details or illustrations (Hutchings & Lavesque 2020). Moreover, type material of these species was often lost (i.e. wars, fires, poor collection management) or simply was never deposited by early taxonomists (e.g. Clarapède, Montagu), who sometimes also provided vague or generalized type localities (Hutchings *et al.* 2021a). Consequently, incorrect names have been widely used at a European scale, with a certain number of genera represented (*a priori*) by a single species with a long list of junior synonymies, being recorded as having wide distributions. Before Fauchald suggested that polychaetes can show interesting biogeographical patterns (Fauchald 1984), there was a widespread perception that many polychaetes were widely distributed and were referred to as “cosmopolitan species” (e.g. the long list of synonyms by Hartman 1959), in part due to the inadequate original description of the species, at least by today’s standards, but in part also due to a broader and looser concept of the morphological variability of the species (Hutchings & Kupriyanova 2018, Hutchings & Lavesque 2020). Also, for many of those early described species representing the name-bearing types of distinct genera and for which no type material is known to exist, there is an increasing necessity to collect fresh material, in order to establish suitable neotypes and therefore to fully characterize these genera and stabilize the systematics of the group.

The second challenging issue concerns the reliability of the available molecular sequences. Actually, many molecular sequences belonging to Terebellidae *s.s.* are now stored in GenBank (Hutchings *et al.* 2021a), providing a useful and free of charge taxonomic tool easily accessible to the whole scientific community and general public, but not always with vouchers having been deposited to support those sequences. As highlighted in a previous study on *Marphysa sanguinea* (Montagu, 1813) by Lavesque *et al.* (2019b), many of these sequences represent misidentifications, which not only complicates the task of relating the information generated from our specimens with previously described species, but also makes determining if the new sequences could belong to potential new species difficult.

During the present study, we undertook a comprehensive survey of specimens from French waters, based on morphological analysis and supplemented by 16S and COI mitochondrial genes analyses. We identified eight genera represented by 17 species, of which nine are herein described as new. A dichotomous key for the identification of the European species of Terebellidae *s.s.* is also provided.

Material and methods

Morphological observations

Specimens were collected during different research programs and specific samplings (see Acknowledgements) along the French coasts (Fig. 1). For morphological analyses, specimens were fixed in 4% formaldehyde in filtered seawater solution, washed and then, transferred to 70% ethanol for preservation. Even if methyl green staining patterns have a low taxonomic value for Terebellidae *s.s.*, this colourant, which can be washed out, was used to improve the contrast of the photos, allowing us to correctly observe selected taxonomic characters. For the molecular studies, several parapodia were removed from several fresh specimens, or from specimens fixed in 96% ethanol.

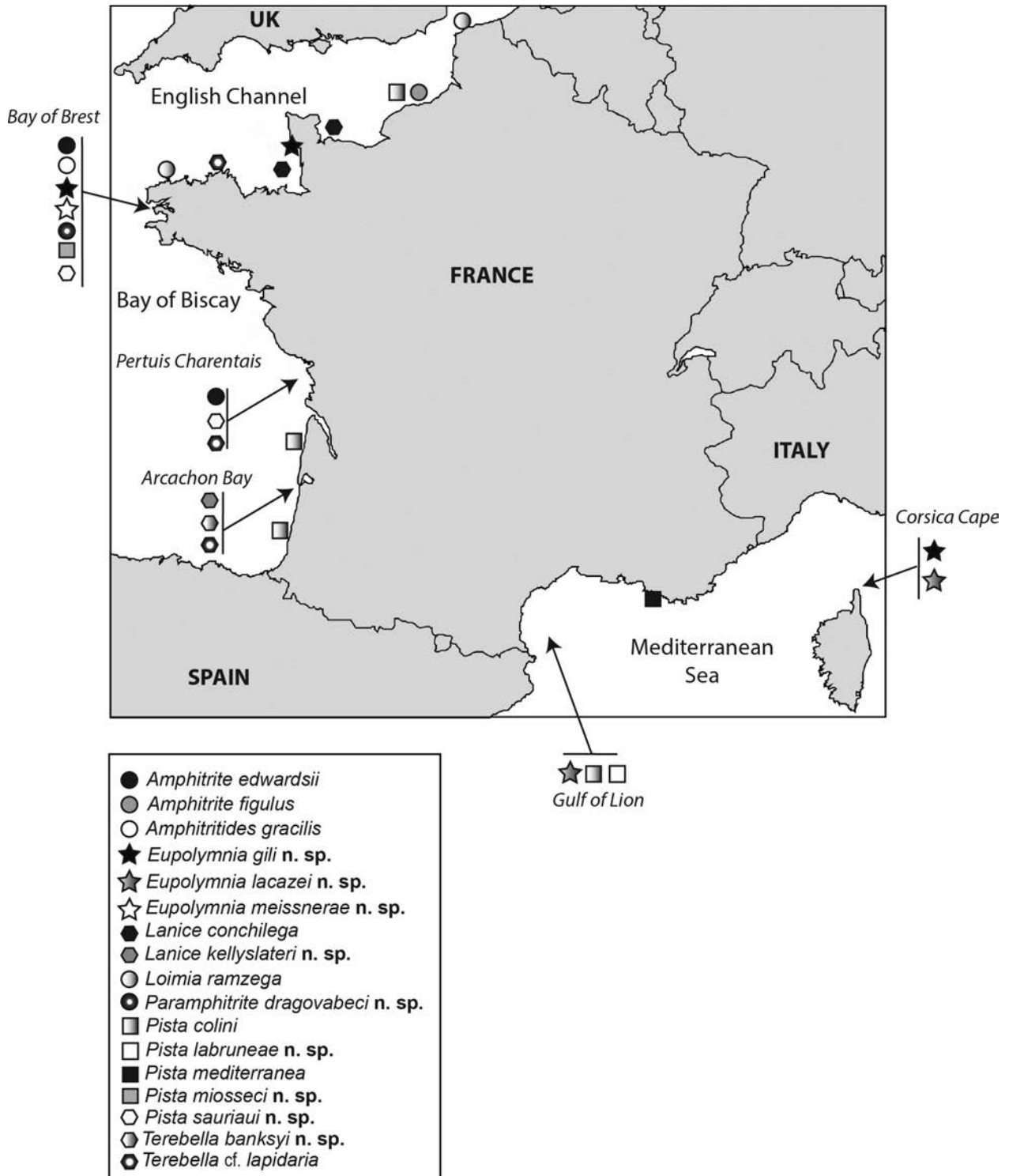


FIGURE 1. Schematic distribution of the different Terebellidae *s.s.* species along the French coasts.

Preserved specimens were examined under a Nikon SMZ25 stereomicroscope and a Nikon Eclipse *Ci* microscope, and photographed with a Nikon DS-Ri 2 digital camera. Measurements were made using the NIS-Elements Analysis software, with width corresponding to the widest thoracic region. Dehydrated specimens used for examination by scanning electron microscopy (SEM) were prepared by critical point drying, coated with gold and examined and photographed with a Hitachi TM3030 at Arcachon Marine Station.

Morphological terminology follows Nogueira *et al.* (2010) and Hutchings *et al.* (2021b), especially concerning the anterior end and the structure of the uncini (Fig. 2).

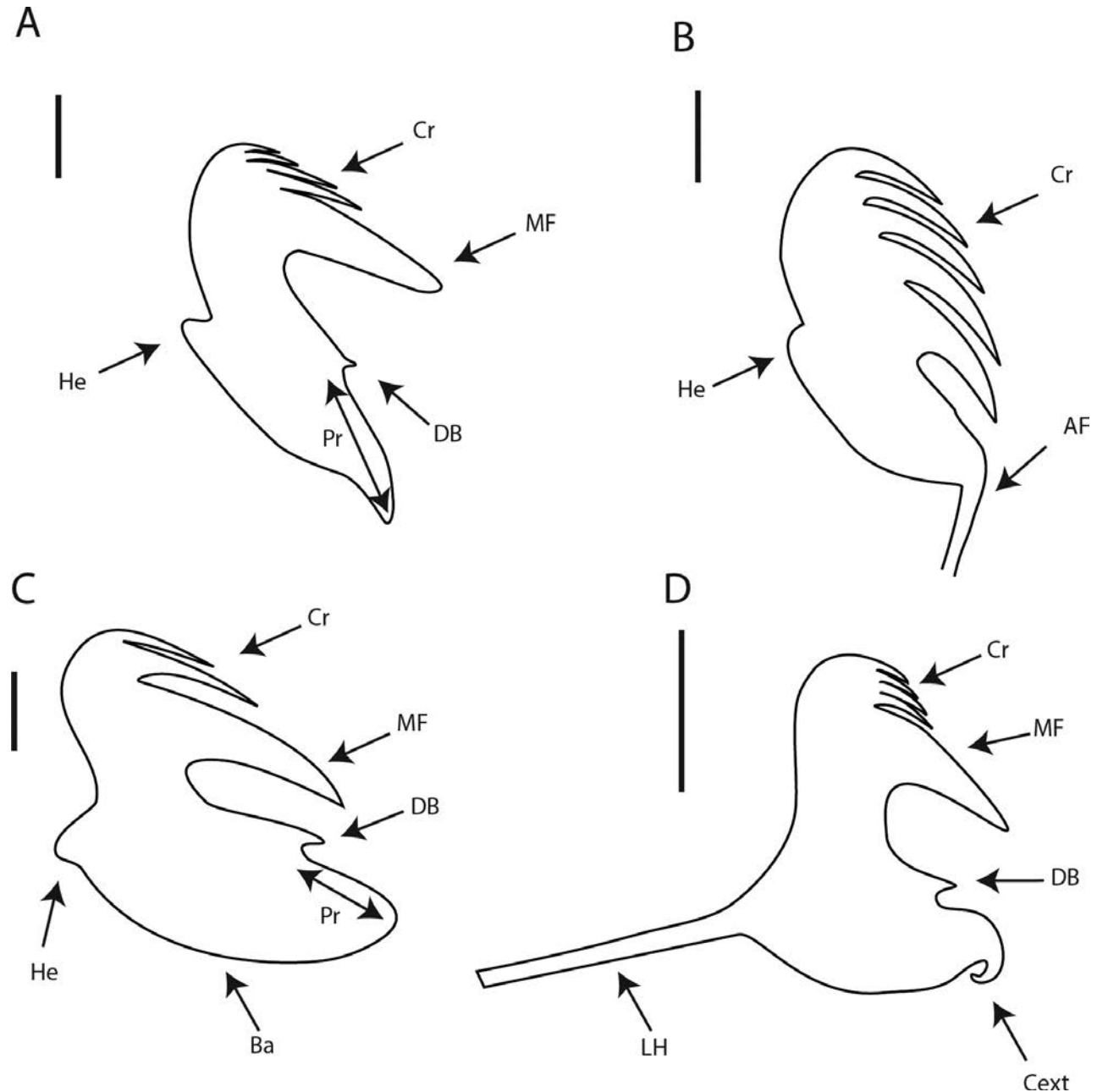


FIGURE 2. Schematic illustrations of different uncini morphologies, in lateral views (following Nogueira *et al.* 2010). A. *Terbella cf. lapidaria*, MNHN-IA-PNT 131, SG X; B. *Lomia ramzega*, paratype MNHN-IA-TYPE 1791, SG XII; C. *Eupolymnia meissnerae* n. sp., holotype MNHN-IA-TYPE 2024, SG X. D. *Pista sauriaui* n. sp., paratype MNHN-IA-TYPE 2036, SG V. Abbreviations: Af, anterior filament; Ba, base; Cext, comma-shape extension; Cr, crest; DB, dorsal button; He, heel; LH, long handle; MF, main fang; Pr, prow. Scale bars: 25 μ m.

Geographical information were obtained using a GPS in the sampling place. The geographical coordinates for specimens not involved in the collecting trips were calculated from the literature or museum information. Reproductive stages of some specimens were documented, when animals were gravid or presented well-developed genital papillae.

Descriptions of new species are based on the holotype, with paratype variations being given in brackets. Measurements provided include total length, maximum width and total number of segments, and it is also recorded if specimens are entire or incomplete. The studied material is deposited at the Muséum National d'Histoire Naturelle, Paris (MNHN) and the Australian Museum, Sydney (AM). Additional material is lodged in the collection of the Arcachon Marine Station (SMA).

Molecular data and analyses

Extraction of DNA was done with ISOLATE II Genomic DNA kit (BIOLINE) following protocol supplied by the manufacturers. The COI (cytochrome c oxidase subunit I) and the 16S genes were amplified using different primers: 16SANNF (GCGGTATCCTGACCGTRCWAAGGTA) (Sjölin *et al.* 2005) with 16SBRH (CCGGTCT-GAACTCAGATCACGT) (Palumbi 1996) for 16S rDNA; jgLCO1490 (TITCIACIAAYCAYAARGAYATTGG) and jgHCO2198 (TAIACYTCIGGRTGICCRAARAAYCA) (Geller *et al.* 2013) for COI. PCR (Polymerase Chain Reaction) occurred with Taq DNA Polymerase QIAGEN Kit in 20 µL mixtures containing: 2µL of 10X Coral-Load PCR Buffer (final concentration of 1X), 1.5 µL of MgCl₂ (25Mm) solution, 1.5 µL of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 0.4 µL of each primer (final concentration of 0.2µM), 0.1 µL of Taq DNA Polymerase (5U/µl), 1 µL template DNA and 13.1 µL of nuclease-free water. The temperature profile was as follows for 16S: 94°C/60s—(94°C/40s-59°C/30s-72°C/90s) *40 cycles—72°C/300s—16°C; for COI: 94°C/300s—(94°C/30s-50°C/15s-72°C/60s)*35 cycles—72°C/240s—16°C. PCR success was verified by electrophoresis in a 1 % p/v agarose gel stained with GelRed. Amplified products were sent to Macrogen Company and Eurofins to complete double strain sequencing, using same set of primers as used for PCR.

Overlapping sequence (forward and reverse) fragments were merged into consensus sequences and aligned using Geneious Prime 2019.0.4. All sequences obtained in this study were deposited in GenBank together with vouchers (Table 1).

Sequences were aligned in Geneious Prime 2019.0.4 using the MUSCLE plugin and default settings. The phylogenetic analysis was performed in MrBayes v3.2.6 (Ronquist and Huelsenbeck 2003) with the GTR + I + G model molecular evolution. The analysis was run for 10 million generations (sampled every 1000), 25 % of the generations were discarded as burn-in and the standard deviation of split frequencies decreased below 0.01. FigTree webserver (Rambaut 2007) was used to visualise the majority-rule consensus tree displaying all nodes with a posterior probability > 0.5.

The COI sequences of *Terebellides lilasae* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019 and *Thelepus japonicus* Marenzeller, 1884, and the 16S sequences of *T. japonicus* and *Trichobranthus glacialis* Malmgren, 1866 were used as the outgroups (Table 1).

Abbreviations and acronyms used

AM	Australian Museum (Sydney, Australia)
BMNH	British Museum of Natural History (London, UK), now called Natural History Museum.
CEMUA	Colección Estuarina y Marina Universidad de Antioquia (Medellín, Colombia)
CH	Chaetiger
LL	Lateral lobes
MNHN	Muséum National d'Histoire Naturelle (Paris, France)
MG	Methyl green
NP	Nephridial papilla
NMW	National Museum Wales (Cardiff, UK)
RESOMAR	French Marine Stations and Observatories Network
SEM	Scanning electron microscope
SG	Segment
SMA	Station Marine d'Arcachon / Arcachon Marine Station (Arcachon, France)
USNM	Smithsonian National Museum of Natural History (Washington, USA)
ZMB	Museum für Naturkunde der Humboldt-Universität (Berlin, Germany)

Table 1. Terminal taxa used in the molecular section of the study (16S and COI genes), with collection localities, voucher specimens, GenBank accession numbers and references (na, not attributed).

Species	Voucher specimen	Type locality	Collection locality	16S	COI
<i>Terebellides lilasae</i>	SMA-VOG8C-A	France, Bay of Biscay	France, Bay of Biscay		MN207183
<i>Thelepus japonicus</i>	AM W.53072	Japan	France, Arcachon Bay	MT566423	MT556446
<i>Trichobranchus glacialis</i>	SMA_Tricho_08	Norway	France, Bay of Biscay	MN219539	
<i>Amphitrite affinis</i>	SIO:BIC:A1117	Canada	Sweden	MT166820	MT167006
<i>Amphitrite figulus</i>	MNHN-IA-PNT 127	UK	France, English Channel	MZ648412	MZ622197
-	SMA-DIEP-Tere-02	-	-	MZ648413	MZ622198
-	HUNTSPOL0384	-	Canada, New Brunswick		HQ023982
-	BIOUG<CAN>:WS0006	-	Russia, Kandalaksha Bay		HM417784
<i>Amphitrite robusta</i>	BAMPOL0406	USA, Washington (State)	Canada, British Columbia		HM473490
<i>Amphitrite undevigintipes</i>	Add Mat	South Korea	South Korea		MN306311
-	-	-	-		MN306312
<i>Artacama crassa</i>	SIO:BIC:A3151	Antarctic, Bransfield Strait	Antarctic, South Sandwich Island	MT166800	
<i>Artacama proboscidea</i>	SIO:BIC:A1125	Norway, Spitsbergen	Sweden, Kostergrund	MT166801	
<i>Eupolymnia crassicornis</i>	SIO:BIC:A9446	Jamaica	Belize, Carrie Bow Cay	MT166805	MT166989
<i>Eupolymnia gili n. sp.</i>	MNHN-IA-TYPE 2021	France, English Channel	France, English Channel	MZ648407	MZ622194
-	MNHN-IA-TYPE 2020	-	-	MZ648408	MZ622195
-	AM W.53325	-	-	MZ648409	
-	SMA-BR-Eupoly-04	-	France, Bay of Brest	MZ648396	
-	SMA-BR-Eupoly-05	-	-	MZ648397	
-	SMA-COR-Tere-01	-	France, Corsica Cape	MZ648395	MZ622193
<i>Eupolymnia lacazei n. sp.</i>	AM W.53326	France, Mediterranean Sea	France, Mediterranean Sea	MZ648384	
-	SMA-COR-Tere-03	-	-	MZ648399	
<i>Eupolymnia meissnerae n. sp.</i>	MNHN-IA-TYPE 2024	France, Bay of Brest	France, Bay of Brest	MZ648410	
<i>Eupolymnia nebulosa</i>	SIO:BIC:A1080	UK, Devon	France, Mediterranean Sea	MT166806	

.....continued on the next page

Tabl E 1. (Continued)

Species	Voucher specimen	Type locality	Collection locality	16S	COI
<i>Eupolyommia rullieri</i>	SIO:BIC:A9447	Mexico, Caribbean Sea	Belize, Carrie Bow Cay	MTI 66807	MTI 66991
<i>Eupolyommia</i> sp A	SMA-COR-Thele-06	Na	France, Corsica	MZ648400	
<i>Eupolyommia</i> sp B	SMA-Arc-Eupoly-03	Na	France, Bay of Biscay	MZ648414	
<i>Eupolyommia</i> sp C	SMA-Ban-Eupoly-04	Na	France, Mediterranean Sea	MZ648385	MZ622189
<i>Eupolyommia</i> sp D	SMA-COR-Tere-02	Na	France, Corsica Cape	MZ648398	
<i>Lanassa venusta</i>	SIO:BIC:A1099	Sweden	Norway, Spitsbergen	MTI 66810	MTI 66994
<i>Lanice conchilega</i>	SMNH 81630	North Sea, Netherlands	UK, Scilly Islands	AY340466	
-	SIO:BIC:A1115	-	-		MTI 66995
-	MNHN-IA-PNT 130	-	France, English Channel	MZ648391	
-	SMA-Din-Lan-02	-	-	MZ648392	
-	SMA-New-Lan-01	-	Belgium, North Sea	MZ648389	
-	SMA-New-Lan-02	-	-	MZ648390	MZ622192
<i>Lanice kelys lateri</i> n. sp.	SMA-ARC-Leg-01	France, Arcachon Bay	France, Arcachon Bay	MZ648394	
-	SMA-Arc-Eyrac-05	-	-	MZ648393	
<i>Lanicola lobata</i>	SIO:BIC:A9450	South Australia	Australia, Tasmania	MTI 66812	
<i>Lanicola carus</i>	SIO:BIC:A9449	Belize, Twin Cays	Belize, Carrie Bow Cay	MTI 66811	MTI 66996
<i>Laphania boeckii</i>	SIO:BIC:A1095	Norway, Finnmark	Norway, Spitsbergen	MTI 66813	MTI 66998
<i>Leaena ebranchiata</i>	SIO:BIC:A1094	Norway	Norway, Spitsbergen	MTI 66814	MTI 66999
<i>Loimia bermudensis</i>	SIO:BIC:A9451	Bermuda	Belize, Carrie Bow Cay	MTI 66815	MTI 67000
<i>Loimia minuta</i>	SIO:BIC:A9452	Southern Florida	Belize, Carrie Bow Cay	MTI 66816	MTI 67001
<i>Loimia ramzega</i>	MNHN-IA-TYPE 1790	France, English Channel	France, English Channel	KY 555060	KY 555063
-	MNHN-IA-TYPE 1789	-	-	KY 555059	KY 555062
-	MNHN-IA-TYPE 1788	-	-	KY 555058	KY 555061
<i>Nicolea zostericola</i>	08PROBE-0203	Québec	Canada, Manitoba		HQ023619
<i>Pista australis</i>	AM W24390	Australia, New South Wales	Australia, New South Wales		AF342682

.....continued on the next page

Tabl E 1. (Continued)

Species	Voucher specimen	Type locality	Collection locality	16S	COI
<i>Pista colini</i>	MNHN-IA-Type 1853	France, Mediterranean Sea	France, Mediterranean Sea		MK584933
<i>Pista cristata</i>	ZMBN 116032	Norway	Norway	MG253107	
<i>Pistella lornensis</i>	SIO:BIC:A1119	Scotland	Sweden	MT166840	
<i>Axionice maculata</i>	SIO:BIC:A1097	UK	Norway, Spitsbergen	MT166803	
<i>Pista miossecci n. sp.</i>	MNHN-IA-TYPE 2033	France, Bay of Brest	France, Bay of Brest	MZ648386	
-	AM W.53330	-	-	MZ648401	
<i>Pista sauriauxi n. sp.</i>	AM W.53331	France, Bay of Brest	France, Bay of Brest	MZ648411	MZ622196
<i>Pista</i> sp A	SMA-Arc-Pista-01	Na	France, Bay of Biscay	MZ648406	MZ622191
<i>Pista</i> sp B	SMA-Cor-Pista-01	Na	France, Corsica	MZ648402	
<i>Spinosphaera hutchingsae</i>	SIO:BIC:A9455	Mexico, Caribbean Sea	Belize, Carrie Bow Cay	MT166842	MT167023
<i>Terebella</i> cf. <i>lapidaria</i>	SIO:BIC:A1102	Mediterranean Sea	UK	JX423683	JX423771
-	SMA-LR-Tere-02	-	France, Bay of Biscay	MZ648403	
-	SMA-LR-Tere-03	-	France, Bay of Biscay	MZ648404	
<i>Terebella banksyi n. sp.</i>	MNHN-IA-TYPE 2037	France, Arcachon Bay	France, Arcachon Bay	MZ648405	
-	SMA-Arc-Terebella-02	-	-	MZ648387	
-	SMA-Arc-Terebella-03	-	-	MZ648388	MZ622190

Results

Taxonomic Account

Family Terebellidae Johnston, 1846 *sensu stricto*

Genus *Amphitrite* O.F. Müller, 1771

Type species: *Amphitrite cirrata* O. F. Müller, 1776, by subsequent designation

Diagnosis (after Hutchings *et al.* 2021b).

Transverse prostomium attached to dorsal surface of upper lip; basal part as a thick crest, eyespots may be present; distal part shelf-like. Buccal tentacles all usually uniformly cylindrical. Peristomium forming lips and continuing dorsally for a short extension, not forming a complete ring; lips expanded, with relatively short upper lip, hood-like, about as long as wide, and with distal margin rounded and slightly undulated; lower lip narrow, rectangular, mid-ventral. Segment I conspicuous all around, dorsally narrow, ventrally developed, with mid-ventral lobe marginal to mouth. Lobes on anterior segments present, of variable length, usually on SG II–IV. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal shields. Two to three pairs of branchiae, usually 3, on SG II–III or SG II–IV; unbranched branchial filaments originating all together from a single point on the body wall, on either side of the branchiferous segments, or originating from a conspicuous main stem, and branching from one to several levels, in dichotomous or arborescent arrangements. Rectangular to conical notopodia beginning on SG IV, extending for 17 segments in most species, until SG XX, or with notopodia extending more posteriorly, sometimes for around 40 segments; notochaetae all broadly-winged medially and finely serrated distally. Neuropodia beginning on SG V, as low, sessile ridges in conjunction with notopodia anteriorly and as short pinnules posteriorly; neurochaetae as short-handled avicular uncini, in partially intercalated double rows, in a face-to-face arrangement, with prows aligned, from SG XI until end of notopodia. Nephridial papillae on SG III, genital papillae on some anterior segments, beginning from SG VI, between parapodial lobes.

Remarks. *Neoamphitrite* Hessle, 1917 and *Amphitrite* have long been considered as two different genera (see references in Jirkov 2020), based on the shape of branchiae (filiform arising directly from body wall in *Amphitrite*, arborescent in *Neoamphitrite*). However, Jirkov (2020) and Hutchings *et al.* (2021b) suggested that *Neoamphitrite* should be synonymized with *Amphitrite*, a synonymy previously suggested by Fauvel (1927) and Hutchings & Glasby (1988), with presence or absence of branching branchiae not being considered a valid generic character. Of the 22 species presently listed in the *Amphitrite*, only three show filiform branchiae (Jirkov 2020).

Amphitrite edwardsii (Quatrefages, 1866)

Figure 3

Terebella edwardsii Quatrefages 1866: 354, pl. XIX, fig. 1.

Amphitrite edwardsii.—Saint-Joseph 1894: 186–198, pl. VII, figs 207–208, pl. VIII, figs 209–223; Fauvel 1927: 245–246, fig. 84, a–h; Jirkov 2020: 329, figs 12–13.

Material examined. MNHN-IA-PNT 125, posteriorly incomplete, Northeastern Atlantic Ocean, Brittany, Bay of Brest, ZE4, 48°17'55"N 4°20'10"W, depth 2 m, June 2016. AM W.53322, posteriorly incomplete, Northeastern Atlantic Ocean, Brittany, Bay of Brest, ZE4, 48°17'55"N 4°20'10"W, depth 2 m, June 2016. MNHN-IA-PNT 126, complete, Northeastern Atlantic Ocean, Bay of Biscay, Pertuis Breton, B29, 46°17'33"N 1°30'57"W, depth 31 m, September 2007. AM W.53323, posteriorly incomplete, Northeastern Atlantic Ocean, Bay of Biscay, Pertuis Breton, B39, 46°15'37"N 1°24'59"W, depth 17 m, September 2007.

Description. Large specimens, with complete one being 156.4 mm long and 9 mm wide, for about 112 segments.

Prostomium at base of upper lip, eyespots absent, distal part forming shelf-like tentacular membrane from which numerous filiform and deeply grooved buccal tentacles originate (Fig. 3A–C). Peristomium forming lips; upper lip thick, hood-like, convoluted, broader than high; lower lip swollen, broader than high (Fig. 3C). Segment

I partially hidden by lobes of SG II, forming protruding lobe below lower lip (Fig. 3C–D). Segments II–IV with lateral lobes; SG II with small lobes, connected ventrally; SG III–IV with well-developed auricular lateral lobes, more dorsal on SG IV (Fig. 3C–D).

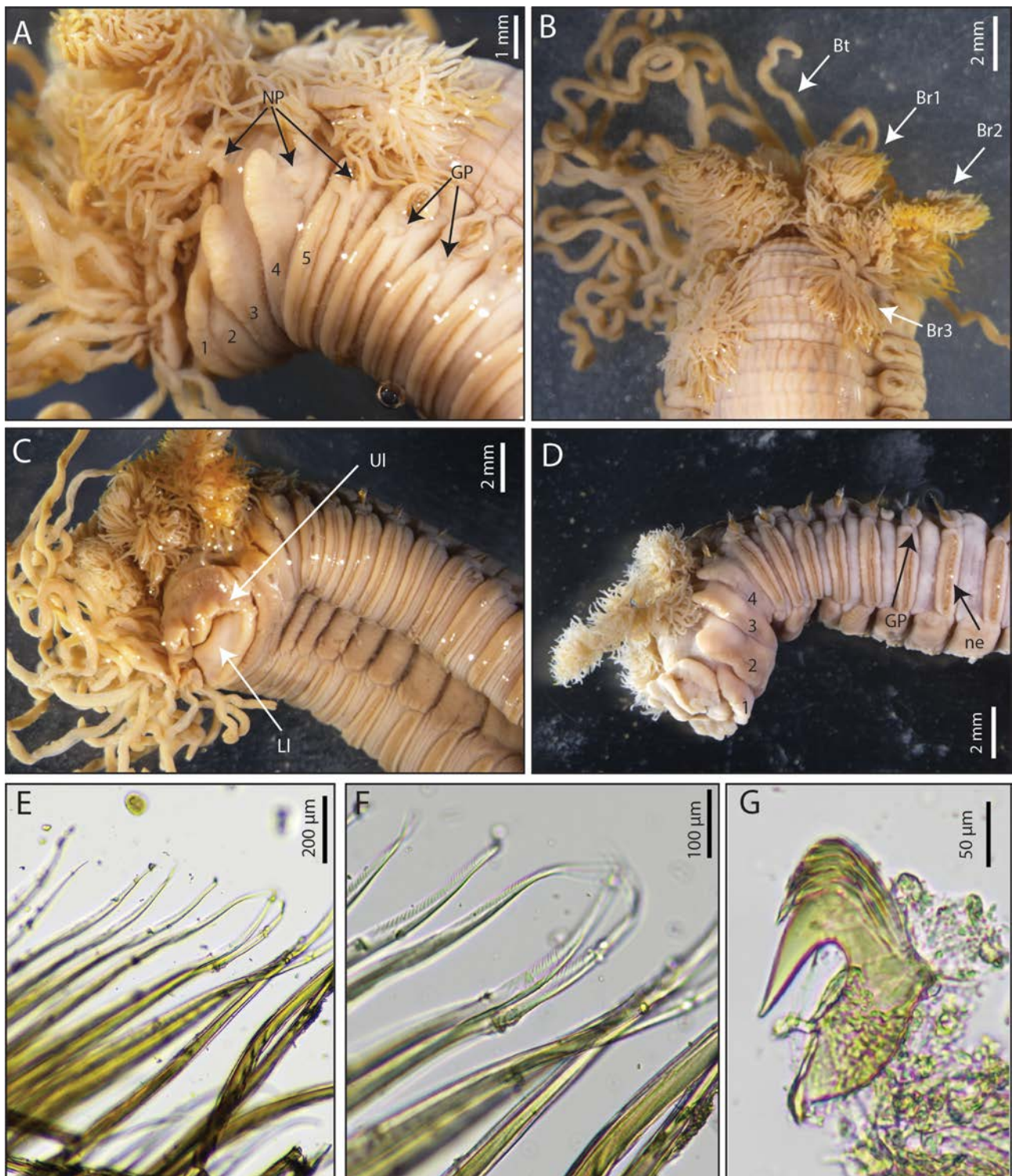


FIGURE 3. *Amphitrite edwardsii* (Quatrefages, 1866) MNHN-IA-PNT 126 (A–C), MNHN-IA-PNT 125 (D), AM W.53322 (E–G). A. Anterior end, lateral view; B. Anterior end, dorsal view; C. Anterior end, ventral view; D. Anterior end, lateral view; E. Notochaetae, SG X; F. Notochaetae of the first row, SG X; G. Uncinus, SG X. Abbreviations: Br, branchiae; Bt, buccal tentacles; CP, genital papillae; LI, lower lip; NP, nephridial papilla; ne, neuropodia; UI, upper lip. Numbers referring to segments.

Three pairs of dichotomous branchiae, on SG II–IV, with wide medial gap (Fig. 3B); second pair inserted more laterally than first and third pairs; with numerous filaments, arising from long annulated stems (Fig. 3A–D). Dorsum of anterior chaetigers tessellated (Fig. 3B). Nine ventral shields, rectangular to trapezoidal, broader than long, present on SG III–XI, fused on SG II–III (Fig. 3C); thereafter shields replaced by mid-ventral groove extending to pygidium (see Morphological variation section).

Notopodia short, rectangular, present on SG IV–XX. Notochaetae slightly curved, medially winged, with wings of same width, and distally serrated; two rows of chaetae, with anterior row about half as long as those on posterior row (Fig. 3E–F).

Neuropodia from SG V, with uncini arranged in single rows on SG V–X, uncini in double rows on SG XI–XX, in a face-to-face arrangement, and in single rows again afterwards; thoracic neuropodia as low ridges (Fig. 3A, C–D), situated latero-ventrally, some neuropodia with undulating margin (see Morphological variation section) (Fig. 3D); abdominal neuropodia raised from the body and displaced more laterally. Uncini avicular, with short triangular heel, distally pointed prow, pointed dorsal button inserted at about halfway between base of main fang and tip of prow, slightly convex base; and crest with four rows of secondary teeth above a distally pointed main fang (Fig. 3G).

Nine pairs of nephridial and genital papillae present on SG III–XI (Fig. 3A), with first pair situated above LL2 (not seen in Fig. 3A); second pair above LL3; third pair between LL4 and first notopodia, posteriorly; subsequent pairs between noto- and neuropodia. Nephridial papillae (on SG III–V) elongated, with first one the longest, clearly geniculate, small and globular genital papillae from SG VI–XI (Fig. 3A).

Pygidium rounded, slightly crenulated.

Morphological variations. The presence of a ventral groove following the ventral shields seems to be dependent on the fixation process. Indeed, this groove is present and well marked on specimens from the Pertuis Charentais, but absent on specimens from Brittany. Similarly, the presence of undulating margins of neuropodia could be also linked to the fixation process, as they are not present on all specimens observed.

Type locality. Saint-Vaast (Normandy, France), approx. 49°35'45"N 1°15'50"W.

Type material. The single type specimen available was lost, according to Quatrefages (1866).

Distribution. Bay of Biscay (Saint-Joseph 1894, this study) (Fig. 1), English Channel (Saint-Joseph 1898), Ireland, Arctic Sea (Fauvel 1927), from Scotland to Portugal (Jirkov 2020), Mediterranean Sea, Adriatic Sea, Aegean Sea, Gulf of Mexico, Puget Sound, Japan (Gil 2011), Falkland Islands, British Columbia (Jirkov 2020). As proposed by Jirkov (2020), all records outside southern boreal Europe should be considered as doubtful.

Habitat. Mud to muddy sands (this study; Fauvel 1927; Gil 2011), in *Zostera* meadow (Fauvel 1927; Gil 2011), shallow waters to 30 m (this study; Gil 2011).

Remarks. Quatrefages (1866) described this species based on a single specimen, collected at low tide at Saint-Vaast (Normandy, France). Unfortunately, the holotype was lost during its study and the description was sparse and incomplete and incomplete. According to Quatrefages, the most notable characteristic is the position of the branchiae, with the second pair being positioned more laterally than the first and third pairs, giving the appearance of a “star” when seen dorsally (Fig. 3B; see also Quatrefages 1866: pl. XIX, fig. 1). As for many species of Terebellidae described in the 19th century, characters now known to be important were not described, and a neotype needs to be designated in the future, and ideally with associated molecular data.

French specimens match the specimens studied by Jirkov (2020) from Ireland and Orkney, although his description is relatively short and lacks details about the position of the branchiae. The only difference concerns the size and shape of the nephridial papillae being described as longer and the first one clearly geniculate in the French specimens instead of being all of the same size.

***Amphitrite figulus* (Dalyell, 1853)**

Figure 4

Terebella figulus Dalyell, 1853: 191–197, pl. XXVII figs 1–2, pl. XXVIII figs 1–2.

Amphitrite johnstoni.—Fauvel 1927: 248–249, fig. 85, a–g.

Neoamphitrite figulus.—Holthe 1986: 100–101, fig. 42.

Amphitrite figulus.—Jirkov 2020: 330, fig. 1c, 14–15.

Other synonym. *Amphitrite stimpsoni* Meyer 1912.

Material examined. MNHN-IA-PNT 127, posteriorly incomplete, English Channel, Dieppe, 49°55'5"N 1°04'28"E, intertidal, May 2020, posterior part used for molecular analysis. SMA-DIEP-Tere-02, posteriorly incomplete, English Channel, Dieppe, 49°55'5"N 1°04'28"E, intertidal, May 2020, posterior part used for molecular analysis. AM W.53324, complete, English Channel, Dieppe, 49°55'5"N 1°04'28"E, intertidal, May 2020, few parapodia used for SEM (plot SMA-DIEP-Tere-04).

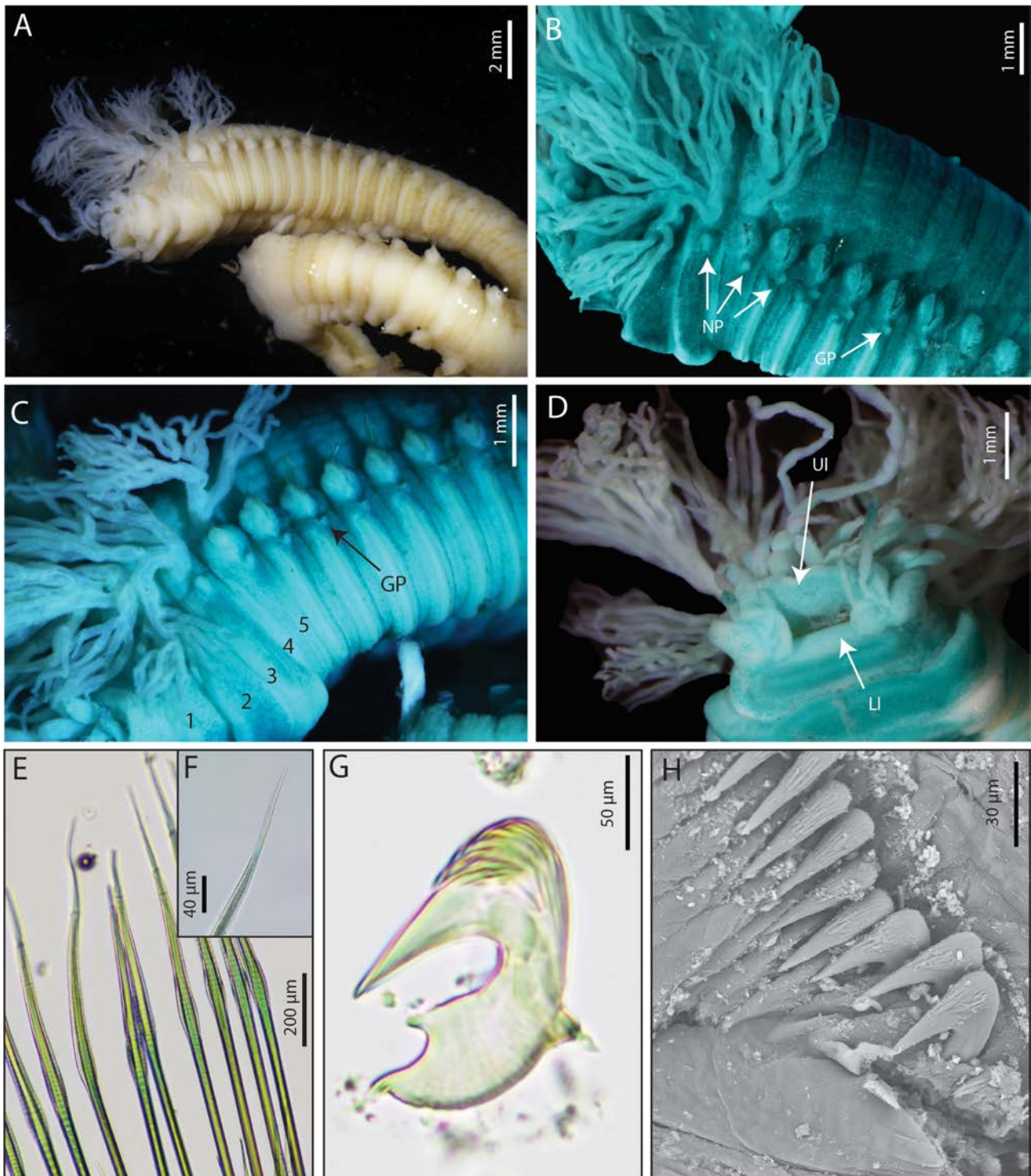


FIGURE 4. *Amphitrite figulus* (Dalyell, 1853) MNHN-IA-PNT 127. A. Anterior end, latero-ventral view; B. Anterior end, lateral view, MG staining; C. Anterior end, lateral view, MG staining; D. Anterior end, ventral view; E. Notochaetae, SG XVI; F. Tip of notochaetae, SG VII; G. Uncinus, SG VIII; H. Uncini, SG X. Abbreviations: GP, genital papillae; LI, lower lip; NP, nephridial papilla; UL, upper lip. Numbers referring to segments.

Description. Moderate-sized specimens, complete one being 47.9 mm long and 4.7 mm wide, for about 155 segments.

Prostomium at base of upper lip, without eyespots, distal part forming shelf-like tentacular membrane from which numerous filiform, wrinkled and deeply grooved buccal tentacles originate (Fig. 4B, D). Peristomium forming lips; upper lip thick, hood-like, convoluted, broader than high; lower lip swollen, broader than high (Fig. 4D). Segment I clearly visible, forming protruding lobe below lower lip. Segments II–III with small ventro-lateral lobes, SG IV without lateral lobes (Fig. 4A–C).

Three pairs of dichotomous branchiae, on SG II–IV, with wide medial gap; first pair the longest, situated slightly more dorsally; with numerous long filaments, arising from short stems (Fig. 4A–C). Dorsum of anterior chaetigers tessellated. Eleven ventral shields, rectangular, broader than long, present on SG III–XIII (Fig. 4A); absence of mid-ventral groove.

Notopodia short, rectangular, present on SG IV–XXVII (n=24). Notochaetae almost straight, medially winged with wings of same width, and distally serrated (Fig. 4E–F); two rows of chaetae, those of anterior row less than half as long as those of posterior row.

Neuropodia beginning from SG V, with uncini arranged in single rows on SG V–X, uncini in double rows on SG XI–XXV or XXVI, in a face-to-face arrangement, and in single rows again from SG XXVI–XXVII; thoracic neuropodia as low ridges, situated latero-ventrally (Fig. 4B–C); abdominal neuropodia raised from body and displaced more laterally (Fig. 4A). Uncini avicular, with short triangular heel, with distally pointed prow, large pointed to digitiform dorsal button inserted halfway between base of main fang and tip of prow, convex base; and crest with five rows of secondary teeth above main fang (Fig. 4G–H).

Fifteen pairs of small globular nephridial and genital papillae present on SG III–XVII (Fig. 4B–C), first pair situated above base of second pair of branchiae, second pair below first notopodia and slightly displaced dorsally, subsequent pairs between noto- and neuropodia, slightly displaced dorsally. Nephridial papillae (first three pairs) larger than genital ones (from SG VI), last pairs difficult to observe.

Pygidium rounded.

Type locality. Probably North Sea coast of Scotland (Gil 2011).

Type material. Could not be traced (Holthe 1986, Jirkov 2020).

Distribution. In Europe, from Norwegian Sea to Aegan Sea (Gil 2011) and White Sea (GenBank accession number: HM417784) (Fig. 26). In France, from North Sea to Bay of Biscay (Fauvel 1927; Jirkov 2020, this study, Resomar database). Also recorded from Canada, Japan, Gulf of Mexico and Sea of Okhotsk (Gil 2011) but all these records have to be considered as doubtful. Mediterranean records could also correspond to misidentifications of *Amphitrite rubra* (Risso, 1826) (see Jirkov 2020).

Habitat. In empty shells in deep water, among rocks in shallow intertidal pools, on mud or sandy mud, among *Zostera*, *Fucus* or *Laminaria*, on mussel and oyster banks (Gil 2011), in mud (this study), upper sublittoral to intertidal (this study, Jirkov 2020). This range of different habitats/depths suggests that these records may represent more than one species.

Remarks. The original description is not sufficiently informative according to current standards, consisting of a mixture of behavioural considerations and morphological data. Specimens examined in our study match those of the description provided by Fauvel (1927, specimens from French coasts), and the description of *Amphitrite johnstoni* Malmgren, 1866, by Holthe (1986, specimens from Scandinavia) and by Jirkov (2020, specimens from White Sea and UK, and also from the Western Pacific). Obviously a detailed review of this species is required including the re-examination of material from all the above localities.

Genus *Amphitritides* Augener, 1922

Type-species: *Terebella gracilis* (Grube, 1860), by subsequent designation.

Diagnosis. (after Hutchings *et al.* 2021b). Transverse prostomium attached to dorsal surface of upper lip; basal part as a thick crest, eyespots may be present; distal part shelf-like. Buccal tentacles usually all uniformly cylindrical. Peristomium forming lips and continuing dorsally for a short extension, not forming a complete annulation; lips expanded, relatively short upper lip, hood-like, about as long as wide, distal margin rounded, slightly undulated;

narrow, rectangular, mid-ventral lower lip. Segment I conspicuous all around, dorsally narrow, ventrally developed, with mid-ventral lobe marginal to mouth; additional lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal shields. Two pairs of arborescent branchiae, on SG II–III, with short main stems. Rectangular to conical notopodia beginning on SG IV, extending for a variable number of segments; notochaetae all medially-winged and finely serrated distally, with basally bulbous wings. Neuropodia beginning on SG V, as low, sessile ridges throughout; neurochaetae as short-handled avicular uncini, in completely separate double rows, beak to beak arrangement, from SG XI until posterior body. Nephridial papillae on SG III, genital papillae on some anterior segments, beginning from SG VI, between parapodial lobes or at anterior bases of notopodia.

Remarks. Recently, Jirkov (2020) proposed the synonymisation of *Amphitritides* with *Amphitrite*, arguing that characters such as the number of pairs of neuropodia with double rows of uncini is not unique to species of *Amphitritides*, but can be also present in species of *Amphitrite*. This is a character highly significant in terms of convergence in the family, and so it could be exhibited by some other genera besides these two. On the other hand, the structure of the lateral lobes is poorly understood in the whole family, and there is a great deal of misinterpretations regarding the shape, structure and orientation of the lateral lobes vs. the lateral ridges. Our suggestion is that *Amphitritides* has no lobes (except mid-ventral one on SGI, as described in the diagnosis), and which clearly differentiates it from *Amphitrite*, which has lobes on anterior segments, of variable length, usually on SG II–IV. It is clear, however, that the diagnosis of a genus is not based on a unique character that distinguishes it from the rest, but on a combination of characters, which defines the genus. It is also clear that a major revision of this group of genera, based on type material, if available, and fresh topotype material, is required in order to solve the relations within this group using both morphological and molecular data.

Amphitritides gracilis (Grube, 1860)

Figures 5 and 6

Terebella gracilis. Grube 1860: 99.

Amphitrite gracilis.—Saint-Joseph 1894: 198–201, pl. VIII, figs. 224; Fauvel 1927: 252–253, fig. 87, a–e; Jirkov 2020: 332–334, figs 2B, 16–17.

Amphitritides gracilis.—Holthe 1986: 104–106, fig. 45; Arvanitidis & Koukouras 1995: Table 1.

Other synonyms. *Physelia scylla* Quatrefages, 1866; *Terebella gelatinosa* Keferstein, 1862; *Terebella laevirostris* Claparède, 1869.

Material examined. MNHN-IA-PNT 128, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, Bay of Brest, 48°21'54"N 4°26'00"W, depth 5 m, February 2013. SMA-BR-Amphi-01, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, Bay of Brest, 48°21'54"N 4°26'00"W, depth 5 m, February 2013, mounted for SEM.

Description. Small specimens, all incomplete, largest specimen 14.7 mm long and 1.9 mm wide, for 33 segments.

Prostomium at base of upper lip without eyespots, distal part forming a shelf-like tentacular membrane from which long, thin and non-grooved buccal tentacles originate (few remaining) (Fig. 5B), continuing ventrally as a thin lobe (Fig. 5C). Peristomium forming lips; upper lip, hood-like, broader than high; lower lip swollen, very glandular and ridged, slightly broader than high (Figs 5A, C; 6A–B).

Segment I dorsally narrow, more developed ventrally, forming protruding lobe below ventral lobe of prostomium and lower lip (Fig. 5C). Segments II–IV without lateral lobes (Figs 5A–B; 6A–B). Ventral shields on SG II–XII (n=11), rectangular, wide and thin, shields separated by deep incision (Fig. 5C); replaced by groove posteriorly.

Two pairs of short, arborescent branchiae on SG II–III, both pairs with short, thick main stem, with dichotomous ramifications starting from close to base and ending with short wrinkled filaments (Fig. 5D); the two pairs inserted dorso-laterally, at the level of the following notopodia (Fig. 6A–B).

Notopodia beginning from SG IV and extending for 19 segments. Notopodia well-developed, approximately rectangular, all similar in size, first two pairs aligned more dorsally, laterally aligned from SG VI (Figs 5A–B; 6A–B). Notochaetae in two rows with symmetrical limbation and curved serrated tips, first row shorter (Fig. 5E–F).

Neuropodia starting from SG V, thoracic neuropodia as long lateral ridges slightly raised from surface of body,

not reaching ventral groove (Figs 5B–C; 6A–B); abdominal neuropodia as short fleshy ridges, close to mid ventral groove. Uncini arranged in double rows from SG XI until end of body, in a face-to-face arrangement, with rows completely separated from each other. Uncini avicular, with short triangular heel, distally pointed prow downwardly directed, short dorsal button inserted halfway between base of main fang and tip of prow, convex base, and main fang surmounted by crest of five rows of secondary teeth (Figs 5G; 6C–D).

Nephridial and genital papillae on SG III and SG VI–XII, inserted laterally and slightly anteriorly to branchial stem on SG III, and anteriorly to base of notopodia on SG VI–XII (NP).

Pygidium not seen.

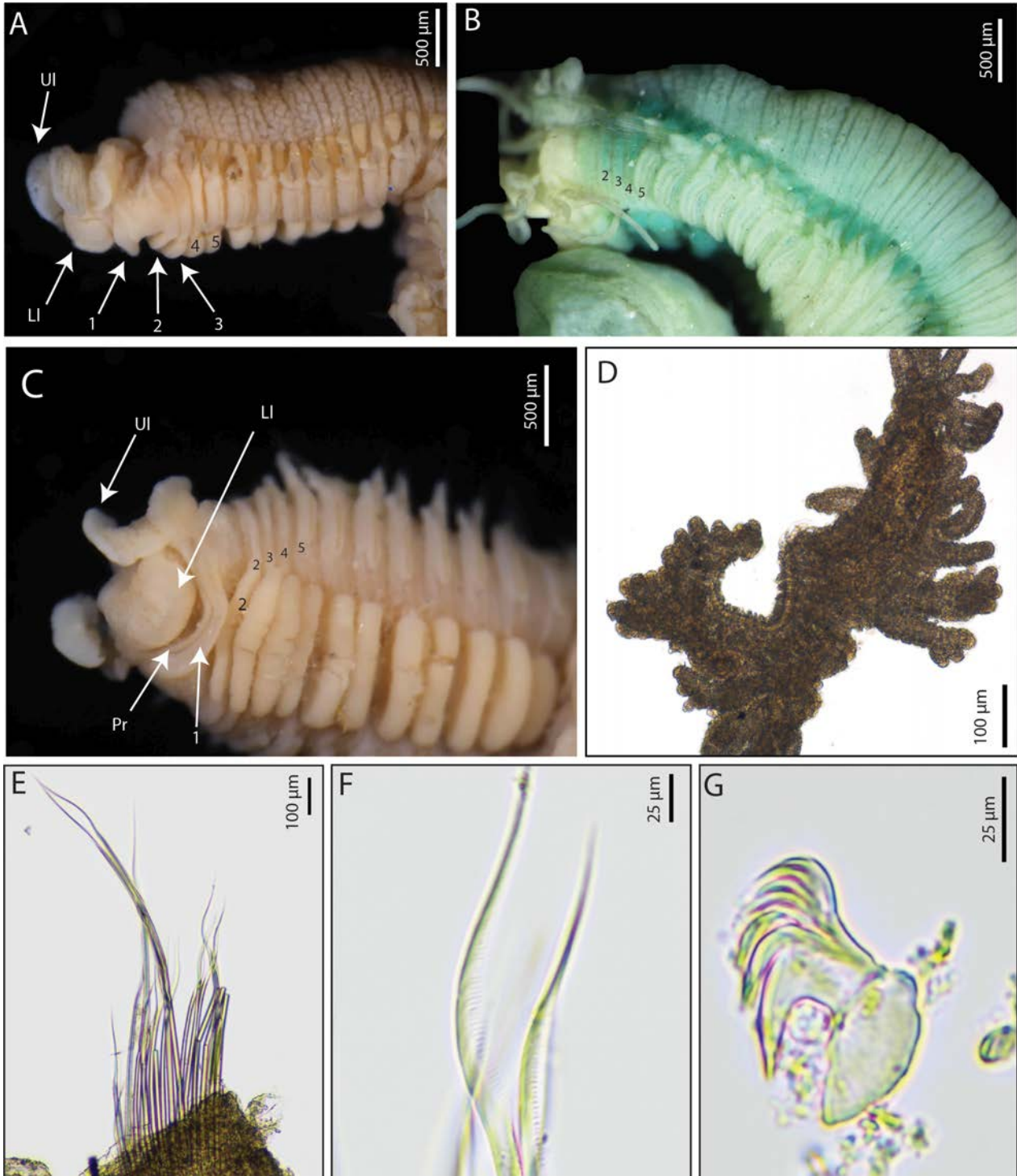


FIGURE 5. *Amphitritides gracilis* (Grube, 1860) MNHN-IA-PNT 128 (A, C, E–G), SMA-BR-Amphitritides-01 (B, D). A. Anterior end, lateral view; B. Anterior end, lateral view, MG staining; C. Anterior end, ventral view; D. Branchia; E–F. Notochaetae, SG XV; G. Uncinus, SG XV. Abbreviations: LI, lower lip; Pr, prostomium; UL, upper lip. Numbers referring to segments.

Type locality. Scilly Isles, off southwest England, approx. 49°56'02"N 6°18'44"W.

Type material. ZMB Q.5045, 2 syntypes.

Distribution. Along all the French coasts (Fauvel 1927, this study, Resomar database). In Europe, from Scotland to Black Sea (Gil 2011; Jirkov 2020). Also recorded from Ivory Coast (Holthe 1986), but this record is considered to be doubtful.

Habitat. Shallow waters, in maërl (rhodolith) beds (this study), soft muddy bottoms and sandy mud, under stones and among *Posidonia*, *Zostera* and algae, eulittoral to 80 m (Fauvel 1927; Holthe 1986; Gil 2011).

Remarks. Our material corresponds closely to the recent description by Jirkov (2020), including the variation in the number of nephridial papillae and notopodia (specimens from UK and Black Sea).

Two morphological differences can be perceived between the present description and the data by Arvanitidis & Koukouras (1995: Table 1, based on the original descriptions and French specimens from the “Collection des Polychètes d’Angers”). Indeed, our specimens, and those of Jirkov, do not show any eyespots (which may fade with time when stored in alcohol), and they also show “rugose” branchial tips, i.e. wrinkled (as in *A. kuehlmanni* Arvanitidis & Koukouras, 1995). This last character was not described by Jirkov (2020) and could be related to method of fixation.

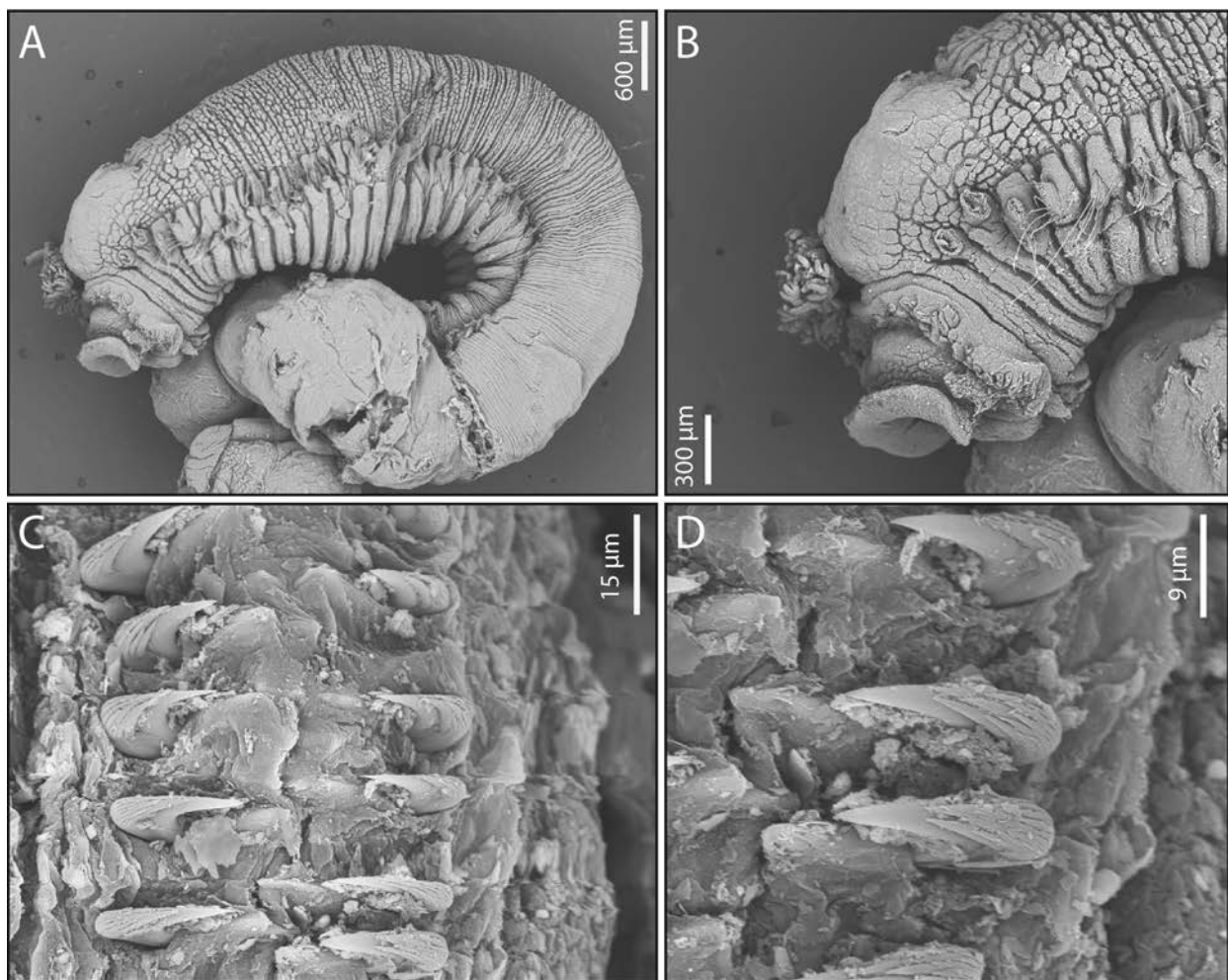


FIGURE 6. *Amphitritides gracilis* (Grube, 1860) SMA-BR-Amphitritides-01, SEM. A–B. Anterior end, lateral view; C–D. Uncini, SG XIV.

Genus *Eupolymnia* Verrill, 1900

Type-species: *Terebella danielsseni* Malmgren, 1866, by monotypy.

Diagnosis. (after Hutchings *et al.* 2021b). Prostomium transverse, attached to dorsal surface of upper lip; basal

part as a thick crest, eyespots usually present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to expanded lips; relatively short upper lip, hood-like, wider than long, distal margin rounded, frequently undulated; lower lip button-like, mid-ventrally, almost completely covered by lobes of SG I. Segment I conspicuous all around, dorsally narrow, with pair of low ventro-lateral lobes connected to each other by mid-ventral lobe marginal to mouth. Segments II–IV with pairs of progressively shorter and more laterally inserted lobes, those on SG II ventro-lateral and frequently connected to each other by low collar-like lobe across ventrum. Anterior segments highly glandular ventrally, with discrete rectangular shields, anterior shields frequently corrugated. Three pairs of branchiae, on SG II–IV, each one with a single short and thick main stem, dichotomously branching to short distal filaments. Conical to roughly rectangular notopodia from SG IV, extending 17 segments, until SG XX; notochoetae all narrowly-winged, wings slightly broader basally on one side and with smooth tips. Neuropodia beginning on SG V, as low, sessile ridges in conjunction with notopodia as conical to rectangular pinnules posteriorly; neurochaetae as short-handled avicular uncini, in completely intercalated double rows in face-to-face arrangement from SG XI until end of notopodia. Nephridial and genital papillae present, from SG II or III, extending for few anterior segments, between parapodial lobes or equivalent position on anterior segments. Pygidium crenulate to papillate.

Remarks. Currently, only two valid species (but with long lists of synonymized species) of this genus occur in European waters, both without any extant type material: *Eupolyornia nesidensis* (Delle Chiaje, 1828) (described from Gulf of Naples, Italy) and *Eupolyornia nebulosa* (Montagu, 1819) (described from Cornwall, UK). The main problem with these two species is that in spite of being widely referred to in the taxonomic literature and used in dichotomous keys, we do not believe that there is a good recent morphological description of any of them as both of the original descriptions are brief. For example, following Holthe (1986), *E. nebulosa* would have “anterior branchiae with long stems” and a “buccal segment forming a broad cushion-like lip”, but this author only observed specimens from Norway. After examination of several specimens from near the type locality (Cornwall, UK), Hutchings & Glasby (1988) concluded that this species has “branchiae with virtually no main stalk” and “peristomium expanded as a discrete narrow elongated raised ventral collar”, though, knowing that there are other species present in the area (as shown in this study) it is possible that the studied material could also belong to a different species. Capa & Hutchings (2006) after observing two specimens sampled close from the type locality (AM W.200882 and BMNH ZK 1950.6.6.21) provided more details concerning this species: presence of 10 ventral shields, branchiae with no stalk and few branches, small spherical lateral lobes on SG II and IV, bilobed on SG III, dental formula of uncini MF:2:3 with dorsal button in the middle of uncini. This species has been widely reported because of its particular “strawberry” colour (e.g. Fauvel 1927) but at least two other species (and probably more) seem to exhibit this pattern of red colour with white spots (see below). Concerning *E. nesidensis*, Delle Chiaje (1828) briefly wrote that the species was yellow, with three pairs of red arborescent branchiae and with parapodia bearing chaetae. There is also a variety, differing from the former by its green colour, the yellowish-red branchiae and the thinner body (Delle Chiaje, 1828). Until a neotype from the Gulf of Naples is selected and described, it is recommended that this name should not be used.

Eupolyornia gili n. sp.

Figure 7

Material examined. Holotype. MNHN-IA-TYPE 2020, complete specimen, gravid, English Channel, Blainville-sur-Mer, 49°04'20"N 1°39'06"W, low intertidal, February 2020, few posterior parapodia used for molecular analysis. **Paratypes.** MNHN-IA-TYPE 2021, one posteriorly incomplete specimen, English Channel, Blainville-sur-Mer, 49°04'20"N 1°39'06"W, lower intertidal, February 2020, few parapodia used for molecular analysis, mounted for SEM. AM W.53325, one posteriorly incomplete specimen, English Channel, Blainville-sur-Mer, 49°04'20"N 1°39'06"W, low intertidal, February 2020, few posterior parapodia used for molecular analysis.

Additional material. SMA-BR-Eupoly-04, one specimen posteriorly incomplete, Northeastern Atlantic Ocean, Brittany, Bay of Brest, 48°21'28"N 4°26'38"W, depth 7 m, May 2018, posterior part used for molecular analysis. SMA-BR-Eupoly-05, one posteriorly incomplete specimen, Northeastern Atlantic Ocean, Brittany, Bay of Brest, 48°21'28"N 4°26'38"W, depth 7 m, May 2018, posterior part used for molecular analysis. SMA-COR-Tere-01, one posteriorly incomplete specimen, Mediterranean Sea, Corsica Cape, 42°47'12"N 9°19'48"E, depth 41 m, May 2019, posterior part used for molecular analysis.

Description. In life, red body covered by with white spots, including branchial stems and branches, buccal tentacles pinkish, prostomial eyespots black (Fig. 7A).

Large sized species, holotype complete 82.5 mm long and 6.8 mm wide (4.1–7.2 mm) for about 100 segments. Transverse prostomium attached to dorsal surface of upper lip; basal part with continuous row of red or black eyespots, without mid-dorsal gap, with eyespots well separated from each other (Fig. 7A–B); distal part forming a shelf-like tentacular membrane; buccal tentacles thick and grooved (Fig. 7A). Peristomium forming lips; hood-like upper lip, rectangular, wider than long with convoluted margin; lower lip swollen, wider than high (Fig. 7C).

Arborescent branchiae present on SG II–IV, first pair the longest, situated slightly more dorsally, third pair the shortest, situated more laterally; with short and thick branchial filaments, branching dichotomously from long basal stem (Fig. 7A–C).

Segment I well visible, ventrally developed, forming ventral lobe below lower lip (Fig. 7B–C). Three pairs of thick, translucent lobes on SG II–IV; SGII with one pair of short rounded ventro-lateral lobes, dorsal margins aligned with ventral edges of following neuropodia; SGIII and IV with short semi-circular lateral lobes, about the same size, situated progressively more dorsally, lobes of SG IV almost aligned with neuropodia of SG V (Fig. 7A–C).

Anterior segments with glandular, trapezoidal, slightly corrugated anteriorly to smooth mid-ventral shields, on SGII–XVII, last three shields distinctly shorter and hexagonal; mid-ventral groove extending posteriorly from SG XVII (Fig. 7D).

Rectangular notopodia beginning from SG IV, extending for 17 segments, until SG XX, laterally aligned, notopodia of first two pairs shorter and dorsally directed (Fig. 7A–C). Narrowly-winged notochaetae in two rows, first row shorter (Fig. 7E).

Neuropodia present from SG V, as low ridges until end of notopodia (Fig. 7B–C), as rectangular pinnules with pointed dorsal tip thereafter (Fig. 7D). Neurochaetae throughout as short-handled avicular uncini, arranged in completely intercalated double rows on SG XI–XX in a face-to-face arrangement. Uncini with well-developed digitiform heel and rounded prow, pointed dorsal button inserted closer to prow than to base of main fang, elongate convex base, and main fang surmounted by a crest with a first row of two large teeth, and a second row with one large middle tooth and several small teeth (Fig. 7F–G).

Nephridial papillae on SG III–V, inserted posteriorly to bases of branchiae and dorsally to notopodia; genital papillae on SG VI–IX, as openings between parapodial lobes, inserted posteriorly to notopodia (Fig. 7B).

Pygidium discoidal, surrounded by short papillae.

Tube made of coarse sand.

Etymology. This species is named after João Gil, an excellent polychaete taxonomist, in recognition of his work on European Fauna of Polychaeta. His thesis is undoubtedly the best reference to correctly identify French worms since Fauvel (1927). This species name was given in agreement with Anne-Laure Janson, Benoit Gouillieux, Vincent Le Garrec and Jean-Philippe Pezy who collected the studied material.

Habitat. Under rocks and in coastal maërl (rhodolith) beds, lower intertidal to shallow waters (depth 7–41 m).

Type locality. Blainville-sur-Mer, English Channel, France, 49°04'20"N 1°39'06"W.

Distribution. French coasts: English Channel (Blainville-sur-Mer), Bay of Biscay (Bay of Brest), Mediterranean Sea (Corsica Cape).

Remarks. Among European species, *Eupolyornia gili* n. sp. differs from *E. meissnerae* n. sp. by the presence of long branchial stems which are inconspicuous in *E. meissnerae* n. sp., by eyespots arranged in a continuous band instead of the eyespots being separated by a mid-dorsal gap as in *E. meissnerae* n. sp. and by uncini surmounted by two and one large teeth on the first and second rows above the main fang, respectively, instead of uncini surmounted by two large teeth in the two first rows for *E. meissnerae* n. sp. *Eupolyornia gili* n. sp. also differs from *E. meissnerae* n. sp. by the absence of a ventral crest on SG II, by the presence of thick and translucent lateral lobes on SG II–IV and the presence of abdominal neuropodia with pointed dorsal projections. Finally, *E. gili* n. sp. differs from *E. meissnerae* n. sp. by the colour pattern of live specimens. Live material of *E. gili* n. sp. have a red body covered by white spots whereas there is an orange pattern in *E. meissnerae* n. sp.

Eupolyornia gili n. sp., *E. lacazei* n. sp. and *E. nebulosa* belong to the same complex of “strawberry worms” due to their colourful pattern, with red body covered by white spots. However, *E. gili* n. sp. differs from *E. lacazei* n. sp. by the absence of ventral crest on SG II, by the presence of thick and translucent lateral lobes on SG II–IV and the presence of abdominal neuropodia with pointed dorsal projections.

Finally, *Eupolyornia gili* n. sp. differs from *E. nebulosa* (Montagu 1819) by the presence of long branchial

stems which are absent for *E. nebulosa*, by the absence of bilobed lateral lobes on SG III, and by the presence of 17 ventral shields instead of 10 for *E. nebulosa* as observed by Hutchings & Glasby (1988) and Capa & Hutchings (2006) on several specimens sampled close to the type locality. The two species also differ by the shape of uncini. Their dorsal buttons are situated closer to the prow than to the base for *E. gili*, and at midway for *E. nebulosa*.

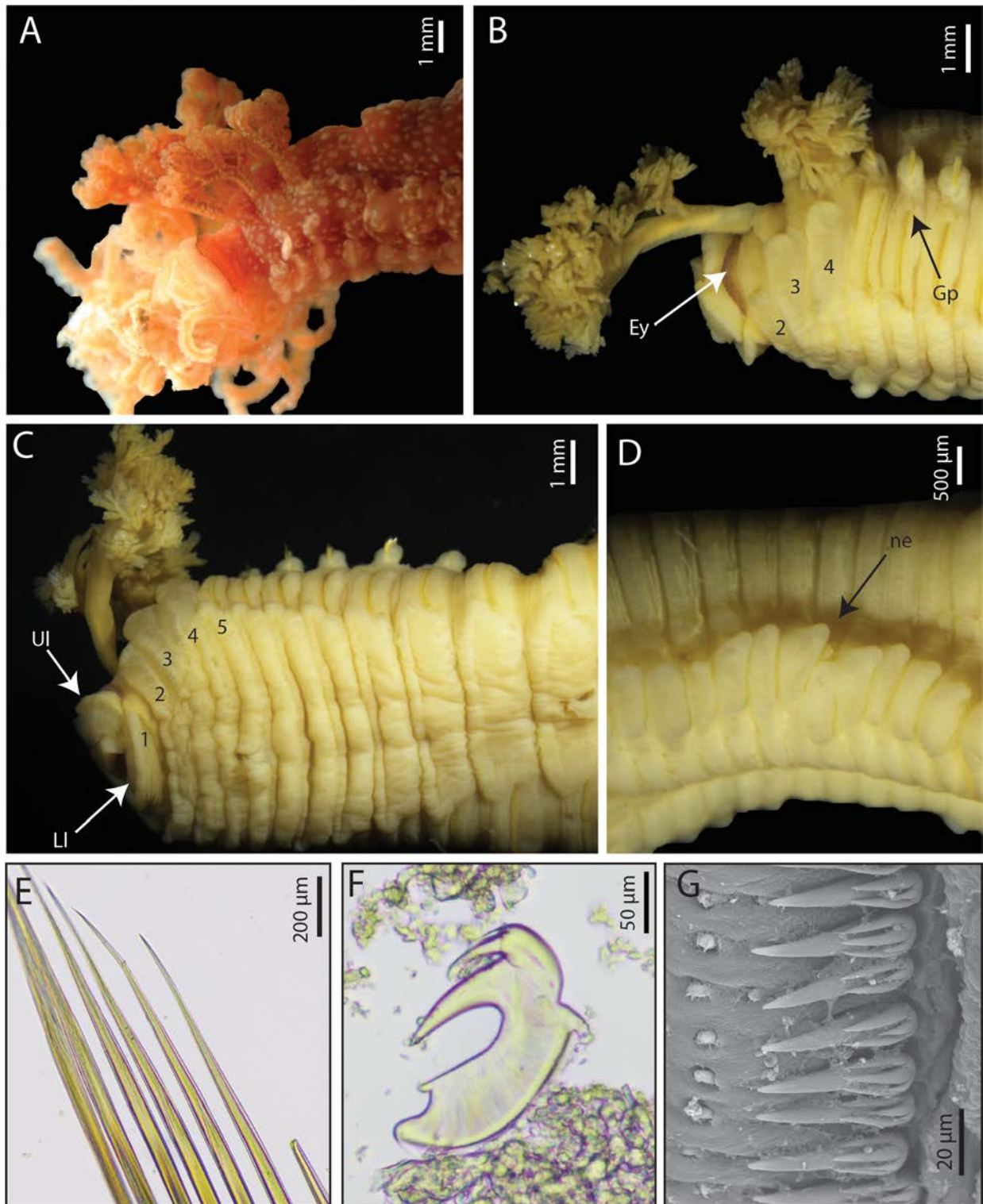


FIGURE 7. *Eupolyornia gili* n. sp. Additional material SMA-BR-Eupoly-04 (A), holotype MNHN-IA-TYPE 2020 (B–C, E), paratype AM W.53325 (D–F), SEM paratype MNHN-IA-TYPE 2021 (G). A. Anterior end, lateral view, live specimen; B. Anterior end, lateral view; C. Anterior end, ventral view; D. Posterior part, lateral view; E. Notochaetae, SG X; F. Uncinus, SG XIII; G. Uncini, SG VII. Abbreviations: Ey, eyespots; Gp, genital papilla; Ll, lower lip; ne, neuropodium; Ul, upper lip. Numbers referring to segments.

Eupolymnia lacazei n. sp.

Figures 8–9

Material examined. Holotype. MNHN-IA-TYPE 2022, posteriorly incomplete, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°28'52"N 3°08'38"E, depth 15 m, December 2020. **Paratypes.** AM W.53326, posteriorly incomplete, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°28'52"N 3°08'38"E, depth 15 m, December 2020, few parapodia used for molecular analysis. MNHN-IA-TYPE 2023, posteriorly incomplete, Mediterranean Sea, Gulf of Lion, Reserve St Troc, 42°28'52"N 3°08'38"E, depth 15 m, December 2020, few parapodia used for molecular analysis, others mounted for SEM.

Additional material. SMA-COR-Tere-03, posteriorly incomplete, Mediterranean Sea, Corsica Cape, 42°47'12"N 9°19'48"E, depth 28 m, May 2019, few parapodia used for molecular analysis.

Description. In life, red body covered with white spots, buccal tentacles pinkish, stems and branches of branchiae red (Fig. 8A).

Small species, holotype incomplete, 29.8 mm long for about 55 segments (complete paratype 45.4 mm; 81 segments) and 1.8 mm wide (complete paratype 5.5 mm).

Transverse prostomium attached to dorsal surface of upper lip; basal part with continuous row of reddish eyespots (Fig. 8C) without mid-dorsal gap, with eyespots well separated from each other; distal part forming a shelf-like tentacular membrane from which numerous thick and deeply grooved buccal tentacles originate (Figs 8A; 9A–B). Peristomium forming lips; hood-like upper lip, rectangular, wider than long; lower lip thin, wider than high, with pharyngeal organ everted (Fig. 8D).

Arborescent branchiae present on SG II–IV, longitudinally aligned, dorsal to line of notopodia; with short and thick branchial filaments, branching dichotomously from long basal stem; first pair longer, following pairs progressively shorter (Figs 8A–C; 9B).

Segment I well visible, ventrally developed, forming ventral lobe below lower lip (Fig. 8D); SG II with one pair of semi-circular ventro-lateral lobes, connected ventrally by a low crest, dorsal margins aligned with ventral edges of following neuropodia; SG III and IV with short semi-circular lateral lobes, about the same size, situated progressively more laterally, lobes of SG IV aligned with neuropodia of SG V (Figs 8B–D; 9A).

Segments II–XVI with glandular, rectangular, smooth to slightly corrugated anteriorly mid-ventral shields, last three shields distinctly shorter; mid-ventral groove extending posteriorly from SG XVII (Fig. 8D).

Rectangular notopodia beginning from SG IV, extending for 17 segments, until SG XX, laterally aligned, notopodia of first two pairs shorter (Fig. 8B). Narrowly-winged notochaetae in two rows, first row shorter (Fig. 8E).

Neuropodia present from SG V, as low ridges until end of notopodia, as rectangular pinnules thereafter (Fig. 8B–D). Neurochaetae throughout as short-handled avicular uncini, arranged in completely intercalated double rows on SG XI–XX, in a face-to-face arrangement. Uncini with short triangular heel and rounded prow, with pointed dorsal button inserted closer to prow than to base of main fang, elongate convex base, and main fang surmounted by a crest with two rows of secondary teeth, first row with two large teeth and second row with several small teeth (middle tooth often larger) (Figs 8F; 9C–D).

Nephridial papillae on SG III–V, posteriorly to bases of branchiae and dorsally to notopodia; genital papillae on SG VI–VIII, as round swellings between parapodial lobes, inserted posteriorly to notopodia.

Pygidium with about 12 papillae.

Etymology. This species is named after the French zoologist Henri de Lacaze-Duthiers (1821–1901), who founded the Laboratoire Arago in Banyuls-sur-Mer more than 100 years ago, and whose 200th birthday is celebrated this year (2021). This species name was chosen by Céline Labrune from the Laboratoire Arago, who provided the type material.

Habitat. Under rocks, shallow waters (depth 15 m).

Type locality. Banyuls-Cerbere nature reserve, Catalan Sea, Western Mediterranean Sea, France, 42°28'52"N 3°08'38"E.

Distribution. Mediterranean Sea, Gulf of Lion and Corsica Cape.

Remarks. Among the European species, *Eupolymnia lacazei* n. sp. differs from *E. meissnerae* n. sp. by having eyespots arranged in a continuous band instead of the eyespots being separated by a mid-dorsal gap as for *E. meissnerae* n. sp., by the presence of long branchial stems which are short for the first pair of branchiae and absent for the second and third ones for *E. meissnerae* n. sp. *Eupolymnia lacazei* n. sp. differs also by the presence of

semi-circular lateral lobes on SG II while *E. meissnerae* n. sp. has auricular-shape lateral lobes and by uncini with two and one large tooth on the first and second rows above the main fang respectively, instead of two large teeth in the two first rows for *E. meissnerae* n. sp. Finally, *E. lacazei* n. sp. differs from *E. meissnerae* n. sp. by the colour pattern of live specimens. They have a red body covered with white spots for *E. lacazei* n. sp. and an orange pattern for *E. meissnerae* n. sp.

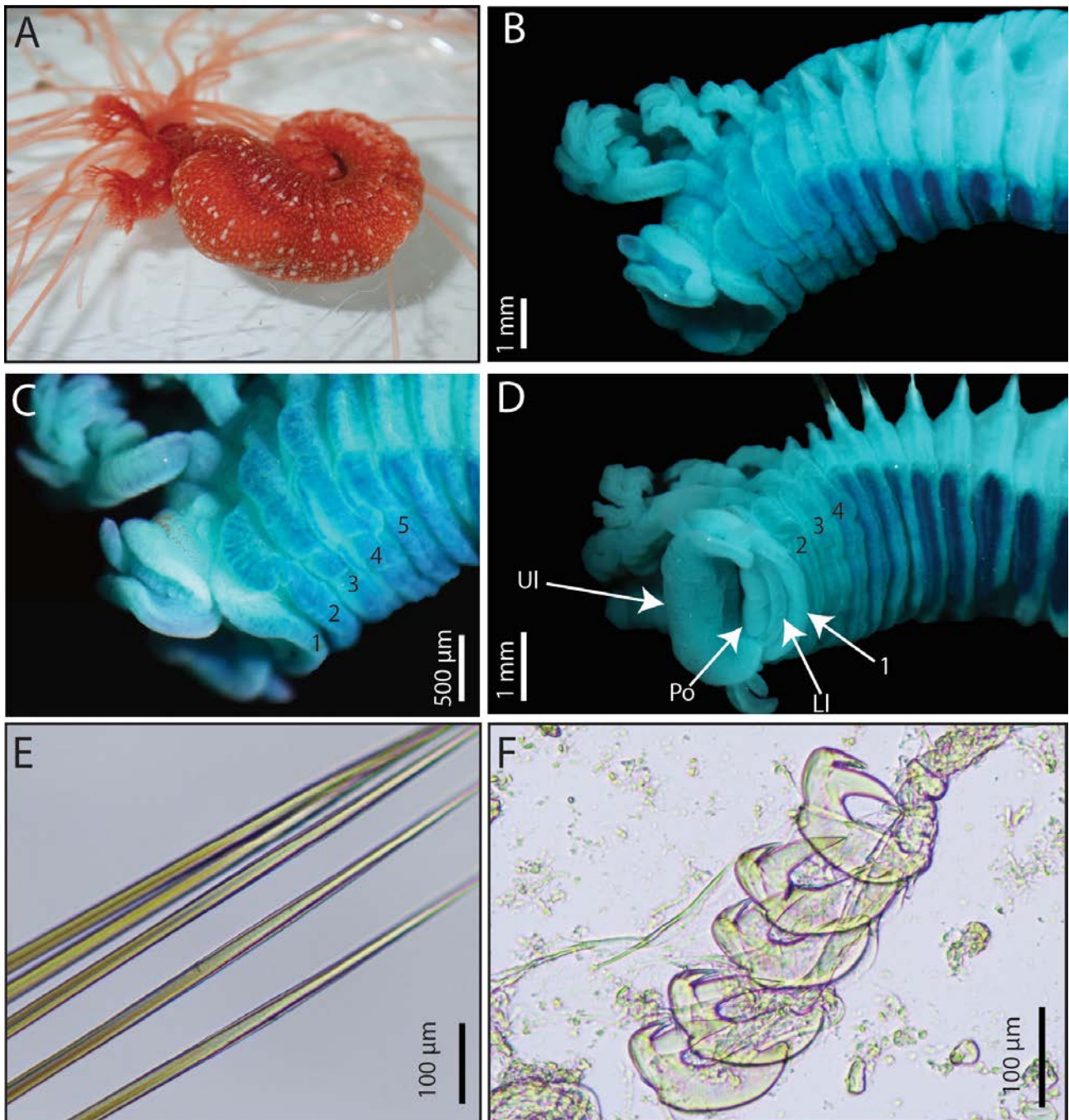


FIGURE 8. *Eupolyornia lacazei* n. sp. Paratype MNHN-IA-TYPE 2023 (A), holotype MNHN-IA-TYPE 2022 (B–F). A. Entire live specimen; B. Entire specimen, lateral view, MG staining; C. Anterior end, lateral view; D. Anterior end, ventral view, MG staining; E. Notochaetae, SG IX; F. Uncinus, SG IX. Abbreviations: Bt, buccal tentacles; LI, lower lip; Po, pharyngeal organ; UI, upper lip. Numbers referring to segments.

Eupolyornia lacazei n. sp., *E. gili* n. sp. and *E. nebulosa* belong to the same complex of “strawberry worms” due to their colourful pattern, with red body covered by white spots. However, *E. lacazei* n. sp. differs from *E. gili* n. sp. by the absence of thick and translucent lateral lobes on SG II–IV, by the absence of abdominal neuropodia with pointed dorsal projections and by the presence of ventral crest on SG II which is absent for *E. gili* n. sp.

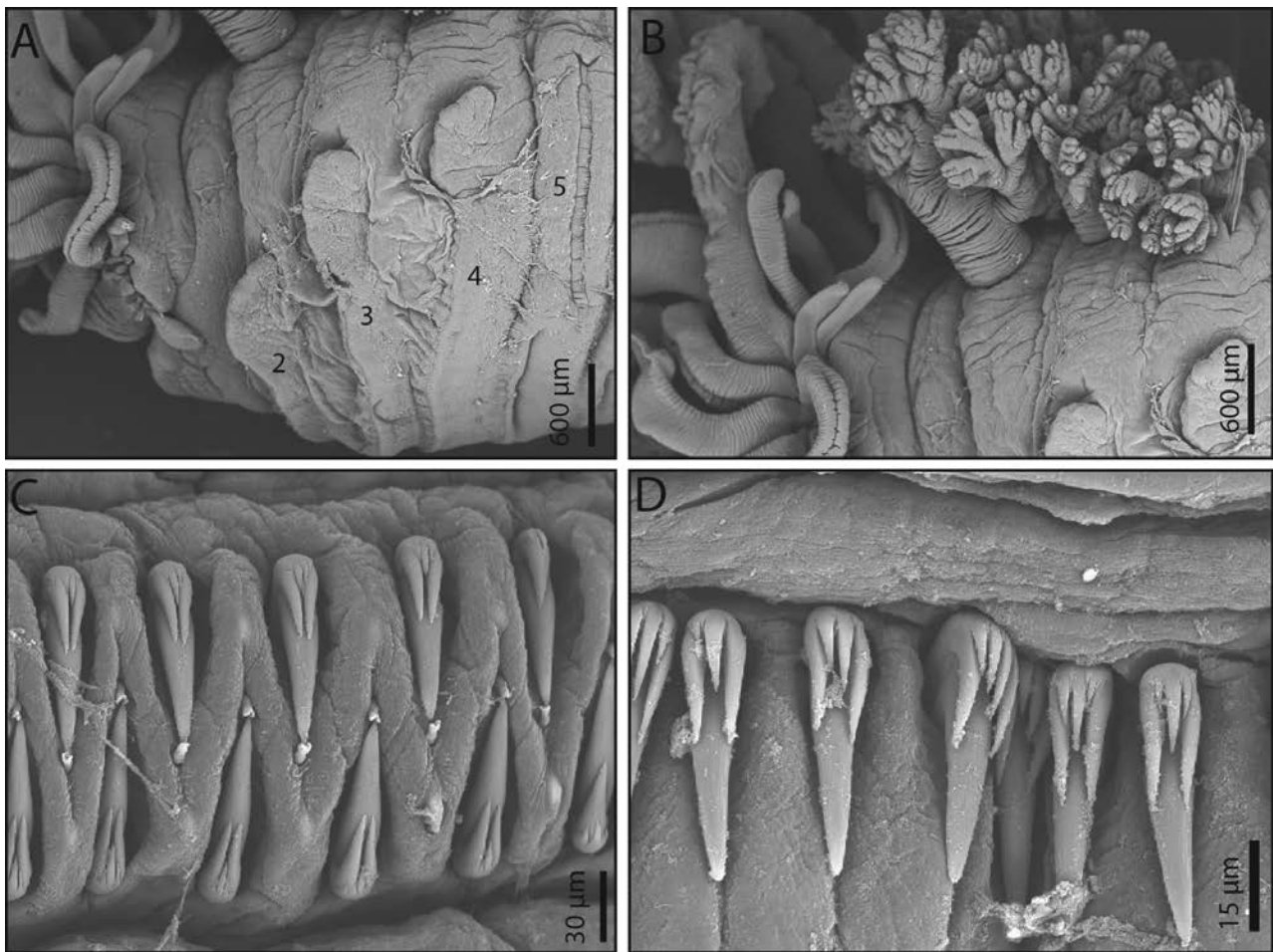


FIGURE 9. *Eupolymnia lacazei* n. sp. SEM paratype MNHN-IA-TYPE 2023. A. Anterior end, lateral view; B. Anterior end, dorso-lateral view; C. Uncini, SG XI; D. Uncini, SG VI. Numbers referring to segments.

Finally, *E. lacazei* n. sp. differs from *E. nebulosa* by the presence of long branchial stems which are absent for *E. nebulosa*, and by the presence of 15 ventral shields instead of 10 for *E. nebulosa*, by the shape of the lateral lobes of SG III, which are semi-circular for *E. lacazei* n. sp. and bilobed for *E. nebulosa*. The two species differ also by the shape of uncini. Their dorsal buttons are situated closer to the prow than to the base for *E. gili* n.sp. and at midway for *E. nebulosa*.

Eupolymnia lacazei n. sp. is relatively similar to two non valid species (Read & Fauchald 2021): *Amphitrite meckelii* Delle Chiaje, 1828 and *Pallonia rapax* A. Costa, 1862. Actually, these two species were described from the Gulf of Naples and have a red colour with white spots. However, the original description of *A. meckelii* states that “the cirri and gills are yellowish and branched, body pinkish with white almost pearly spots, feet with yellow bristles”. In contrast, *E. lacazei* n. sp. has a red body covered by white spots, buccal tentacles pinkish, stems and branchiae red. Moreover, as mentioned by Jirkov (2020), *A. meckelii* should be considered as *nomen dubium* because this “original description does not provide enough information even to be sure about generic affiliation”. Concerning the original description of *P. rapax*, Costa says that “the following twenty rings (after the first ring) have on each side a small fleshy foot, in the form of an auricle, bearing a bundle of bristles” and “it lives in sandy bottoms in a tube consisting of grains of sand and crushed shells”. Even if *P. rapax* shares exactly the same colour pattern as *E. lacazei* n. sp., this species has 20 notopodia and thus should not belong to *Eupolymnia*. The two species occur in very different habitats, associated with sandy bottoms for *P. rapax* and under rocks for *E. lacazei* n. sp. In the absence of type material, *Pallonia rapax* should be considered as *nomen dubium*, as for *A. meckelii* it is not possible to be sure about its correct generic affiliation.

Eupolymnia meissnerae n. sp.

Figures 2C; 10–11

Material examined. Holotype. MNHN-IA-TYPE 2024, posteriorly incomplete specimen, gravid, Northeastern Atlantic Ocean, Brittany, Bay of Brest, station ZC, 48°18'55"N 4°21'53"W, depth 5 m, May 2018, posterior part used for molecular analysis. **Paratypes.** AM W.53327, posteriorly incomplete specimen, Northeastern Atlantic Ocean, Brittany, Bay of Brest, Rozegat, 48°18'19"N 4°22'16"W, depth 1 m, March 2009. MNHN-IA-TYPE 2025, posteriorly incomplete specimen, Northeastern Atlantic Ocean, Brittany, Bay of Brest, Rozegat, 48°18'19"N 4°22'16"W, depth 1 m, March 2009, mounted for SEM.

Description. In life, body uniformly light orange, except branchiae, buccal tentacles and upper lip, which are dark orange, and prostomial eyespots brown (Fig. 10A).

Small species, holotype incomplete (22 segments), 11.7 mm long (11.5–13.6 mm) and 1.8 mm wide (1.2–2.8 mm).

Transverse prostomium attached to dorsal surface of upper lip; basal part with continuous row of black to reddish eyespots, without short mid-dorsal gap, with eyespots more or less separated from each other (Fig. 10A, C); distal part forming a shelf-like tentacular membrane from which the few remaining filiform and grooved buccal tentacles originate (Fig. 10D). Peristomium forming lips; hood-like upper lip, circular, wider than long; lower lip thin, wider than long, pharyngeal organ everted (Fig. 10B).

Arborescent branchiae present on SG II–IV, longitudinally aligned, dorsal to line of notopodia; with long branches and few short branchial filaments branching dichotomously; with a short basal stem on the first pair only; second and third pairs without stem; first pair longer, following ones progressively shorter (Figs 10A–D; 11A–B).

Segment I conspicuous all around, ventrally developed, forming ventral lobe below lower lip (Fig. 10B–D); SG II with one pair of auricular-shaped ventro-lateral lobes, connected ventrally by a low crest, anterior margins undulating; SG III with almost spherical short dorso-lateral lobes; SG IV with a pair of short rounded dorso-lateral lobes; dorsal margins of lateral lobes on SG II–IV aligned with dorsal margins of neuropodia (Figs 10C–D; 11A–B).

SG II–XV with glandular, rectangular, smooth to slightly corrugated anteriorly mid-ventral shields (Fig. 10D); mid-ventral groove extending posteriorly from SG XVI.

Rectangular notopodia beginning from SG IV, extending for 17 segments, until SGXX, laterally aligned (Figs 10B–C; 11A–B). Narrowly-winged notochaetae in two rows (Fig. 10E), first row shorter.

Neuropodia present from SG V, as low ridges until end of notopodia (Figs 10B–C; 11A–B), as rectangular pinnules thereafter. Neurochaetae throughout as short-handled avicular uncini, arranged in completely intercalated double rows on SG XI–XX, in a face-to-face arrangement. Uncini with short triangular heel and pointed prow, dorsal button inserted at about halfway distance between base of main fang and tip of prow, elongate convex base, and main fang surmounted by crest with two rows of secondary teeth, first row with two large teeth, second row with two large teeth and several small ones (Figs 2C; 10F–G; 11C–D).

Nephridial papillae on SG III–V, posteriorly to bases of branchiae and dorsally to notopodia (Fig. 10C); genital papillae on SG VI–VIII, globular, inserted posteriorly to neuropodia.

Pygidium unknown.

Etymology. This species is dedicated to Karin Meißner, for her great contribution to polychaete taxonomy and her friendship with NL and PH.

Habitat. Shallow waters (depth 1–5 m), in maërl (rhodolith) beds.

Type locality. Bay of Brest, Bay of Biscay, Northeastern Atlantic Ocean, France, 48°18'55"N, 4°21'53"W.

Distribution. Only known from the type locality.

Remarks. Among the European species, *Eupolymnia meissnerae* n. sp. differs from *E. gili* n. sp. by the absence of long branchial stems which are long for *E. gili* n. sp., by having eyespots with a mid-dorsal gap instead of a continuous band of eyespots for *E. gili* n. sp. and by having uncini with two large teeth on both first and second rows above main fang instead of uncini with two and one large tooth on the first and second rows above the main fang, respectively for *E. gili* n. sp. *Eupolymnia meissnerae* n. sp. differs also from *E. gili* n. sp. by the presence of a ventral crest on SG II, by the absence of thick and translucent lateral lobes on SG II–IV and the absence of abdominal neuropodia with pointed dorsal projections which are present for *E. gili* n. sp. Finally, *E. meissnerae* n. sp. differs from *E. gili* n. sp. by the colour pattern of live specimens, with specimens having orange pattern for *E. meissnerae* n. sp. and red body covered by white spots for *E. gili* n. sp.

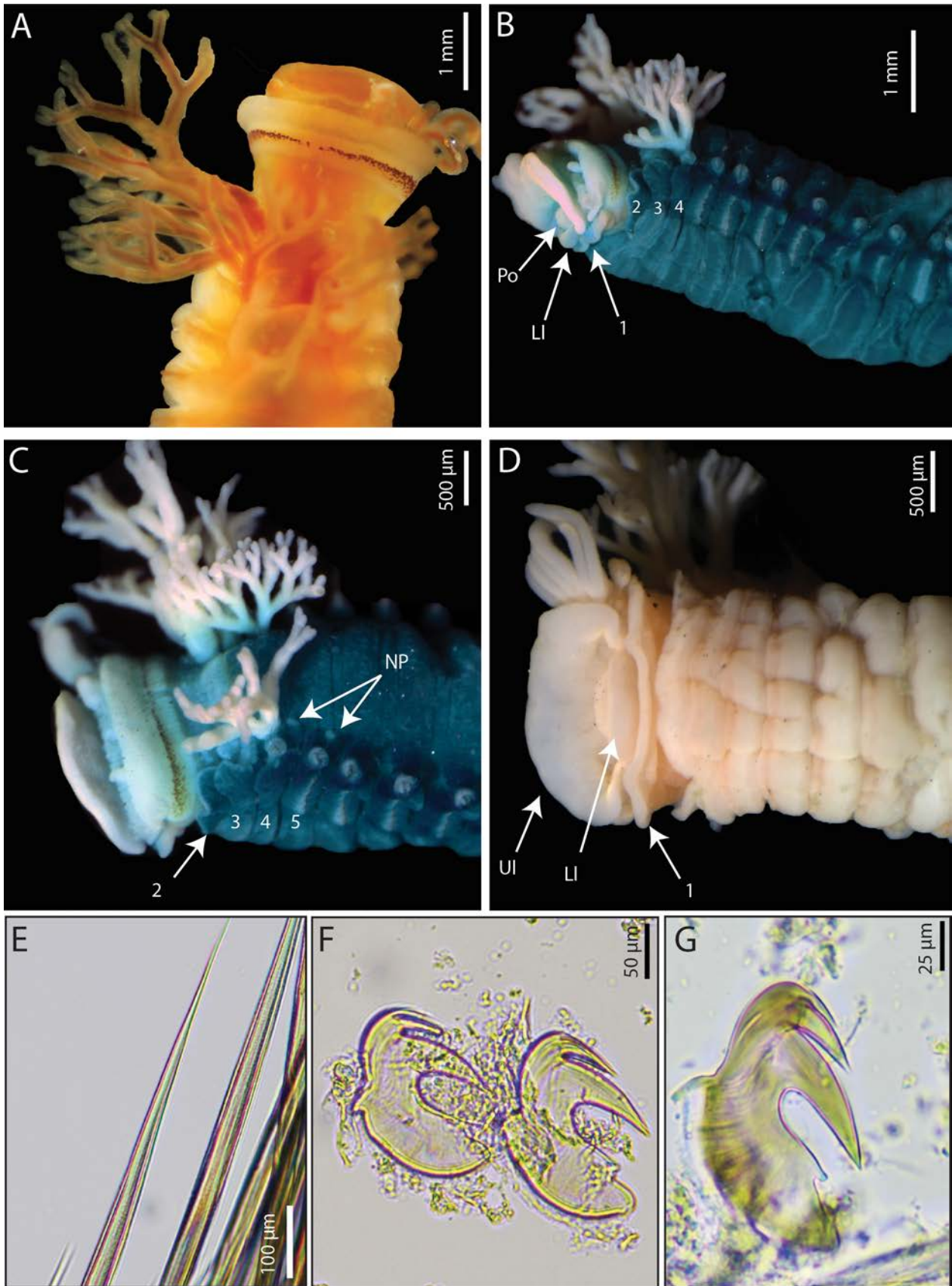


FIGURE 10. *Eupolymnia meissnerae* n. sp. holotype MNHN-IA-TYPE 2024 (A–D, G), paratype AM W.53327 (E–F). A. Anterior end, dorsal view, live specimen; B. Anterior end, lateral view, MG staining; C. Anterior end, dorso-lateral view, MG staining; D. Anterior end, ventral view; E. Notochaetae, SG VII; F. Uncini, SG VIII; G. Uncinus, SG X. Abbreviations: LI, lower lip; NP, nephridial papillae; Po, pharyngeal organ; UL, upper lip. Numbers referring to segments.

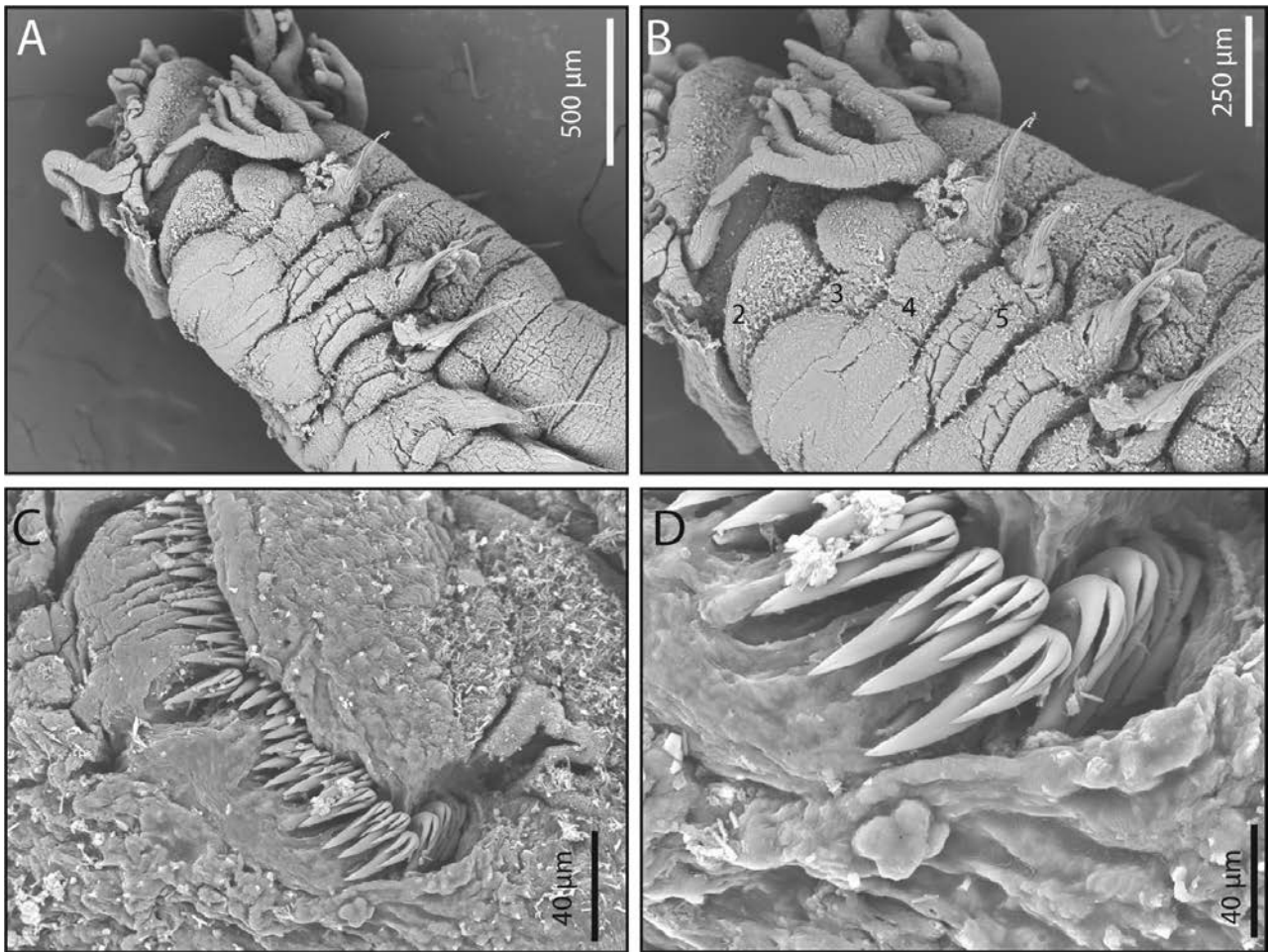


FIGURE 11. *Eupolymnia meissnerae* n. sp. SEM paratype MNHN-IA-TYPE 2025. A–B. Anterior end, lateral view; C–D. Uncini, SG VIII. Numbers referring to segments.

Eupolymnia meissnerae n. sp. differs from *E. lacazei* n. sp. by the presence of a short branchial stem for the first pair of branchiae and the absence of stem for the second and third pairs, instead of the presence of long stems for *E. lacazei* n. sp. *Eupolymnia meissnerae* n. sp. also differs from *E. lacazei* n. sp. by the presence of eyespots that are separated by a mid-dorsal gap instead of a continuous band of eyespots for *E. lacazei* n. sp. and by uncini with two large teeth on both first and second rows above main fang instead of uncini with two and one large tooth on the first and second rows above the main fang, respectively for *E. lacazei* n. sp. *Eupolymnia meissnerae* n. sp. has auricular-shaped lateral lobes on SG II and *E. lacazei* n. sp. semi-circular lateral lobes. Finally, *E. meissnerae* n. sp. differs from *E. lacazei* n. sp. by the colour pattern of live specimens; live specimens of *E. lacazei* n. sp. have an orange body whereas *E. meissnerae* n. sp. have a red body covered by white spots.

Eupolymnia meissnerae n. sp. differs from *E. nebulosa* by the presence of 14 ventral shields instead of 10 in *E. nebulosa*, by the shape of the lateral lobes of SG III, which are spherical in *E. meissnerae* n. sp. and bilobed in *E. nebulosa*. The two species also differ by the denticulation of the uncini. The main fang is surmounted by a crest with two rows of secondary teeth, first row with two large teeth, second row with two large teeth and several small ones for *E. meissnerae* n. sp., and with first row with two large teeth, second row with one large tooth and several small ones in *E. nebulosa*.

Terebella abbreviata Quatrefages, 1866, a non valid species synonymised with *E. nesidensis*, was described from the same area (La Rochelle or St Vaast). We have observed the syntype (MNHN-IA-TYPE0390) but this specimen is in very poor condition and we were not able to identify it to genus, as branchiae are missing and lateral lobes are absent (or damaged?). This species should be considered as *species inquirenda*.

Genus *Lanice* Malmgren, 1866

Type-species: *Nereis conchilega* Pallas, 1766, by monotypy.

Diagnosis. (after Hutchings *et al.* 2021b). Transverse prostomium attached to dorsal surface of upper lip; basal part as a thick crest, eyespots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like, about as wide as long; short, button-like, mid-ventral lower lip. Segment I conspicuous all around, dorsally narrow, with pair of dorso-lateral to lateral lobes extending anteriorly to level of upper lip or beyond, and ventrally connected to each other by lower membrane across ventrum, partially exposing lower lip; SG III with large lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth to markedly corrugated, rectangular to trapezoidal shields. Three pairs of progressively shorter arborescent branchiae, on SG II–IV, with short main stems. Cylindrical to rectangular notopodia beginning on SG IV; notochaetae all narrowly-winged. Neuropodia beginning on SG V, as low, sessile ridges in conjunction with notopodia and as short pinnules posteriorly; neurochaetae as short-handled uncini, in partially intercalated to completely separated double rows, in back to back arrangement, from SG XI until end of notopodia, on SG XX. Nephridial and genital papillae usually poorly developed, almost inconspicuous, of variable position and distribution. Pygidium smooth to papillate.

Remarks. Recently, Jirkov & Leontovitch (2017) proposed the synonymy between the genera *Lanice* and *Axionice*, based on the great variability that the arrangement of the uncini in double rows in the posterior thoracic segments can exhibit. So, these authors suggested that the uncinal alignment in the the double rows character, in a back-to-back or a face-to-face arrangement, is not a sufficiently stable character in order to define genera, and that, together with other characters, such as the development of lateral lobes, the arrangement of the uncini is not a consistent character. In contrast, Londoño-Mesa *et al.* (in prep.) sustain that the different arrangement of uncini in double rows in the posterior thoracic segments is a useful taxonomic character in the family that would have evolved only once and very early, according to both morphological and molecular data.

Lanice conchilega (Pallas, 1766)

Figures 12–13

Nereis conchilega Pallas, 1766: 131–138, pl. 9, figs 14–22.

Lanice conchilega.—Saint-Joseph 1894: 211–218, pl. IX, figs 241–245; Fauvel 1927: 255–257, fig. 88; Holthe 1986: 120–122, fig. 53.

Other synonyms. *Amphitrite flexuosa* Delle Chiaje, 1828; *Amphitrite tondi* Delle Chiaje, 1828; *Terebella artifex* Sars, 1863; *Terebella flexuosa* Delle Chiaje, 1828; *Terebella littoralis* Dalyell, 1853; *Terebella pectoralis* Quatrefages, 1866; *Terebella prudens* Quatrefages, 1866; *Wartelia gonotheca* Giard, 1878.

Material examined. MNHN-IA-PNT 129, posteriorly incomplete, English Channel, Luc-sur-Mer, 49°19'10"N 0°20'57"W, intertidal, July 2016. MNHN-IA-PNT 130, posteriorly incomplete, English Channel, Chausey Islands, 48°54'29"N 1°46'54"W, depth 15 m, March 2016, posterior part used for molecular analysis. SMA-Din-Lan-02, posteriorly incomplete, English Channel, Chausey Islands, 48°54'29"N 1°46'54"W, depth 15 m, March 2016, posterior part used for molecular analysis. SMA-Din-Lan-03, incomplete, English Channel, Chausey Islands, 48°54'29"N 1°46'54"W, depth 15 m, March 2016.

Comparative material. SMA-NEW-01, posteriorly incomplete, North Sea, Belgium, Nieuwpoort, 51°09'13"N 2°43'18"E, intertidal, August 2019, posterior part used for molecular analysis. SMA-NEW-02, posteriorly incomplete, North Sea, Belgium, Nieuwpoort, 51°09'13"N 2°43'18"E, intertidal, August 2019, posterior part used for molecular analysis.

Description. Relatively small species with the longest incomplete specimen studied being 42.3 mm long and 1.7 mm wide, for 25 segments.

Prostomium at base of upper lip, without eyespots, distal part forming a shelf-like tentacular membrane from which numerous filiform, wrinkled and deeply grooved buccal tentacles originate (Fig. 12D). Peristomium well developed with conspicuous hood-like convoluted upper lip, dorsally with brown pigment, and short and swollen lower lip, partially covered by lobes of SG I (Figs 12B–D; 13A).

Segment I with pair of large lobes directed anteriorly and reaching distal part of upper lip; lobes almost oval, pointed anteriorly, with thin margin; continuing across dorsum as narrow crest, connected mid-ventrally by thin convoluted membrane, mid-ventrally indented to partially expose lower lip (Fig. 12A–C). Segment II short without lateral lobes and laterally covered by lobes of SG III, visible ventrally with a pointed anterior projection; absence of glandular membrane connecting first pair of branchiae. Segment III with pair of large, auricular lobes, reaching mid-length of lobes of SG I laterally; ventral edges fused laterally to first mid-ventral shield. Absence of lateral lobes on SG IV (Figs 12A–C; 13A–B).

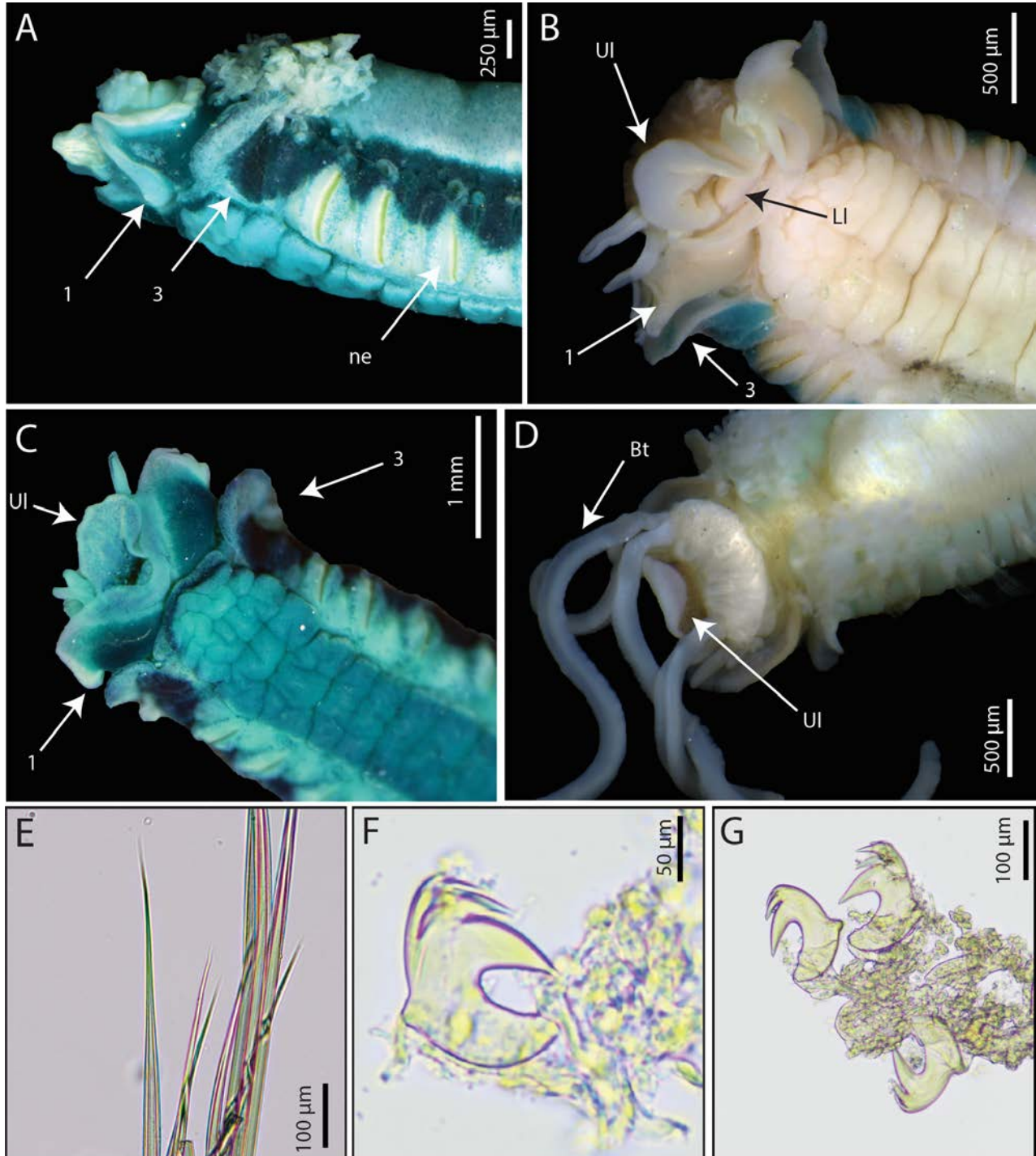


FIGURE 12. *Lanice conchilega* (Pallas, 1766) SMA-Din-Lan-03 (A, C), SMA-Din-Lan-02 (B), MNHN-IA-PNT 129 (D), MNHN-IA-PNT 130 (E–F), SMA-New-Lan-02 (G). A. Anterior end, lateral view, MG staining; B. Anterior end, ventral view; C. Anterior end, ventral view, MG staining; D. Anterior end, dorsal view; E. Notochaetae, SG X; F–G. Uncini, SG X. Abbreviations: Bt, buccal tentacles; Li, lower lip; ne, neuropodia; Ul, upper lip. Numbers referring to segments.

Three pairs of arborescent branchiae on SG II–IV, dorsally aligned, with short branchial filaments, with short basal stems (Figs 12A; 13A–B). Rectangular corrugated mid-ventral shields on SG II–SGXV (XVI), fused on SG II–IV, followed by 3–4 smaller trapezoidal shields from SG XVI (XVII) (Fig. 12B–C).

Notopodia beginning on SG IV, extending until SG XX; notopodia short, globular, almost inconspicuous on several specimens (Figs 12A; 13A–C). Narrowly-winged notochaetae in two rows (Fig. 12E), with first row shorter.

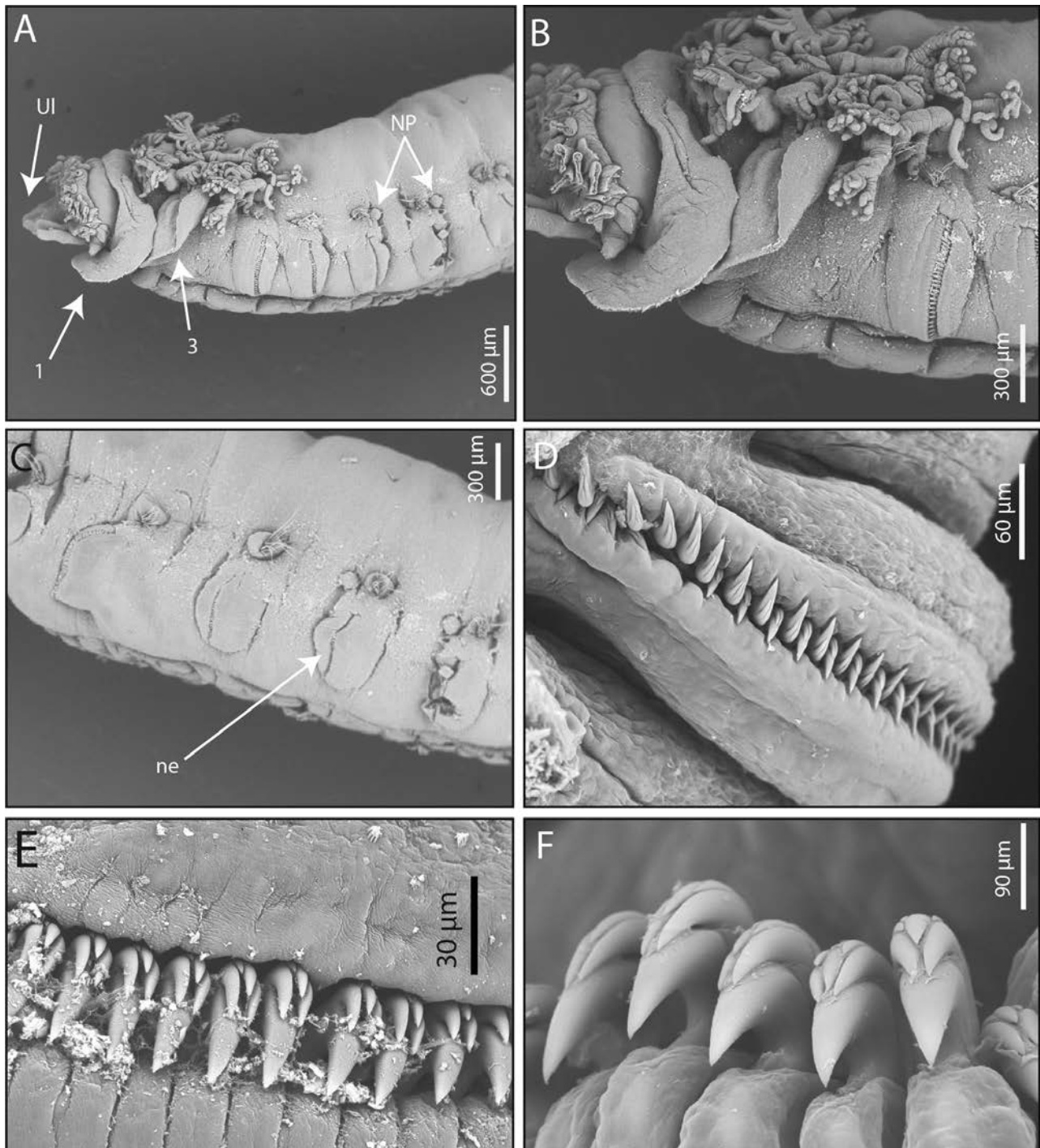


FIGURE 13. *Lanice conchilega* (Pallas, 1766) SEM SMA-Din-Lan-03, SEM. A–B. Anterior end, lateral view; C. Thoracic part, lateral view; D. Thoracic uncini in double row; E. Uncini, SG V; F. Abdominal uncini. Abbreviations: ne, neurochaetae; NP, nephridial papillae; Ul, upper lip. Numbers referring to segments.

Neurochaetae present from SG V, as low sessile ridges until end of notopodia (Figs 12A–C; 13A–D), short and reaching mid-ventral shields; as elongate and thin, rectangular pinnules from SG XXI; inserted laterally to mid-ventral groove on posterior segments. Neurochaetae throughout as short-handled avicular uncini, arranged in inter-

calated back-to-back double rows on SG XI–XX (Fig. 13D). Uncini with short triangular heel and rounded prow, with almost inconspicuous dorsal button inserted closer to prow than to base of main fang, convex base, main fang surmounted by crest with three rows of secondary teeth, first row with two large teeth, second row with one large and several irregularly-sized teeth, and third row with very small teeth (Figs 12F–G; 13D–F).

Genital papillae on SG VI–IX, small, dorsally to notopodia (Fig. 13A).

Pygidium not seen.

Tube with sandy-branched projections on anterior margin.

Type locality. Holland, North Sea.

Type material. Probably lost or never designated (Holthe 1986; Hutchings & Glasby 1988).

Distribution. Considered as a cosmopolitan species, present from Greenland to Antarctic (Gil 2011), but probably restricted to Western Europe.

Habitat. Sandy beaches, intertidal to shallow waters (depth 15 m) (this study).

Remarks. Specimens sampled from the Belgian part of the North Sea, close to the type locality situated on the Dutch coast, are similar to the French specimens studied herein, both morphologically and molecularly (Fig. 27). Moreover, these specimens match with the information provided by Hutchings & Glasby (1988), who examined specimens from the type locality (voucher USNM 44397). However, as for other species described during the 18th century, the designation of a neotype, supported with molecular sequences, is desirable, as probably several different species may occur in Europe (see below).

Lanice kellyslateri n. sp.

Figures 14–15

Material examined. Holotype. MNHN-IA-TYPE 2026, complete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Eyrac pier, 44°39'53"N 01°09'49"W, depth 5 m, October 2016. **Paratypes.** MNHN-IA-TYPE 2027, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Eyrac pier, 44°39'53"N 01°09'49"W, depth 5 m, October 2016. AM W.53328, complete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Eyrac pier, 44°39'53"N 01°09'49"W, depth 5 m, October 2016. MNHN-IA-TYPE 2028, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Eyrac pier, 44°39'53"N, 01°09'49"W, depth 5 m, October 2016, mounted for SEM.

Additional material. SMA-Arc-Eyrac-05, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Eyrac pier, 44°39'53"N 01°09'49"W, depth 5 m, October 2016, posterior part used for molecular analysis. SMA-Arc-Leg-01, complete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Legallais Beach, 44°39'50"N 01°10'29"W, intertidal, December 2017, posterior part used for molecular analysis.

Description. In life, pinkish body, with buccal tentacles translucent; areas around notopodia and neuropodia reddish; lateral lobe on SG I white, on SG III with reddish anterior margin; anterior ventral shields reddish (SG III–XI), following ones blood red (SG XII–XVIII); branchiae blood red (Fig. 14A).

Large species, complete holotype 63.3 mm long (61.1 mm), 4.0 mm wide (3.8 mm) for about 130 segments.

Prostomium at base of upper lip, without eyespots, distal part forming shelf-like tentacular membrane from which numerous filiform and deeply grooved buccal tentacles originate (Figs 14A, C; 15A–B). Peristomium well developed, with conspicuous hood-like rectangular upper lip, directed anteriorly, and short and swollen lower lip, partially covered by lobes of SG I (Figs 14B, D; 15A–B).

Segment I with pair of large lobes directed anteriorly and reaching distal part of upper lip; lobes almost oval, pointed anteriorly, with thin undulating margin; continuing across dorsum as narrow crest, connected mid-ventrally by thin convoluted membrane, mid-ventrally indented to partially expose lower lip (Figs 14A–D; 15A). Segment II, short without lateral lobes and laterally covered by lobes of SG III; visible dorsally, with a thick glandular membrane connecting the first pair of branchiae, and ventrally with a pointed anterior projection. Segment III with a pair of large, rectangular lobes, distal margins undulating, with rounded corners, reaching less than mid-length of lobes of SG I laterally; ventral edges fused laterally to first mid-ventral shield. Absence of lateral lobes on SG IV (Figs 14A–D; 15A–B).

Three pairs of arborescent branchiae on SG II–IV, dorsally aligned, with short branchial filaments, with short basal stems (Figs 14A–C; 15A–B); the two first pairs of branchiae connected by a dorsal crest (Fig. 14B). Rectan-

gular corrugated mid-ventral shields on SG III–XVIII (XIX), followed by three (two) smaller trapezoidal shields (Fig. 14D).

Notopodia beginning on SG IV, extending until SG XX; notopodia of SG IV–XII short, longer from SG XIII, inserted progressively more laterally (Figs 14B–C; 15C–D). Narrowly-winged notochaetae arranged in two rows (Fig. 14F), with first row shorter.

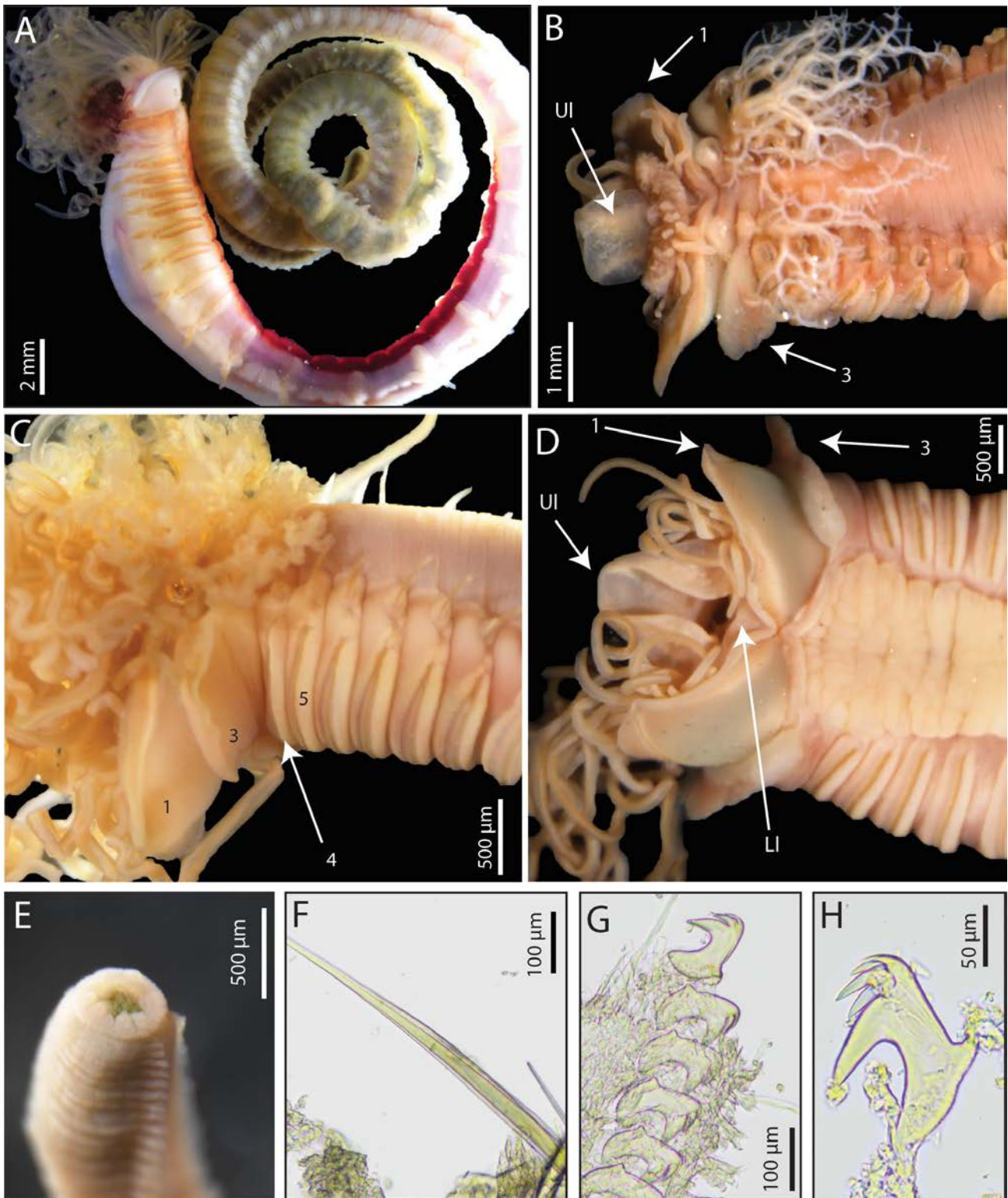


FIGURE 14. *Lanice kellyslateri* n. sp. holotype MNHN-IA-TYPE 2026 (A, E), paratypes MNHN-IA-TYPE 2027 (B), AM W.53328 (C, D), additional material SMA-ARC-Eyrac-05 (F), SMA-ARC-Leg-01 (G–H). A. Live entire specimen, lateral view; B. Anterior end, dorsal view; C. Anterior end, lateral view; D. Anterior end, ventral view; E. Pygidium; F. Notochaetae, SG XII; G. Uncini, SG VIII; H. Uncinus, SG VI. Abbreviations: Ll, lower lip; Ul, upper lip. Numbers referring to segments.

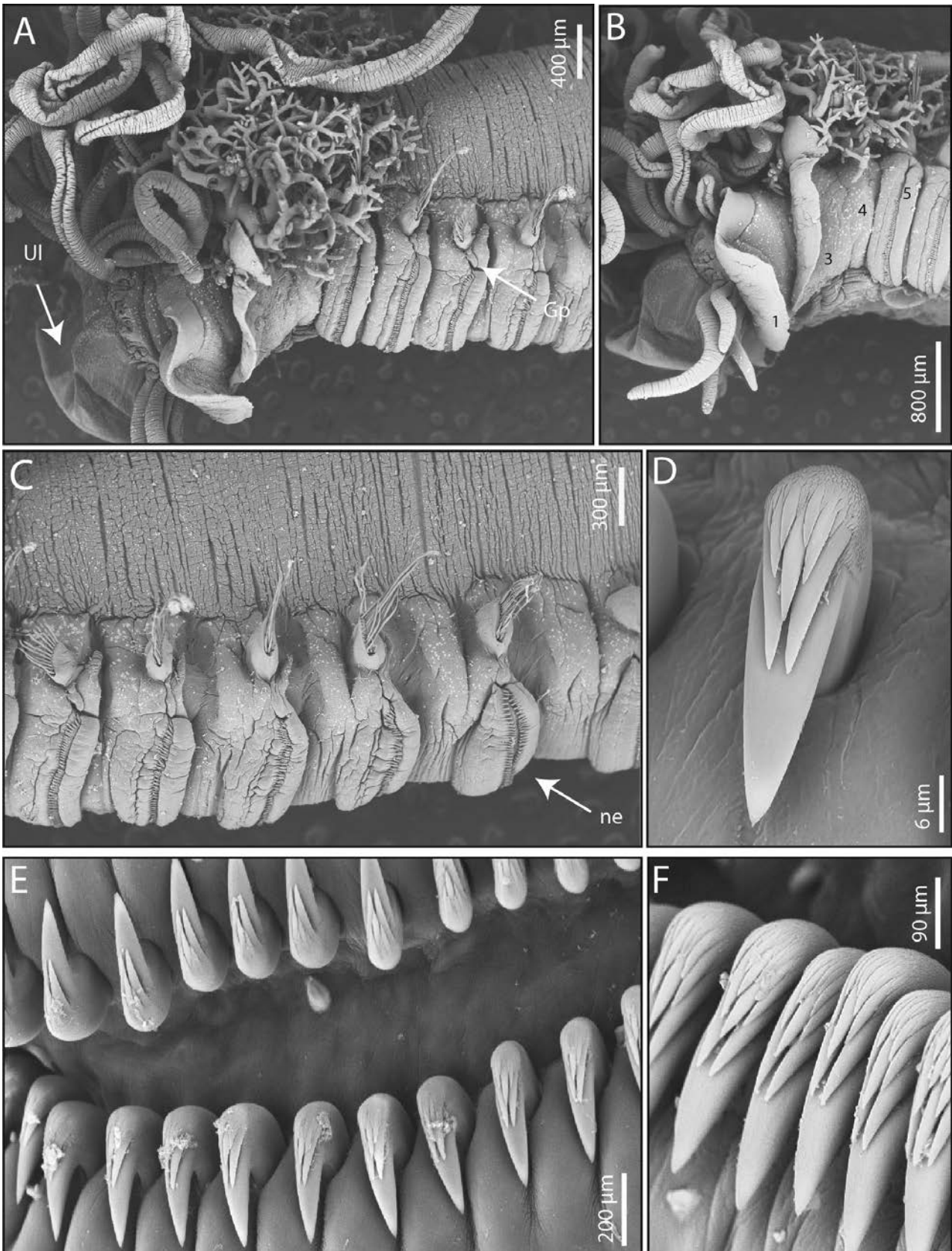


FIGURE 15. *Lanice kellyslateri* n. sp. SEM paratype MNHN-IA-TYPE 2028. A. Anterior end, dorso-lateral view; B. Anterior end, lateral view; C. SG VII–XI, lateral view; D. Uncinus, SG11. E. Thoracic uncini in double row; F. Abdominal uncini. Abbreviations: Gp, genital papilla; ne, neuropodia; UI, upper lip. Numbers referring to segments.

Neuropodia present from SG V, as prominent sessile ridges until end of notopodia, reaching mid-ventral shields (Figs 14A–D; 15A–C); from SG XXI as elongate and thin, rectangular pinnules, inserted laterally to mid-ventral groove on posterior segments (Fig. 15A). Neurochaetae throughout as short-handled avicular uncini, arranged in back to back double rows on SG XI–XX (Fig. 15E). Uncini with triangular heel and rounded prow, with inconspicuous dorsal button, slightly convex base, and main fang surmounted by crest with three rows of secondary teeth, first row with two large teeth, second row with one large and several irregularly-sized teeth, and third row with very small teeth (Figs 14G–H; 15D–F).

Genital papillae on SG VI–XIX, globular, inserted under base of notopodia, slightly displaced dorsally.

Pygidium with eight small globular papillae (Fig. 14E).

Tube with sandy-branched projections on anterior margin.

Etymology. This species is named after the “King” Kelly Slater, 11-time Surf World Champion, and also an environmental activist for the protection of the oceans.

Habitat. Sandy beaches, from intertidal to shallow waters (depth 5 m).

Type locality. Eyrac Beach, Arcachon Bay, Bay of Biscay, France; 44°39'53"N 01°09'49"W.

Distribution. Arcachon Bay (France) (this study); Scilly Islands (England) (Stiller *et al.* 2020 as *L. conchilega*, based on molecular results).

Remarks. Until this study, one single valid species was recorded from European waters: *L. conchilega*. Molecular analyses (Figs 26, 27) confirmed the existence of a second cryptic species in France: *L. kellyslateri* **n. sp.**, which is morphologically very similar. However, *L. kellyslateri* **n. sp.** can be differentiated from *L. conchilega* by the well-defined ventral shields on SG III–IV instead of the presence of ventral shields fused on SG II–IV for *L. conchilega*, by the upper lip which is never pigmented as in *L. conchilega*, which is dorsally pigmented with numerous brown spots, by the shape of the neuropodia which are very prominent instead of low sessile ridges as in *L. conchilega* and by the two first pairs of branchiae connected by dorsal crests, which are absent in *L. conchilega*.

We have compared *L. kellyslateri* **n. sp.** to *Terebella pectoralis* Quatrefages, 1866 (holotype MNHN-IA-Type 0480), a species described from Atlantic coasts of France and synonymised with *L. conchilega*. Even though this material is not in good condition, this species clearly differs from *L. kellyslateri* **n. sp.** by the presence of a large ventral homogeneous glandular region instead of well-defined ventral shields present in *L. kellyslateri* **n. sp.**, by the neuropodia present as low ridges instead of the prominent ones which are present for *L. kellyslateri* **n. sp.** and by the presence of short lateral lobes on SG III, with a straight vertical anterior margin instead of the presence of large lobes with undulating margins and rounded corners for *L. kellyslateri* **n. sp.** Finally, the tube of *T. pectoralis* is composed of a smooth membrane and made of gravel and shell fragments while those of *L. kellyslateri* **n. sp.** is made of fine sand grains, giving a homogeneous appearance. As pointed out by Quatrefages (1866) and later by Saint-Joseph (1894), the difference of tube morphology within the French *Lanice* could correspond to different species. The tube of *T. pectoralis* is indeed very different from *L. conchilega* and *L. kellyslateri* **n. sp.** ones but based on the overall condition of the holotype of *T. pectoralis*, we are not able to confirm that this species should be considered as valid.

Terebella prudens Quatrefages, 1866 was also described from the same area and later synonymised with *L. conchilega*. As for *T. pectoralis*, the description is very brief and lacks important taxonomic details. However, unlike *T. pectoralis*, no material of *T. prudens* was deposited in the MNHN collection and thus a comparison was not possible.

Molecularly, *L. kellyslateri* **n. sp.** is similar to the *L. conchilega* identified by Stiller *et al.* (2020), from Scilly Islands (England) (Figs 26; 27).

Genus *Loimia* Malmgren, 1866

Type-species: *Terebella medusa* Savigny, 1822, by original designation.

Diagnosis. (from Hutchings *et al.* 2021b). Transverse prostomium attached to dorsal surface of upper lip; basal part as a thick crest, eyespots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, relatively short upper lip, hood-like; short, button-like, mid-ventral lower lip. Segment I conspicuous all around, dorsally narrow, with pair of dorso-lateral to lateral lobes extending

anteriorly to level of upper lip or beyond, and ventrally, connected to each other by lower membrane across ventrum, partially exposing lower lip. Large lateral lobes present on SG III; SG IV sometimes also with pair of short lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth to strongly corrugated, rectangular to trapezoidal shields. Three pairs of progressively shorter arborescent branchiae, on SG II–IV, with short main stems. Conical to rectangular notopodia beginning on SG IV, extending for 17 segments, until SG XX; notochaetae all narrowly-winged. Neuropodia beginning on SG V, as low, sessile ridges in conjunction with notopodia and as short pinnules posteriorly; neurochaetae as short-handled uncini throughout, with high, pectinate crest, in partially intercalated to completely separated double rows, arranged in back to back arrangement, from SG XI until end of notopodia. Nephridial papillae on SG III, genital papillae on SG VI–VIII, posterior to notopodia and dorsal. Pygidium smooth to papillate.

Remarks. Recently, Jirkov & Leontovitch (2017) proposed the synonymy of the genera *Loimia* and *Axionice* suggesting that the position of the uncini in a back-to-back arrangement, the presence of pectinate uncini, the number of double rows of uncini, and the shape of the lateral lobes were insufficient to consider *Loimia* as monophyletic. Nevertheless, this synonymization is not followed here, since we consider the genus *Loimia* as being well defined, with all species having three pairs of arborescent branchiae, uncini in double rows until SG XX, uncini pectinate (at least on the thoracic segments) and lateral lobes well-developed on the SG I. Londoño-Mesa & Glasby (*in prep.*), after the revision of the existing type material of all currently described species also support *Loimia* as a valid genus using phylogeny based on morphological information, concluding that the characters listed above as defining the genus are valid and, decline the synonymy suggested by Jirkov & Leontovitch (2017).

Loimia ramzega Lavesque, bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017

Figure 2B

Loimia ramzega Lavesque *et al.* 2017a: 935–942, figs 2–5.

Diagnosis. (for a detailed description, see Lavesque *et al.* 2017a). Large sized animals with live specimens up to 650 mm long. Three pairs of arborescent branchiae on SG II–IV, two pairs of lateral lobes on SG I and III; first pair more ventral, second pair more developed and lateral, but oblique, with undulating edge, sixteen ventral shields from SG II (fused on SG II–III); uncini pectinate with five or six teeth in vertical row (Fig. 2B), pygidium with about 14 long conical papillae.

Type locality. France, English Channel, Brittany, Plouguerneau, Lilia beach; 48°36'38"N 04°36'24"W.

Type material. Holotype MNHN-IATYPE 1788, four paratypes MNHN-IATYPE 1789 to 1992. NMW.Z.2017.002.0001, one paratype, and six individuals. CEMUA-POLY-TERE-0100, one paratype.

Distribution. Only known from the French coasts: Bay of Biscay (Bay of Brest, Grall *pers. obs.*), English Channel (Lavesque *et al.* 2017a), southern North Sea (Dunkerque, Lavesque *pers. obs.*).

Habitat. Sandy beaches, intertidal (Lavesque *et al.* 2017a), shallow waters, fine sands (this study).

Remarks. *Loimia ramzega* is very distinct from other European species of *Loimia* (see Lavesque *et al.* 2017a), but surprisingly quite similar to *Terebella gigantea* Montagu, 1819. Despite the very sparse original description given by Montagu (1819) and the absence of type material, several morphological details can be found in this paper. These two species have a very large size (650 mm long for *L. ramzega*, 406 mm for *T. gigantea*) and approximately the same type locality (Brittany, English Channel, France for *L. ramzega* and Devon, English Channel, UK, for *T. gigantea*). Moreover, as Montagu wrote “with seventeen pairs of exerted fasciculi” in the description, this species probably does not belong to the genus *Terebella* genera which generally have notopodia until the end of the body, or on more than 25 segments (Hutchings *et al.* 2021b).

However, Montagu’s description lacks some taxonomic details, particularly concerning uncini and shape of lateral lobes, which are very important in the genus *Loimia*. Montagu described the branchiae as relatively short, while they are very long on *L. ramzega*, and that ventral shields are brown, while they are blood red on *L. ramzega*. Finally, the tubes of the five *Terebella* species described by Montagu (1819) in his paper are “extremely delicate”, while a membrane (together with shells fragments and gravels) allows the tube of *L. ramzega* to “maintain a hard consistency”.

Later, McIntosh (1922) moved *T. gigantea* to the genus *Amphitrite*. Even if several taxonomic characteristics, like the shape of the branchiae, the size of the animals, or the presence of lateral lobes are similar with *L. ramzega*,

the shape of the uncini is very different (McIntosh 1922, plate CXXV, Fig. 10b). In that paper, McIntosh also suggested that *A. gigantea* could be the same as *Terebella edwardsii* Quatrefages, 1866, but this last species is different and valid as *Amphitrite edwardsii* (this study).

Finally, we suggest that *T. gigantea* should be considered as a *nomen dubium* considering that the species probably does not belong to the genus *Terebella* and that there is no known type material. Montagu appears to have never designated and deposited type material, and the original descriptions lacks important information, so it should be a *nomen dubium* until a neotype is designated and described.

***Paramphitrite* Holthe, 1976**

Type-species: *Paramphitrite tetrabanchia* Holthe, 1976, by original designation.

Diagnosis. (from Hutchings *et al.* 2021b). Transverse prostomium attached to dorsal surface of upper lip; basal part as a thick crest, eyespots absent; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and mid-ventral lower lip. Segment I reduced dorsally, expanded ventrally, with low mid-ventral lobe marginal to mouth; SG II–IV with pairs of low lateral lobes. Anterior segments highly glandular ventrally, with discrete, smooth, rectangular to trapezoidal mid-ventral shields. Two pairs of arborescent branchiae, on SG II–III, much shorter than body width, with short main stems. Rectangular to conical notopodia beginning on segment IV, extending for 13 segments, until SG XVI; notochaetae all medially limbate and distally serrated. Neuropodia beginning on SG V, as low ridges until SG XX, shortly after end of notopodia, and short pinnules posteriorly; neurochaetae as short-handled avicular uncini with high crest, in completely separated double rows, in face-to-face arrangement, on SG XI–XX. Nephridial papillae present on SG III, genital papillae on SG VI–VIII, between parapodial lobes. Pygidium smooth.

Remarks. Recently, Jirkov (2020) proposed the synonymy between the genera *Paramphitrite* and *Amphitrite*. This synonymy is not followed here, as the characters mentioned by this author are perceived as being variable within both genera. As in the case of many other genera of Terebellidae, the variability of some characters, such as the number of the thoracic chaetigers, the number of pairs of nephridial papillae, or the arrangement of the double rows of uncini, among others, are shared with animals of several other genera, and cannot be used to synonymise genera. On the contrary, it supports our view about the need to find additional morphological characters in order to perform a more robust revision of the genera, supported by molecular data. Ideally and whenever possible, it should include the redescription of the type species of each genus.

***Paramphitrite dragovabeci* n. sp.**

Figures 16 and 17

Material examined. Holotype. MNHN-IA-TYPE 2029, posteriorly incomplete, Northeastern Atlantic Ocean, Brittany, Bay of Brest, Camaret, 48°17'48"N 4°34'59"W, depth 15 m, October 2016. **Paratype.** MNHN-IA-TYPE 2030, posteriorly incomplete, Northeastern Atlantic Ocean, Brittany, Bay of Brest, Camaret, 48°17'48"N 4°34'59"W, depth 15 m, October 2016, mounted for SEM.

Description. Holotype posteriorly incomplete with 22 segments, 17.3 mm long (9.9 mm) and 1.2 mm wide (1.4 mm).

Transverse prostomium attached to dorsal surface of upper lip; basal part with eyespots regularly arranged in short lateral rows (Fig. 16C). Buccal tentacles thick and grooved (Figs 16B–D; 17A). Peristomium forming lips; upper lip broad, rounded, hood-like, with dorsal surface distinctly annulated; pharyngeal organ everted, followed by a small, rounded lower lip, restricted to mouth (Fig. 16A–D).

Well-developed ventral lobe on SG I, developed lateral lobes on SG II–IV, lobes from SG II connected by a ventral crest. Ten ventral shields present on SG III to SG XIII (Figs 16A–D; 17A–C).

Two pairs of dichotomous branchiae, on SG II–III, each situated dorso-laterally, with wide medial gap; branchial filaments annulated, arising from short stems; filaments of the first pair longer (Figs 16A–C; 17A–C).

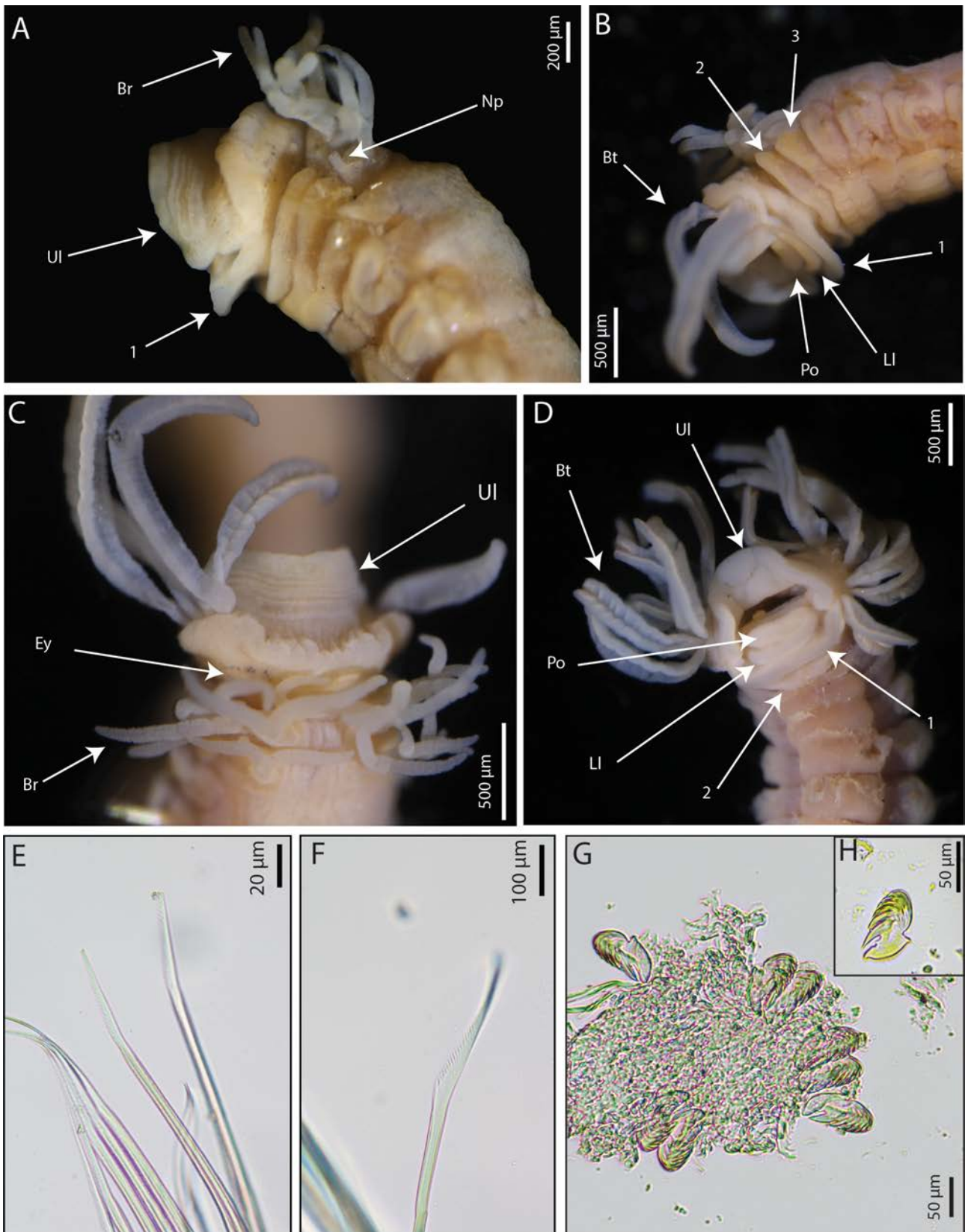


FIGURE 16. *Paramphitrite dragovabeci* n. sp. holotype MNHN-IA-TYPE 2029 (A–D, G), paratype MNHN-IA-TYPE 2030 (E–F, I). A–B. Anterior end, lateral view; C. Anterior end, dorsal view; D. Anterior end, ventral view; E–F. Notochaetae, SG XI; G. Uncini, abdominal segment; I. Uncinus, SG XI. Abbreviations: Br, branchiae; Bt, buccal tentacle; Ey, eyes; Ll, lower lip; Np, nephridial papilla; Po, pharyngeal organ; Ul, upper lip. Numbers referring to segments.

Notopodia on SG IV–SG XVI (n=13), inserted progressively more laterally (Figs 16A–B; 17A); notopodia small, almost rectangular, distally rounded. Notochaetae arranged in two rows, with first row shorter. Notochaetae almost straight, medially winged with limbs of same width, and distally serrated (Fig. 16E–F).

Neuropodia from SG V, as fleshy lateral ridges until SG XIV, slightly raised from SG XV and displaced more ventrally. Uncini in double rows from SG XI–SG XX, in a face-to-face arrangement. Uncini avicular, with triangular heel, distally pointed prow downwardly directed, short dorsal button inserted closer to the base of main fang than to tip of the prow, convex base, and main fang surmounted by crest with six rows of secondary teeth (Figs 16G–H; 17D).

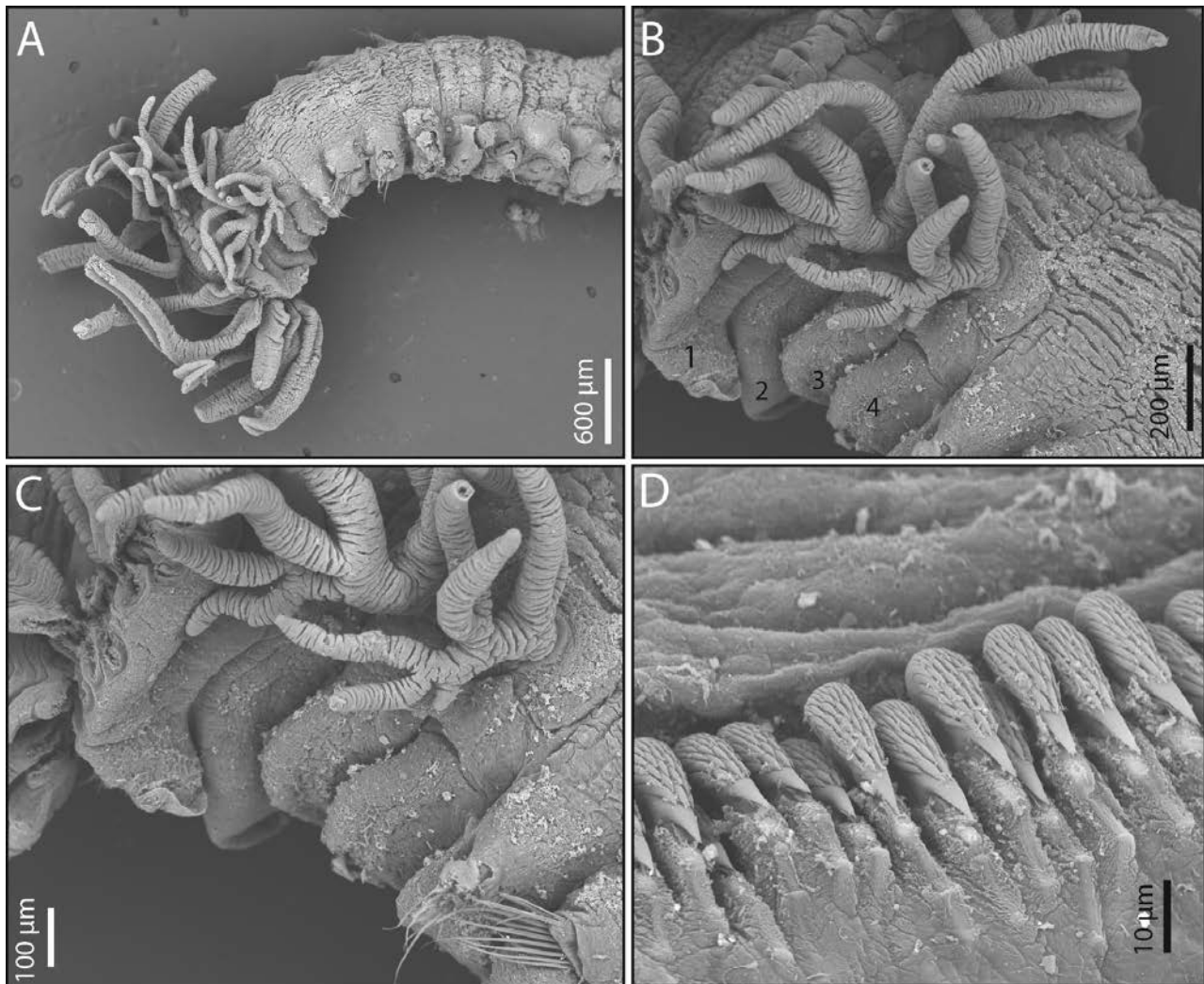


FIGURE 17. *Paramphitrite dragovabeci* n. sp. SEM paratype MNHN-IA-TYPE 2030. A–C. Anterior end, lateral view; D. uncini, SG XIV. Numbers referring to segments.

Nephridial and genital papillae present on SG III and SG VI–VIII; nephridial papillae on SG III large and elongate, situated laterally at branchial base (Fig. 16A); genital papillae situated laterally below notopodia and slightly posteriorly to neuropodia on SG VI–VIII.

Pygidium unknown.

Etymology. This species is dedicated to the Yugoslav football player Drago Vabec, legend of the “Stade Bretois” Football Club from 1979 to 1983. This species name was proposed by Jacques Grall (IUEM laboratory—Brest), who collected the type material and who is a great fan of both this club and this player.

Habitat. Shallow waters (depth 15 m), in maërl (rhodolith) beds.

Type locality. Bay of Brest (Camaret), Bay of Biscay, Northeastern Atlantic Ocean, France. 48°17'48"N 4°34'59"W.

Distribution. Only known from the type locality.

Remarks. Two species of *Paramphitrite* are known to occur in the European waters: *P. birulai* Ssolowiew, 1899 and *P. tetrabranchia* Holthe, 1976. This last species was recently synonymised with *P. birulai* by Jirkov (2020) but Holthe had already doubts about its status earlier (Holthe 1986).

Branchiae of *P. dragovabeci* **n. sp.** are separated by a wide medial gap while those of *P. birulai* are relatively close (Loia *et al.* 2017: fig. 3b; Jirkov 2020: fig. 4c). *Paramphitrite dragovabeci* **n. sp.** differs by the presence of well-developed lateral lobes on SG II–IV which are small for *P. birulai*, and by the absence of nephridial papillae on SG IV which are present for *P. birulai* (Jirkov 2020). Finally, based on the figure 4A from Jirkov's paper (2020), the shape of the large elongate nephridial papillae of SG III of *P. dragovabeci* **n. sp.** seems different but this character was not described either by Loia *et al.* (2017) nor by Jirkov (2020). According to Jirkov (2020), *P. birulai* has pectinate branchiae while specimens of *P. dragovabeci* **n. sp.** described herein have dichotomous ones. However, based on Jirkov's fig. 4A, the branchiae are clearly not pectinate (as in Eunicidae for example) but with filaments arising from a main stem (as also written by the author).

French specimens are similar to Spanish ones studied by Parapar *et al.* (1991). Indeed, Spanish specimens have a wide gap between branchiae and well-developed lateral lobes on SG II–IV. Unfortunately, no information about nephridial papillae appear in this paper. They were sampled in the same geographical area, the Bay of Biscay. We suspect that Spanish and French specimens belong to a single species: *P. dragovabeci* **n. sp.** Finally, the wide distribution of *P. birulai*, from the High Arctic Sea to the Mediterranean Sea (Loia *et al.* 2017; Jirkov 2020), seems doubtful, given the very different environmental conditions. Loia *et al.* (2017) proposed that this species was introduced in the Adriatic Sea, but molecular comparisons are necessary to confirm it, as several cryptic species probably occur in Europe, but also to confirm if *P. birulai* has such a wide distribution and if the Spanish specimens actually belong to *P. dragovabeci* **n. sp.**

Paramphitrite pauciseta (Day, 1963), described from South Africa, differs from *P. dragovabeci* **n. sp.** by the presence of small (and not obvious) lateral lobes on SG II–IV, by branchiae which are not dichotomous and which consist of a tuft of stout filaments and by the presence of characteristic reddish subdermal spots at the base of each branchia (but these spots probably disappear after fixation and storage in alcohol).

***Pista* Malmgren, 1866**

Type-species: *Amphitrite cristata* Müller, 1776 by monotypy.

Diagnosis. (after Hutchings *et al.* 2021b). Transverse prostomium attached to dorsal surface of upper lip; basal part as a thick crest, eyespots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; upper lip relatively short, hood-like; lower lip swollen, cushion-like and mid-ventral. Segment I reduced dorsally, with pair of lobes of variable size and position; SG II–IV also with pairs of lobes of variable size and position, sometimes extending for a few more segments. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal mid-ventral shields. One, two or three pairs of arborescent, pectinate or plumous branchiae from SG II, typically two pairs, on SG II and III, less typically a single pair, and rarely 3 pairs. Conical to rectangular notopodia beginning on SG IV, typically extending for 17 segments, until SG XX; notochaetae all distally winged, frequently broadly-winged. Neuropodia beginning on SG V, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as long-handled avicular uncini, at least on anterior neuropodia, frequently until SG X or end of notopodia, then short-handled; uncini in partial to completely intercalated double rows on SG XI–XX, in a face-to-face arrangement. Nephridial papillae present on SG III, genital papillae on a variable number of segments, usually on SG VI–VII, posterior and dorsal to notopodia. Pygidium smooth to slightly crenulated.

Remarks. The genus *Pista* is probably the most problematic one within the Terebellidae *s.s.* The main issue concerns the diagnostic characters of the type species, *P. cristata* (Müller, 1776). This species was reported around the world (Hutchings & Lavesque 2020) because of: (1) a very brief original description and lack of type material, (2) a doubt concerning the number of pairs of branchiae and the arrangement of the branching filaments, and thus (3) confusion in several taxonomic keys. This species was described as having one pair of branchiae, while Malmgren who erected the genus *Pista* and designated *P. cristata* as the type species, stated that it has two pairs of branchiae. Some authors, as Jirkov & Leontovich (2017), have discussed the validity of the generic boundaries, trying to understand the vague information contained in the original description of this species. Nevertheless, since the

type material does not exist, and since these authors did not revise material from type locality, their comments are not very helpful. Fortunately, one of the present authors (M.H.L-M) has recently examined material from the type locality (Kristiansand fjord, Norway) and will soon stabilize the taxonomic issues of this species by designating a neotype, in order to give not only a full description of the species, but also morphological boundaries of the genus (Londoño-Mesa *et al. in prep.*). Based on his observation, *Pista cristata* is characterized by the presence of two pairs of pompom-like branchiae with tufts of branched filaments coming off the main stem (as followed by several authors: Nogueira *et al.* 2011; Mikac & Hutchings 2017; Labrune *et al.* 2019; Hutchings *et al.* 2021a, b), by the absence of dorsal ridges on SG II–III, by short lateral lobes on SG I and well-developed lateral lobes on SG II–IV, by uncini short-necked, with long-handle posterior process restricted until SG VIII, and finally by genital papillae present on SG VI–VII.

***Pista colini* Labrune, Lavesque, Bonifácio & Hutchings, 2019**

Pista colini Labrune *et al.* 2019: 71–83, figs 2–4.

Diagnosis (for a detailed description, see Labrune *et al.* 2019). Live specimens with ventral shields divided in two regions, anterior part pinkish, posterior part blood red, dark pigmentation on dorsal side of the upper lip. One pair of unequal-sized pompom-like branchiae inserted on SG II, branchial filaments arranged in spiral around the central axis with dichotomous filaments. Two pairs of lateral lobes on SG II–III; well developed on SG II, with rounded anterior margins, merging with ventral shields; half width of segment, asymmetrical and slightly displaced dorsally on SG III, connected across ventrum; absent on SG IV. Neurochaetae as long-handled avicular uncini on SG V–VI, short-handled thereafter.

Type locality. France, Western Mediterranean Sea, Gulf of Lion, Banyuls-sur-Mer harbour.

Type material. Holotype MNHN-IA-TYPE 1850, four paratypes MNHN-IATYPE 1851 to 1855. Two other paratypes: AM W.50625, AM W.50626.

Distribution. Mediterranean Sea, Gulf of Lion (Labrune *et al.* 2019); Aquitanian coast, Bay of Biscay (this study); English Channel, Bay of Seine (this study).

Habitat. Shallow water (depth 3 m), on gravelly sands (Labrune *et al.* 2019), coastal waters from depths of 15–50 m, sandy bottoms (this study).

Remarks. Examination of fresh specimens allowed us to add pigmentation patterns to the diagnosis, such as the dark pigmentation on the dorsal side of the upper lip of these animals.

***Pista labroneae* n. sp.**

Figure 18

Material examined. Holotype. MNHN-IA-TYPE 2031, posteriorly incomplete, Mediterranean Sea, Gulf of Lion, Redit F20, 42°46'44"N 3°3'21"E, depth 20 m, August 2010. **Paratypes.** AM W.53329, posteriorly incomplete, Mediterranean Sea, Gulf of Lion, Redit F20, 42°29'20"N 3°8'19"E, depth 17 m, October 2020. MNHN-IA-TYPE 2032, posteriorly incomplete, Mediterranean Sea, Gulf of Lion, Beauduc, 43°24'47"N 4°30'7"E, depth 14 m, 2012.

Description. Holotype posteriorly incomplete, 22.3 mm long (5.8 mm) and 1.5 mm wide (0.5 mm), for 29 segments.

Transverse prostomium attached to dorsal surface of upper lip; basal part without eyespots; distal part of prostomium convoluted. Buccal tentacles filiform and deeply grooved (Fig. 18B–F). Peristomium forming lips, upper lip hood-like, large, wider than long, rectangular, with convoluted margin, slightly pointed anteriorly; lower lip swollen, crescent-shaped, wider than long (Fig. 18B–C).

Segment I conspicuous, with one pair of rounded lateral lobes, connected to each other by a thin and smooth membrane with rounded ventral indentation, surrounding lower lip (Fig. 18B–C, E). Segment II with one pair of large ventro-lateral lobes, trapezoidal, with long ventral base and rounded margins, connected to each other by large mid-ventral crenulated crest. Segment III with one pair of auricular dorso-lateral lobes, much shorter than those of SG II, connected to each other by thin, slightly crenulated mid-ventral crest. Segment IV without lateral lobes.

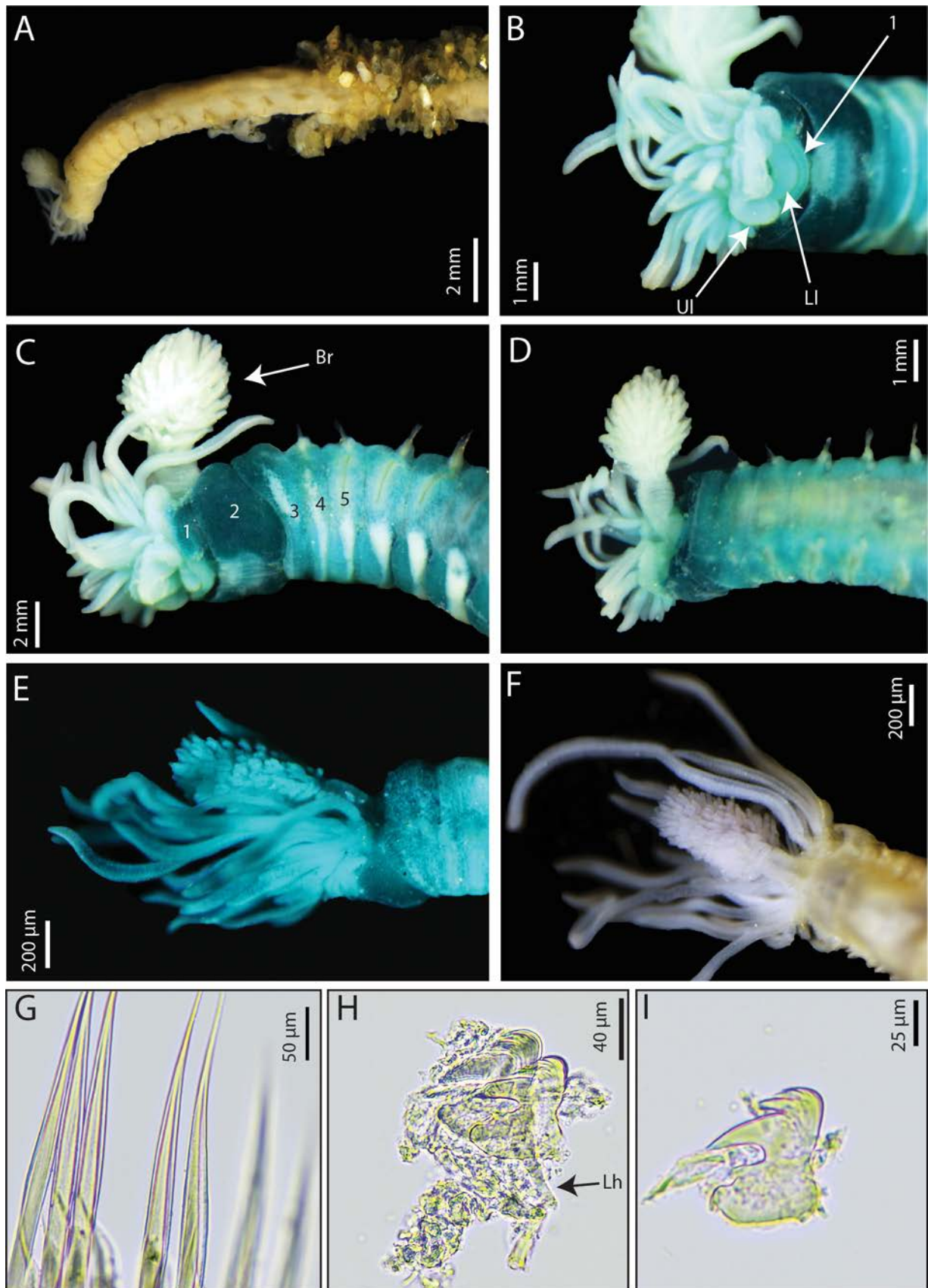


FIGURE 18. *Pista labruneae* n. sp. holotype MNHN-IA-TYPE 2031 (A–D; G–I), paratype AM W.53329 (E–F). A. Entire specimen, lateral view; B. Anterior end, ventral view, MG staining; C. Anterior end, lateral view, MG staining; D. Anterior end, dorsal view, MG staining; E. Anterior end, lateral view, MG staining; F. Anterior end, dorsal view. G. Notochaetae, SG XI; F–G. Uncini, SG V. Abbreviations: Br, branchiae; Lh, long-handle; Ll, lower lip; Ul, upper lip. Numbers referring to segments.

Dorsal anterior margins of SG III as protruding crest (Fig. 18D). A single plume-shaped branchia present on SG II inserted mid-dorsally; with conspicuous, annulated basal stem, branches arranged in spiral around the main stem, with short filaments (Fig. 18A, C–E). Smooth mid-ventral shields present on SG V–XIX, rectangular shields, becoming progressively longer and wider posteriorly.

Notopodia beginning on SG IV, extending until SG XX; notopodia short, rectangular, first four pairs shorter, inserted progressively more laterally, then longitudinally aligned (Fig. 18C–D). Broadly-winged notochaetae in two rows, broader on one side (Fig. 18G), with first row shorter.

Neuropodia present from SG V, as low, almost sessile ridges until end of notopodia, as low rectangular pinnules thereafter (Fig. 18 C–D). Neurochaetae as long-handled uncini on SG V–X, with well-developed handles originating from heel, progressively thinner; uncini arranged in partially intercalated double rows on SG XI–XX in a face-to-face arrangement. Avicular uncini with slightly convex base, large rounded heel, distally rounded prow, dorsal button inserted halfway between base of main fang and prow, and well-developed pointed main fang, surmounted by crest with 5 rows of numerous and progressively shorter secondary teeth above the main fang (Fig. 18H–I). Genital papillae on SG VI–VII, tubular, situated dorsally behind notopodia. Pygidium unknown.

Etymology. This species is dedicated to Céline Labrune, from the Banyuls-sur-Mer Arago Laboratory, for her friendship with NL for about 15 years and for providing the type material of eight new species since the beginning of the “*Spaghetti Project*”, including this new one.

Habitat. Fine sand, depth 17–20 m.

Type locality. Gulf of Lion, Western Mediterranean Sea, Gulf of Lion. 42°46′44″N 3°3′21″E.

Distribution. Only known from the type locality, but probably present in Italy and other parts of the Mediterranean Sea (see below).

Remarks. Among the European species, *P. labruneae* n. sp. is easily recognizable by the presence of a single branchia situated mid dorsally on SG II. The type material was carefully checked to ensure that only a single branchia was ever present, and that another one had been lost but no evidence of a branchial scar was ever found, so we are confident that only a single branchia was present. Moreover, specimens with only a single branchia are regularly found in this area (Labrune pers. com.) confirming that only a single branchia is present.

Pista labruneae n. sp. differs from *P. colini* recently described from the same area (Labrune *et al.* 2019). First, *P. colini* has one pair of branchiae instead of a single mid-dorsal branchia. The two species differ also by the number and shape of lateral lobes. The lateral lobes on SG II of *P. labruneae* n. sp. are larger than those of *P. colini*. Finally, *P. colini* has neurochaetae as long-handled avicular uncini on SG V–VI, short-handled thereafter while *P. labruneae* n. sp. has long-handled uncini at least until SG X.

Pista labruneae n. sp. has probably been previously confused and misidentified in the Mediterranean Sea as *P. unibranchia* Day, 1963, a species from South Africa also described as having a single branchia. However, as underlined recently by Langeneck *et al.* (2020), the presence of this last species as a non-indigenous species is doubtful. Moreover, *P. unibranchia* is characterised by the absence of long-handled uncini on SGV (Day 1963) and should be transferred to the genus *Pistella* Hartmann-Schröder, 1996. In addition to the different shape of uncini, *Pista labruneae* n. sp. differs from *P. unibranchia* by the absence of lateral lobes on SG IV.

***Pista mediterranea* Gaillande, 1970**

Figure 19

Pista mediterranea Gaillande 1970: 443–448, figs 1–7.

Synonym. *Pista malmgreni* Saphronova & Jirkov in Jirkov, 2001

Material examined. Holotype (examined by M.H.L-M): USNM 42795, Port Miou, near Marseille, S. France, Mediterranean Sea, depth 2.5 m, January 1969. Paratype MNHN-IA-TYPE0819 (10 posteriorly incomplete specimens), Mediterranean Sea, Cassis, Port Miou, approx. 43°12′29″N 5°31′05″E, depth 2.5 m, January 1969.

Additional type material. Paratypes USNM 42796, seven specimens. Not examined.

Description (based on paratype MNHN-IA-TYPE0819). Relatively large species, all specimens posteriorly incomplete, with longest specimen being 39.1 mm long and 2.6 mm wide.

Transverse prostomium attached to dorsal surface of upper lip; basal part without eyespots; distal part of pros-

tomium shelf-like. Buccal tentacles long, filiform, deeply grooved. Peristomium forming lips, upper lip hood-like, large, wider than long, convoluted; lower lip swollen and squared shaped (Fig. 19C).

Segment I partially covered by lateral lobes of SG II, with small ventral lobes, projecting anteriorly (Fig. 19 A–B), connected to each other by a smooth membrane with rounded ventral indentation, surrounding lower lip. Segment II with pair of rounded ventro-lateral lobes, connected to each other by a large mid-ventral crest, indented and crenulated ventrally. Segment III with pair of developed lateral lobes, larger than those of SG II, auricular-shape, connected to each other by a thin mid-ventral crest, ventrally crenulated. Segment IV with pair of small latero-dorsal rounded lobes (Fig. 19A–B).

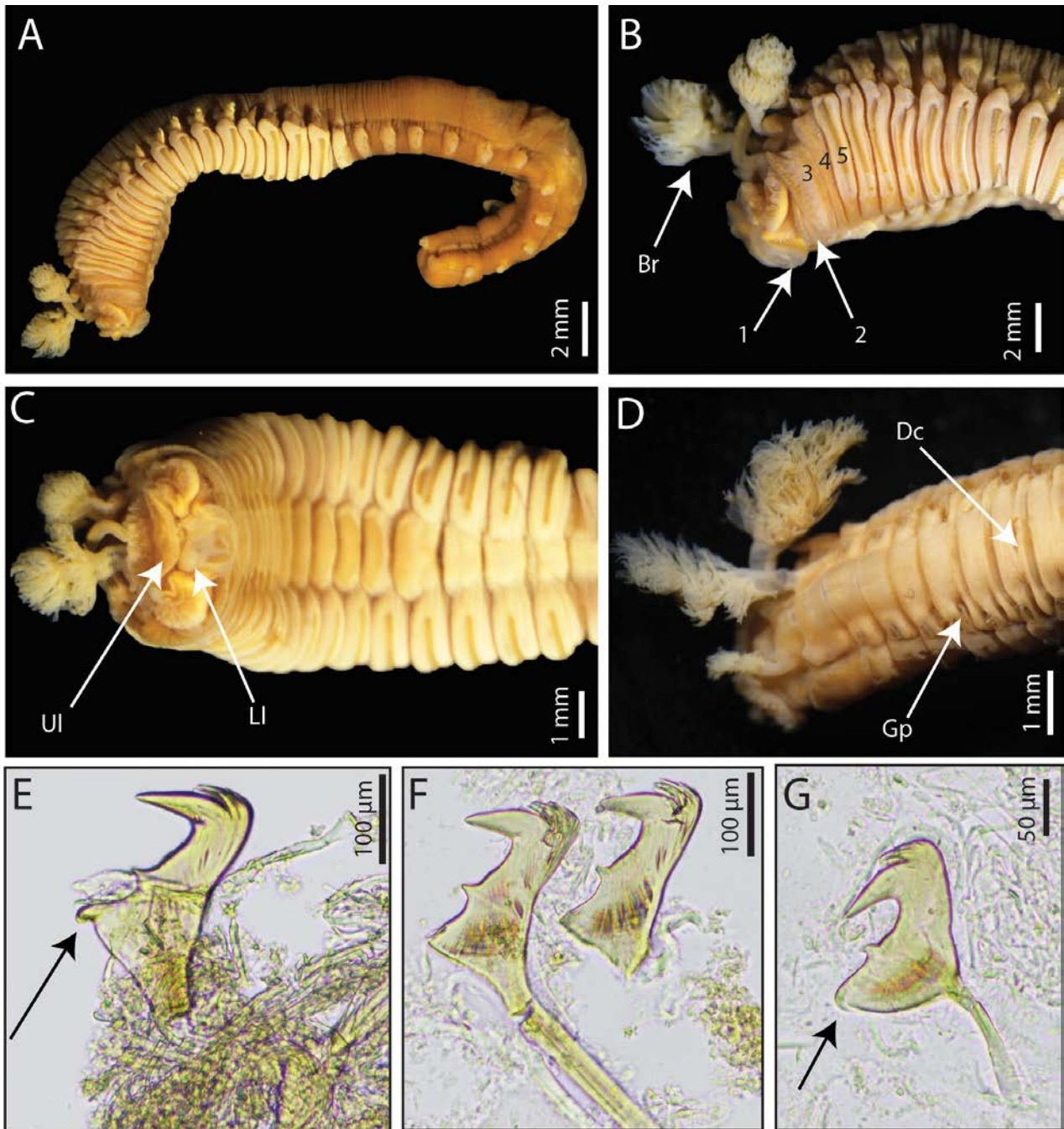


FIGURE 19. *Pista mediterranea* Gaillande 1970 Paratype MNHN-IA-TYPE0819. A. Entire specimen, lateral view; B. Anterior end, ventral view; C. Anterior end, ventral view; D. Anterior end, dorsal view; E–F. Uncini, SG V; G. Uncinus, SG X. Abbreviations: Br, branchiae; Dc, dorsal crests; Gp, genital papilla; Ll, lower lip; Ul, upper lip. Numbers referring to segments; black arrows pointing to comma-shaped extension.

Dorsal anterior margins of SG III–XI as protruding crests (Fig. 19D). Two pairs of dorso-lateral arborescent branchiae present on SG II–III, second pair slightly smaller, first pair inserted more dorsally; each branchia with long, annulated basal stem, branches arranged in spiral and highly dichotomous, with long filaments (Fig. 19A–D). Smooth mid-ventral shields present on SG –XXI, rectangular, of uniform width anteriorly, and becoming progressively longer posteriorly (Fig. 19C).

Notopodia beginning on SG IV, extending until SG XX; notopodia short, rectangular, first four pairs inserted progressively more laterally, then longitudinally aligned (Fig. 19A–B, D). Broadly-winged notochaetae arranged in two rows, broader on one side, with first row shorter (see Gaillande 1970: fig. 3).

Neuropodia present from SG V, as low, almost sessile ridges until end of notopodia, as low rectangular pinnules thereafter (Fig. 19A–C). Neurochaetae as long-handled uncini on SG V–X, with well-developed handles originating from heel, becoming progressively shorter; uncini arranged in partially intercalated double rows on SG XI–XX, in a face-to-face arrangement. Uncini from SG V very high, with a vertical prow (Fig. 19E–F). Uncini of following segments with the typical shape (i.e. normal size) (Fig. 19G); uncini with distally rounded prow with a comma-shaped extension, rounded heel, conspicuous dorsal button inserted halfway between base of main fang and prow, and main fang surmounted by a crest with five rows of numerous and progressively shorter secondary teeth.

Genital papillae on SG VI–VII, situated dorsally behind notopodia.

Pygidium not known.

Type locality. France, Western Mediterranean Sea, Cassis (Port Miou). Approx. 43°12'29"N 5°31'05"E.

Distribution. Mediterranean Sea (Gaillande 1970, Jirkov & Leontovitch 2017).

Habitat. Mud, in *Lithophyllum* algae (Gaillande 1970), shallow water, depth 2–4 m (Gaillande 1970, Jirkov & Leontovitch 2017).

Remarks. In the original description, Gaillande (1970) wrote that the long-handled processes of the uncini were difficult to see from SG VII to SG X, but we are able to observe these processes, which are thinner than in the previous chaetigers but clearly visible (Fig. 19G).

Pista malmgreni Saphronova & Jirkov in Jirkov, 2001 was synonymised with *P. mediterranea* by its own authors (Jirkov & Leontovitch 2013). When they described this species, whose type locality is situated in Bahuslän (Western Sweden), the authors also used a paratype from the Mediterranean Sea (Marseille) (Gil 2011). Further investigations based on holotype should be conducted to confirm this synonymy or to reinstate *P. malmgreni*.

Pista miossecai n. sp.

Figure 20

Material examined. Holotype. MNHN-IA-TYPE 2033, posteriorly incomplete (posterior part used for molecular analysis), Northeastern Atlantic, Bay of Biscay, Bay of Brest, VC, 48°18'59"N 4°23'28"W, depth 2.2 m, February 2019. **Paratypes.** AM W.53330, posteriorly incomplete (posterior part used for molecular analysis), Northeastern Atlantic, Bay of Biscay, Bay of Brest, VC, 48°18'59"N 4°23'28"W, depth 2.2 m, May 2018. MNHN-IA-TYPE 2034, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, Bay of Brest, VC, 48°18'59"N 4°23'28"W, depth 2.2 m, October 2015, mounted for SEM.

Description. In life, yellowish body, with buccal tentacles translucent; posterior areas of neuropodia dark red as posterior margin of ventral shields (Fig. 20A).

Holotype posteriorly incomplete, 16.8 mm long (14.2–36.0 mm) and 1.7 mm wide (1.9–2.8 mm), for 38 segments. Transverse prostomium attached to dorsal surface of upper lip; basal part with isolated eyespots, laterally covered by lobes on SG I and dorsally by prostomium (difficult to see); distal part of prostomium shelf-like. Buccal tentacles deeply grooved (Fig. 20A–D). Peristomium forming lips, upper lip hood-like, large, wider than long, and circular; lower lip large and swollen, rectangular, wider than long (Fig. 20D).

Segment I long, without lateral lobes; connected ventrally by a thin and smooth (crenulated) membrane with rounded ventral indentation, surrounding lower lip (Fig. 20A–D). Segment II with pair of rounded ventro-lateral lobes, connected to each other by a large mid-ventral crest, indented and crenulated ventrally. Segment III with pair of developed lateral lobes, larger than those of SG II, rounded, almost semi-circular lobes, connected to each other by a thin mid-ventral crest, ventrally crenulated (indented). Segment IV with pair of very short latero-dorsal rounded lobes, almost inconspicuous (Fig. 20A–D).

Dorsal anterior margins of SG III–VIII as protruding crests (Fig. 20B). Two pairs of dorso-lateral plume-shaped branchiae present on SG II–III, about the same size (or second pair smaller), first pair inserted more dorsally; each branchia with annulated basal stem, branches arranged in spiral with few dichotomies, branchial filaments long (Fig. 20B–D). Smooth to corrugated mid-ventral shields present on SG IV–XVII, rectangular (squared) shields, of uniform width anteriorly, and becoming progressively longer posteriorly (Fig. 20D).

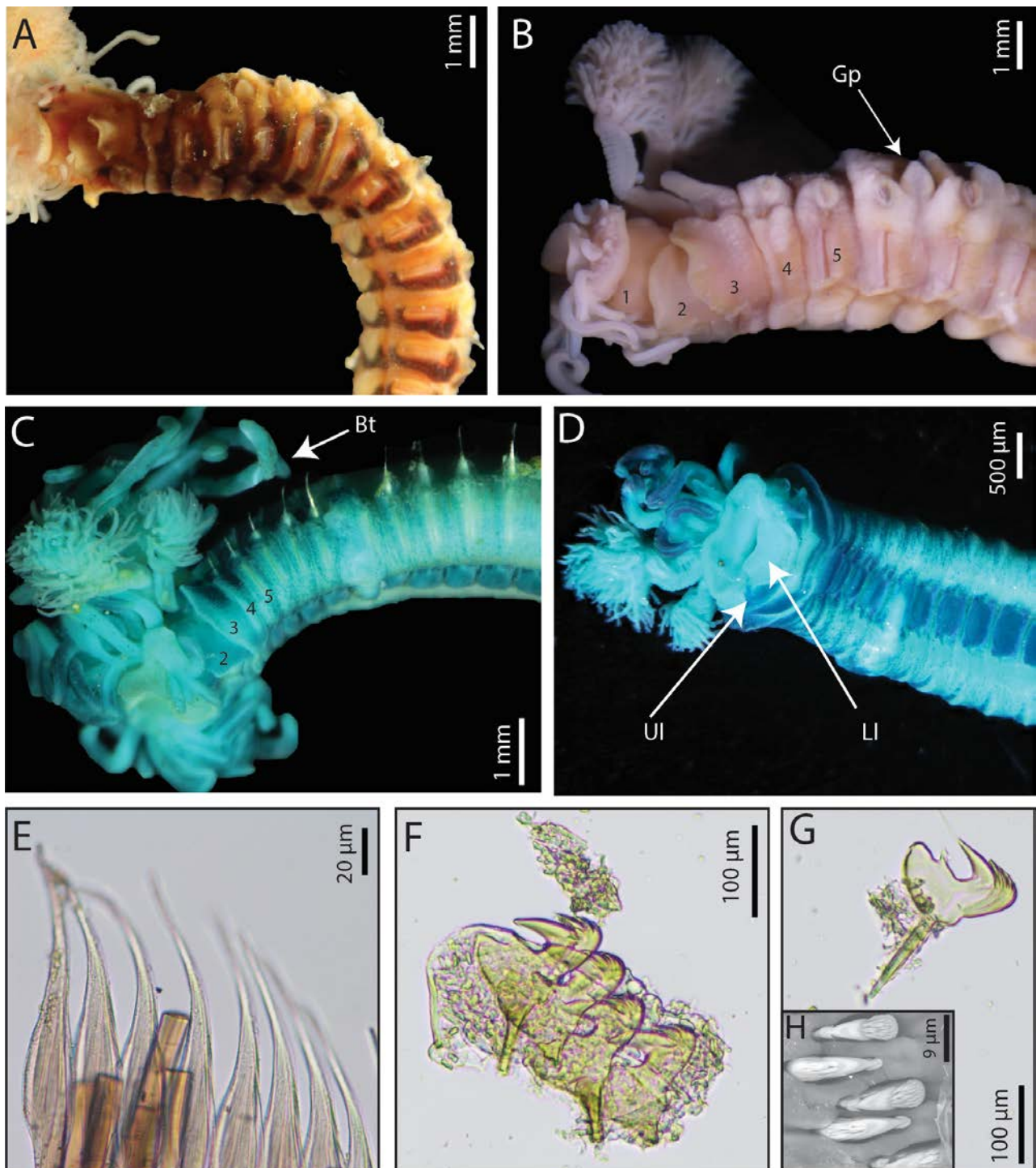


FIGURE 20. *Pista miossecai* n. sp. paratype AM W.53330 (A–B, E–F), holotype MNHN-IA-TYPE 2033 (C–D), paratype MNHN-IA-TYPE 2034 (G). A. Anterior end, lateral view, live specimen; B. Anterior end, lateral view, MG staining; C. Anterior end, lateral view, MG staining; D. Anterior end, ventral view, MG staining; E. Notochaetae, SG X; F. Uncini, SG V; G. Uncinus, SG X; H. Uncini, SG VIII. Abbreviations: Bt, buccal tentacles; Gp, genital papilla; Ll, lower lip; Ul, upper lip. Numbers referring to segments.

Notopodia beginning on SG IV, extending until SG XX; notopodia short, rectangular, first four pairs inserted progressively more laterally, then longitudinally aligned (Fig. 20A–C). Broadly-winged notochaetae arranged in two rows, broader on one side (Fig. 20E), with first row shorter.

Neuropodia present from SG V, as low, almost sessile ridges until end of notopodia (Fig. 20A–C), as low rectangular pinnules thereafter. Neurochaetae as long-handled uncini on SG V–X (Fig. 20F–G), with well-developed handles originating from heel. Uncini arranged in partially intercalated double rows on SG XI–XX; in a face-to-face arrangement. Uncini avicular, with short, triangular heel, distally rounded prow, pointed dorsal button inserted halfway between base of main fang and prow, convex base, and main fang surmounted by crest with five rows of numerous, progressively shorter secondary teeth (Fig. 20F–H).

Genital papillae on SG VI–VII, globular, situated dorsally behind notopodia (Fig. 20B).

Pygidium unknown.

Etymology. This species is dedicated to the famous Brest singer Christophe Miossec, whose music has accompanied NL for 25 years, especially when writing. This name was chosen in agreement with Jacques Grall and Vincent Le Garrec from the IUEM Brest laboratory who provided the type material.

Habitat. Shallow waters (depth 2 m), in maërl (rhodolith) beds.

Type locality. Bay of Brest, Bay of Biscay, Northeastern Atlantic Ocean, France. 48°18'59"N 4°23'28"W.

Distribution. Only known from the type locality.

Remarks. With two pairs of branchiae, *P. miosseci* n. sp. belongs to the *Pista cristata* (Müller, 1776) complex. *Pista miosseci* n. sp. differs from this last species by the presence of eyespots, the presence of dorsal crests on SG III–VIII and the presence of long-handled uncini on SG X. *Pista miosseci* n. sp. does not have lateral lobes on SG I while those of *P. cristata* are short and SG IV with pair of very short latero-dorsal rounded lobes while they are well-developed for *P. cristata*. However, investigations should be done concerning the presence of the dorsal crests, as they could be dependent on fixation.

Among the other European *Pista* species with this two pairs of branchiae, *P. miosseci* n. sp. differs from *P. mediterranea* by the absence of lateral lobes on SG I instead of presence of short ones for *P. mediterranea*. *P. miosseci* n. sp. differs also from *P. mediterranea* by the shape of thoracic uncini. Indeed, *P. mediterranea* has very high uncini on SG V, with a vertical prow and anterior comma-shaped uncini extension that are absent in *P. miosseci* n. sp. The comma-shaped uncini extension is a robust part of the uncini but its observation depends on the angle of the final preparation of the microscope slide. Thus, several uncini should be observed to confirm this character.

Pista miosseci n. sp. differs from *P. sauriaui* n. sp. by the absence of anterior comma-shaped extension on thoracic uncini that are present for *P. sauriaui* n. sp. and by the presence of long-handled uncini on SG X that are restricted to the SGV–VII for *P. sauriaui* n. sp. *Pista miosseci* n. sp. does not have lateral lobes on SG I while those of *P. sauriaui* n. sp. are large. Finally, *P. miosseci* n. sp. has eyespots which are absent in *P. sauriaui* n. sp.

Finally, *Pista miosseci* n. sp. differs from *P. wui* Saphronova, 1988 by the absence of large lobes on SG I (instead of small ones) and very short lateral lobes on SG IV, instead of well-developed ones for *P. wui* and by the presence of dorsal crests and eyespots which are absent on *P. wui*. The presence of dorsal crests may depend on fixation of specimens. Moreover, these crests were not considered a valuable taxonomic character until recently, and may be present in several species but have not been described.

In European waters, two other species of *Pista* with two pairs of branchiae, but with invalid status, occur: *Terebella turrita* Grube, 1860, synonymised with *P. cristata* (Fauvel 1927; Hartman 1959) and *Pista malmgreni* Saphronova & Jirkov in Jirkov, 2001 synonymised with *P. mediterranea* (see above). With a type locality situated in Adriatic Sea, *T. turrita* is probably valid under the genus *Pista*, belonging to the *P. cristata* complex. However, it is not possible to reinstate this species based on the original description and further investigations should be conducted.

***Pista sauriaui* n. sp.**

Figures 2D; 21–22

Material examined. Holotype. MNHN-IA-TYPE 2035, Northeastern Atlantic Ocean, Brittany, Bay of Brest, 48°19'58" N 4°26'59"W, depth 3 m, February 2013. **Paratypes.** MNHN-IA-TYPE 2036, Northeastern Atlantic Ocean, Brittany, Bay of Brest, MF1, 48°18'05" N 4°19'26"W, depth 2 m, January 2016, mounted for SEM. AM

W.53331, Northeastern Atlantic Ocean, Brittany, Bay of Brest, 48°18'59"N 4°23'28"W, depth 2.2 m, May 2018, posterior part used for molecular analysis.

Additional material. SMA-LR_Pista_01, Northeastern Atlantic Ocean, Brittany, Pertuis Breton, 46°13'53" N 1°22'28"W, depth 2 m, April 2013; SMA-LR_Pista_02, Northeastern Atlantic Ocean, Brittany, Pertuis Breton, 46°13'53" N 1°22'28"W, depth 2 m, April 2013.

Description. Holotype posteriorly incomplete, 21.1 mm long (28.5 mm) long and 2.2 mm wide (1.9 mm), for 25 segments.

Transverse prostomium attached to dorsal surface of upper lip; basal part without eyespots; distal part of prostomium shelf-like. Buccal tentacles deeply grooved (Fig. 22A–B). Peristomium forming lips, upper lip hood-like, large, wider than long; lower lip large and swollen, rectangular, wider than long (Fig. 21A).

Segment I narrow, with one pair of large lobes directed anteriorly; lobes originating dorso-laterally, at level of first pair of branchiae, partially covered laterally by prostomium; connected to each other by thin and smooth membrane with rounded ventral indentation, surrounding lower lip (Figs 21A–C; 22A–B). Segment II with one pair of rounded ventro-lateral lobes, connected to each other by a large mid-ventral crest, ventrally crenulated. Segment III with one pair of lateral lobes, same size as those of SG II, auricular-shaped, connected ventrally to the corresponding ventral pad. Segment IV with pair of very small latero-dorsal rounded lobes, almost inconspicuous (Figs 21B–C; 22A–B).

Dorsal anterior margins of SG III–VIII as protruding crests (Fig. 21D). Two pairs of arborescent branchiae situated dorso-lateral on SG II–III, of about the same size, first pair inserted more dorsally; each branchia with long, annulated basal stem, dichotomously branching for some levels, with long branchial filaments (Figs 21B–D; 22A). Corrugated mid-ventral shields present on SG III–XXIII, rectangular, of uniform width anteriorly, and becoming progressively longer (Fig. 21A).

Notopodia from SG IV to SG XX; notopodia short, rectangular, first four pairs inserted progressively more laterally, then longitudinally aligned (Figs 21B–D; 22A). Notochaetae broadly-winged of two sizes, arranged in two rows (Fig. 21E), with first row shorter.

Neuropodia present from SG V, as low, almost sessile ridges until end of notopodia (Figs 21B–C; 22A), thereafter as low rectangular pinnules. Neurochaetae as avicular uncini, with well-developed handle on SG V–VII (Figs 2D; 21F–G), uncini without handles from SG VIII (Fig. 22H), uncini arranged in partially intercalated double rows on SG XI–XX in a face-to-face arrangement. Uncini with short, triangular heel, rounded prow with a comma-shape extension (Figs 2D; 21F–H), short dorsal button inserted halfway between base of main fang and prow, convex base, and main fang surmounted by a crest with five rows of numerous and progressively shorter secondary teeth above the main fang (Figs 2D; 21F–H; 22C–D).

Genital papillae on SG VI–VII, situated dorsally behind notopodia (Fig. 21D). Pygidium unknown.

Etymology. This species is named after Pierre-Guy Sauriau, benthic ecologist from the Laboratory of La Rochelle who provided some of the studied material and who was the first supervisor of NL. This name was chosen in agreement with Jérôme Jourde (La Rochelle), Jacques Grall and Vincent Le Garrec (IUEM Brest) who worked with Pierre-Guy for a long time.

Habitat. Shallow waters (depth 2–3 m), in maërl (rhodolith) beds and *Zostera marina* meadows.

Type locality. Bay of Brest, Bay of Biscay, Northeastern Atlantic Ocean, France.

Distribution. Bay of Brest and Pertuis Breton (Biscay of Biscay), 48°19'58" N 4°26'59"W.

Remarks. *Pista sauriaui* n. sp. belongs to the two-pairs of branchiae group in *Pista* genus, as well as *P. cristata*, the type species, *P. miosseci* n. sp. and *P. mediterranea*, previously included here. *Pista sauriaui* n. sp. differs from *P. cristata* by the presence of anterior comma-shaped extension on thoracic uncini (see *P. miosseci* n. sp. Remarks) and by the presence of dorsal crests on SG III–VIII (these crests are absent in *P. cristata*) (see *P. miosseci* n. sp. Remarks). Finally, these two species differ by the shape of their lateral lobes: *P. sauriaui* n. sp. has large ones on SG I and very small ones on SG IV, while *P. cristata* has short ones on SG I and very large ones on SG IV.

Pista sauriaui n. sp. differs from *P. miosseci* n. sp. by the presence of anterior comma-shaped extension on thoracic uncini which are absent in *P. miosseci* n. sp. and by long-handled uncini restricted to the SGV–VII, instead of presence of these long-handled uncini at least until SG X in *P. miosseci* n. sp. Also, *P. sauriaui* n. sp. has no eyespots, which are present in *P. miosseci* n. sp. and has large lateral lobes on SG I, while those of *P. miosseci* n. sp. are absent. Both species, *P. sauriaui* n. sp. and *P. miosseci* n. sp. occur in the same geographical area (Bay of Brest, Brittany), in the same habitat (shallow waters, in maërl beds) and share several morphological features. The use of

molecular analysis confirms that they belong to different species but they have probably evolved differently. This study clearly highlights the need of integrative taxonomy, combining molecular approach and careful morphological observation, especially for the species complexes.

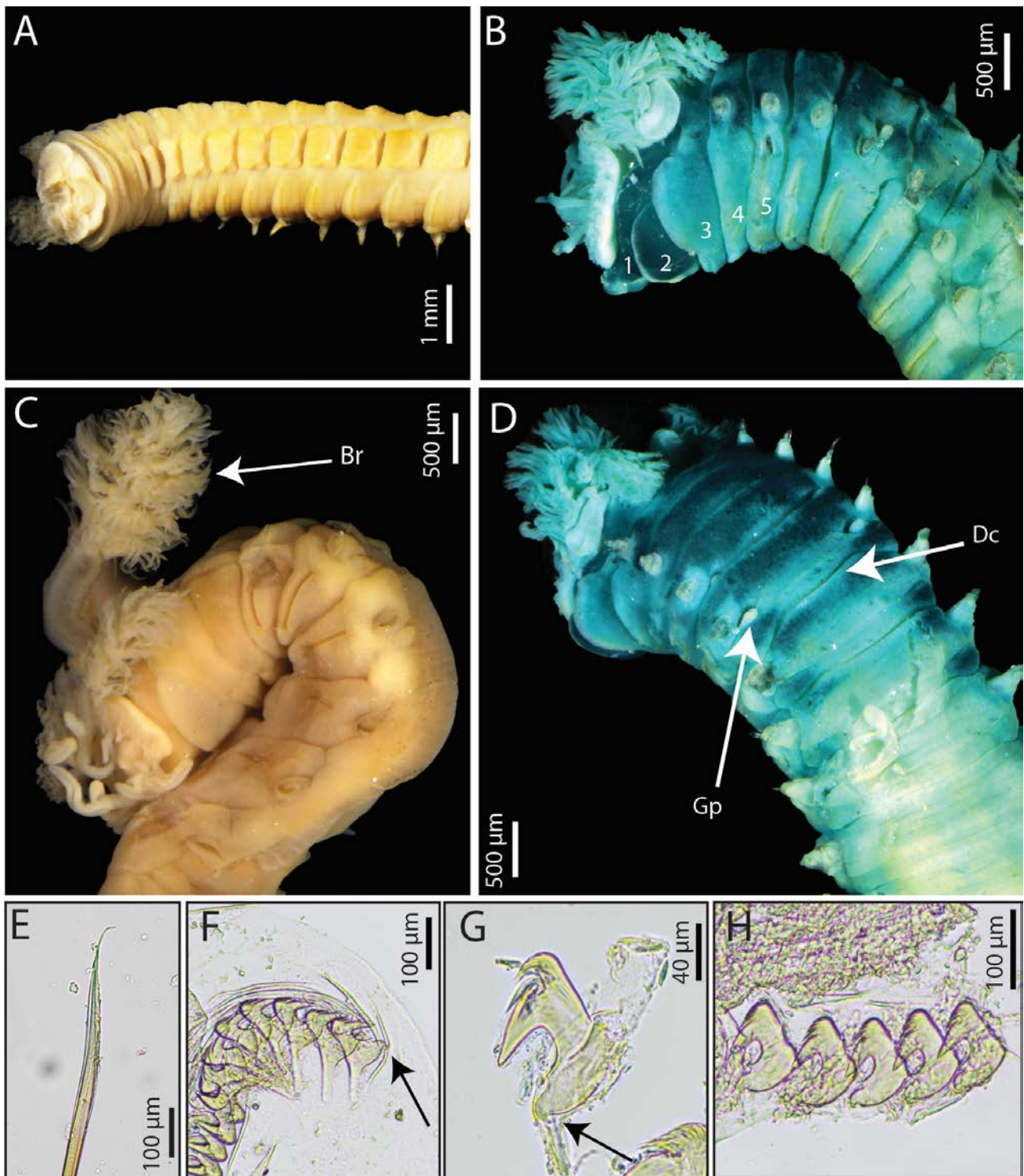


FIGURE 21. *Pista sauriaui* n. sp. holotype MNHN-IA-TYPE 2035 (A–B, D), paratype MNHN-IA-TYPE 2036 (C), paratype AM W.53331 (E), additional material SMA-LR-Pista-01 (F–H). A. Anterior end, ventral view; B. Anterior end, lateral view, MG staining; C. Anterior end, lateral view; D. Anterior end, dorso-lateral view, MG staining; E. Notochaetae, SG XI; F–G. Uncini, SG V; H. Uncini, SG X. Abbreviations: Br, branchiae; Dc, dorsal crests; Gp, genital papillae. Numbers referring to segments; black arrows pointing to comma-shaped extension.

Pista sauriaui **n. sp.** differs from *P. wui* Saphronova, 1988 (described from British Columbia), both with two pairs of branchiae, by the presence of long-handled uncini restricted to the SGV–VII, instead of presence of these long-handled uncini at least until SG X for *P. wui*, by the presence of large lobes on SG I (instead of small ones) and very short lateral lobes on SG IV, instead of well-developed ones for *P. wui*. Finally, *P. sauriaui* **n. sp.** has dorsal crests on SG III–VIII which are absent for *P. wui* (see Remarks *P. miosseci* **n. sp.**).

Finally, *Pista sauriaui* **n. sp.** differs from *P. mediterranea* by the absence of very high uncini with vertical prow on SG V and by the presence of long-handled uncini restricted to the SGV–VII, instead of presence of these long-handled uncini at least until SG X in *P. mediterranea*. Also, *Pista sauriaui* **n. sp.** differs also by the presence of large lobes on SG I, which are small for *P. mediterranea*.

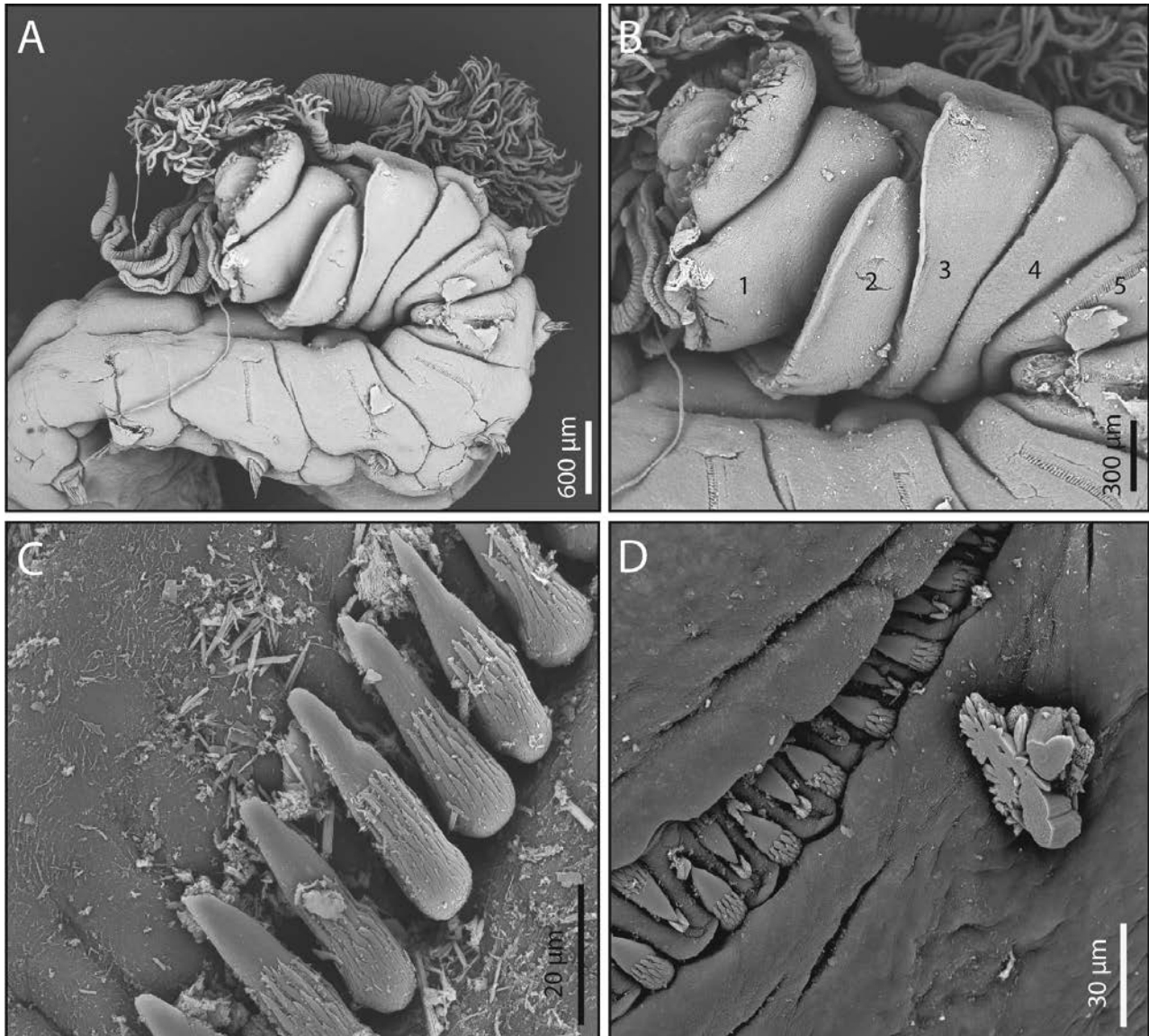


FIGURE 22. *Pista sauriaui* **n. sp.** SEM paratype MNHN-IA-TYPE 2036. A–B. Anterior end, lateral view; C. Uncini, SG VII; D. Uncini, SG XI. Numbers referring to segments.

Terebella **linnaeus**, 1767

Type-species: *Terebella lapidaria* Linnaeus, 1767, by monotypy.

Diagnosis. (after Hutchings *et al.* 2021b). Transverse prostomium attached to dorsal surface of upper lip; basal part as a thick crest, eyespots frequently present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; lips expanded, upper lip relatively short, hood-like, about as long as wide; large,

button-like to cushion-like, mid-ventral lower lip. Segment I conspicuous all around, dorsally narrow, expanded ventrally, frequently with low mid-ventral lobe marginal to mouth; other lobes on anterior segments absent. Anterior segments highly glandular ventrally, with discrete, smooth to slightly crenulated, rectangular to trapezoidal mid-ventral shields. Three pairs of branching branchiae with short main stems, usually on SG II–IV, but sometimes on discontinuous segments. Conical notopodia beginning on SG IV, extending for a variable number of segments, frequently to posterior body; notochaetae medially winged and distally serrated, and alimbate and serrated, frequently with blade at an angle, usually with transition on types of chaetae from anterior to midbody notopodia. Neuropodia beginning on SG V, as low sessile ridges throughout; neurochaetae as short-handled avicular uncini, in completely intercalated to partially back to back double rows from SG XI until posterior body. Nephridial papillae on SG III, genital papillae usually present from SG VI, extending for a variable number of segments, between parapodial lobes. Pygidium smooth to slightly crenulated.

***Terebella banksyi* n. sp.**

Figures 23–24

Material examined. Holotype. MNHN-IA-TYPE 2037, complete in two parts, gravid, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Grand Banc, approx. 44°40'27"N 01°11'46"W, intertidal, October 2017, few parapodia used for molecular analysis. **Paratypes.** AM W.53332, complete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Jacquets, 44°43'17"N 01°11'24"W, intertidal, in oyster reefs, January 2018. MNHN-IA-TYPE 2038, complete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Le Cla, 44°40'43"N 01°08'11"W, intertidal, in oyster reefs, August 2017. MNHN-IA-TYPE 2039, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Jacquets, 44°43'17"N 01°11'24"W, intertidal, in oyster reefs, January 2018, mounted for SEM.

Additional material. SMA-Arc-Eupoly-Jac02, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Jacquets, 44°43'17"N 01°11'24"W, intertidal, in oyster reefs, January 2018, mounted for SEM. SMA-Arc-Terebella-02, one specimen, complete, Northeastern Atlantic Ocean, Arcachon Bay, Le Cla, 44°40'43"N 01°08'11"W, intertidal, in oyster reefs, August 2017, some parapodia used for molecular analysis. SMA-Arc-Terebella-03, one specimen, complete, Northeastern Atlantic Ocean, Arcachon Bay, Le Cla, 44°40'43"N 01°08'11"W, intertidal, in oyster reefs, August 2017, some parapodia used for molecular analysis.

Description. Holotype complete, 33.9 mm long (12.1 mm) long and 2 mm wide (0.6 mm), for about 80 segments.

Transverse prostomium attached to dorsal surface of upper lip; basal part with few red eyespots (absent on holotype, probably faded), well separated and situated laterally only; distal part shelf-like. Numerous long and deeply grooved buccal tentacles, reaching end of the body (Fig. 23A–D). Peristomium forming lips, upper lip hood-like and slightly convoluted, higher than broad; lower lip swollen, cushion-like, broader than high (Figs 23B–C, 24B).

Segment I narrow, forming ventral lobe (Fig. 23B–C); absence of lateral lobes on anterior SG I–IV. Three pairs of dichotomous branchiae, on discontinuous segments, SG II–III and V (Figs 23C–D; 24A), with wide medial gap; first pair situated laterally, third pair more dorsally; with numerous short filaments, arising from long stems and branches (Figs 23A, C–D; 24A–B). Dorsum of anterior chaetigers tessellated. Ventral shields on SG II–XIV (n=13), rectangular, well defined, inflated on SG III–IV, absence of mid-ventral groove posteriorly.

Notopodia beginning on SG IV, extending posteriorly until last few chaetigers (n>75); notopodia short, rectangular; decreasing in size posteriorly (Fig. 23A–D). Notochaetae identical on all segments, narrowly-winged from mid-length, with blade at an angle of about 45° with the shaft and curled serrated tip (Fig. 23E–F).

Neuropodia present from SG V, as low, almost sessile ridges throughout (Figs 23A–D; 24B). Neurochaetae as short-handled avicular uncini, arranged in double rows from SG XI to posterior body, in face-to-face arrangement. Uncini with triangular heel; long digitiform prow, pointing downwards and prolonged by a thin curved tendon, pointed dorsal button inserted halfway between base of main fang and prow, convex base, and main fang surmounted by crest with four rows of secondary teeth (Figs 23G; 24C–D).

Twelve pairs of nephridial and genital papillae, a large globular one on SG III at base of branchiae, and small globular ones on SG V–XV, situated between notopodia and neuropodia and slightly displaced posteriorly (Fig. 23C–D).

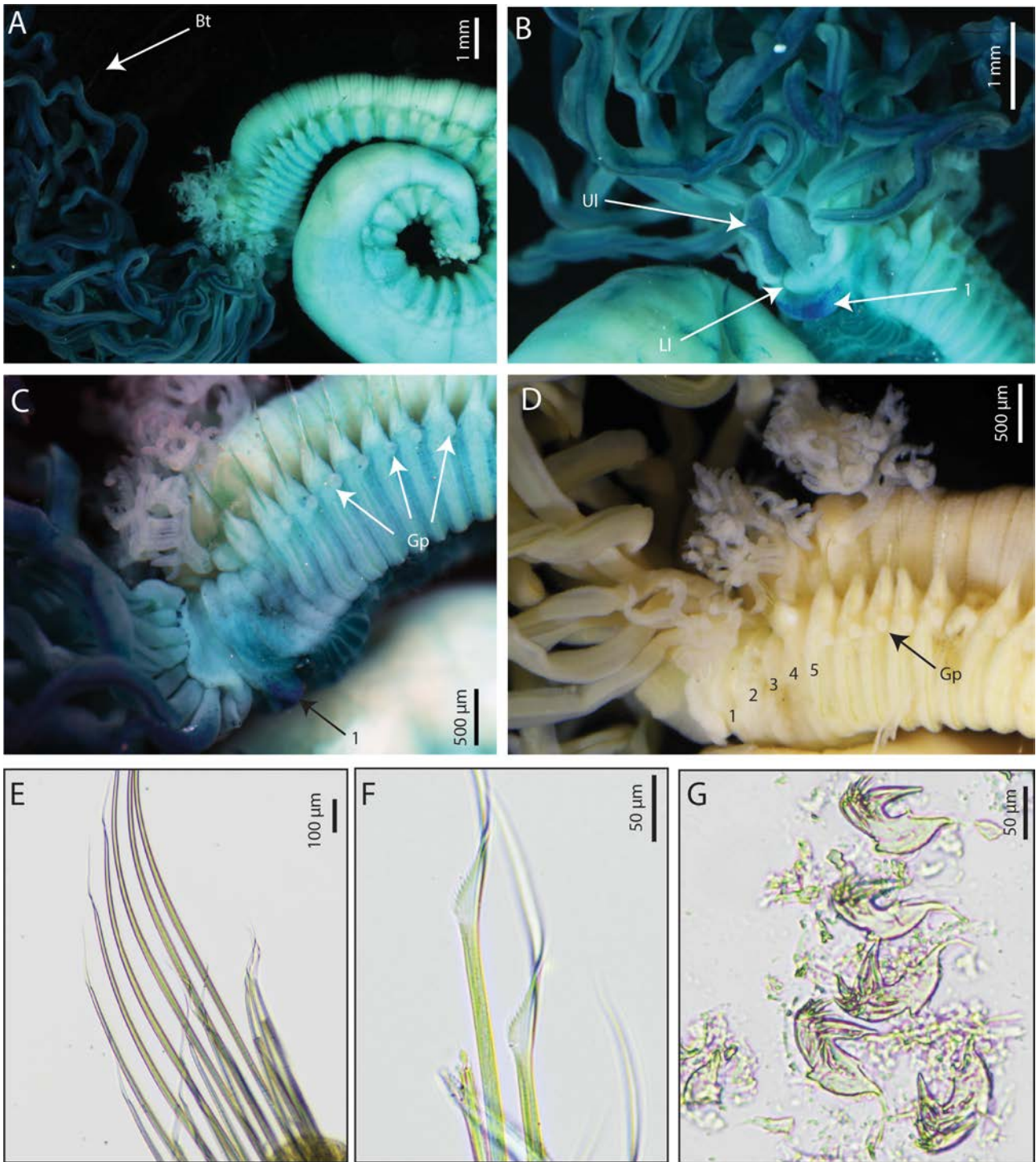


FIGURE 23. *Terebella banksyi* n. sp. holotype MNHN-IA-TYPE 2037. A. Entire specimen, lateral view, MG staining; B. Anterior end, ventral view, MG staining; C. Anterior end, lateral view, MG staining; D. Anterior end, dorso-lateral view; E. Notochaetae, SG X; F. Notochaetae, posterior segments; G. Uncini, SG X. Abbreviations: Br, branchiae; Bt, buccal tentacles; Gp, genital papillae; Ll, lower lip; Ul, upper lip. Numbers referring to segments.

Pygidium rounded.

Etymology. This species is dedicated to Banksy, a brilliant street artist whose graphic work always conveys powerful messages.

Type locality. Jacquets, Arcachon Bay, Bay of Biscay, Northeastern Atlantic Ocean, France, 44°43'17"N 01°11'24"W.

Distribution. Only known from type locality.

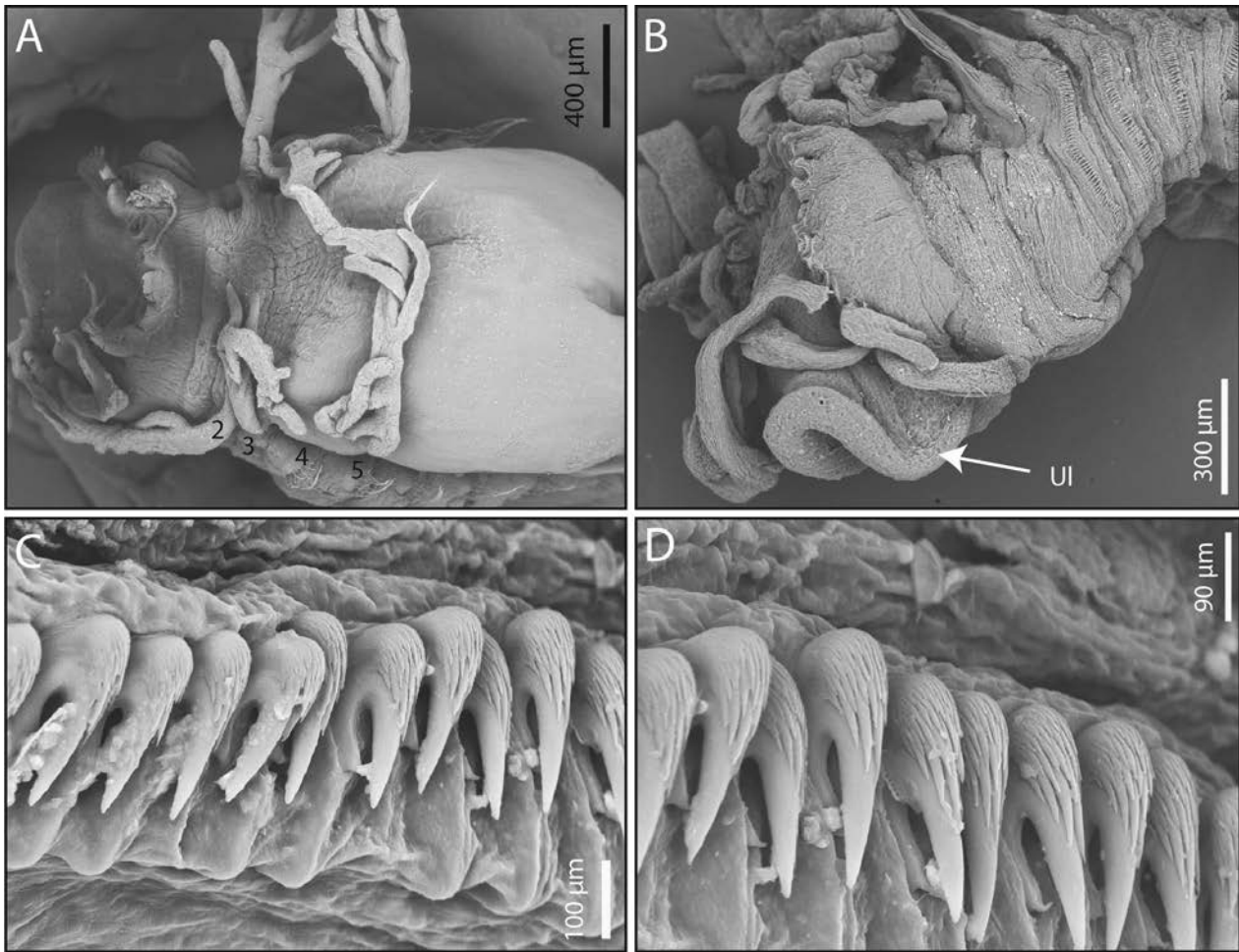


FIGURE 24. *Terebella banksyi* n. sp. paratype MNHN-IA-TYPE 2039 (A), additional material SMA-MNHN-Arc-Eupoly-Jac02 (B–D). A. Anterior end, dorsal view; B. Anterior end, lateral view; C–D. Uncini, SG V. Abbreviations: UI, upper lip. Numbers referring to segments.

Habitat. Under oyster shells, on oyster farms, intertidal.

Remarks. Until now, a single species of *Terebella* was considered to be valid in the European waters, *T. lapidaria* Linnaeus, 1767 described from the Mediterranean Sea. *Terebella banksyi* n. sp. differs from *T. lapidaria* by the presence of twelve pairs of nephridial and genital papillae, instead of the five pairs as in members of *T. lapidaria*, by the branchiae present on discontinuous segments (SG II–III and V), instead of the more usual distribution of the branchiae on consecutive segments (SG II–IV) for *T. lapidaria*, and by the absence of a spur on notochaetae from posterior chaetigers (instead of the blades at 90° with the shafts of the posterior notochaetae for *T. lapidaria*).

Two other species of *Terebella* were described from European waters, but are now synonymised with *T. lapidaria*: *Terebella constrictor* Montagu, 1819 and *Heterophyselia bosci* Quatrefages, 1866 (Read & Fauchald 2021). As Montagu never deposited his type material, it is impossible to confirm the identity of his species. The description is very sparse but the figure (plate XII, Fig. 1, Montagu 1819) clearly shows absence of branchiae on SG V, and thus differs from *T. banksyi* n. sp. For the second species, we have compared our material with the syntype of *Heterophyselia bosci* (MNHN-IA-TYPE0405) which is in very good condition. With the presence of branchiae on SG II–IV and of nephridial and genital papillae until SG X, this species is very similar with *T. lapidaria* and we suggest these two species should be synonymized, see below.

Finally, another species was described from Canary Islands, close to European waters: *Terebella orotavae* (Langerhans, 1881). This species differs from *T. banksyi* n. sp. by the distribution of the branchiae on consecutive segments (SG II–IV) instead of the branchiae not present on consecutive segments (SG II–III and V), by the presence of a single nephridial papillae instead of the presence of twelve pairs of nephridial and genital papillae for *T. banksyi* n. sp. and by the presence of two types of notochaetae, instead of one as in *T. banksyi* n. sp.

In Arcachon Bay, *Terebella banksyi* **n. sp.** was always found associated with the Japanese oysters *Crassostrea gigas* Thunberg, 1793, either on oysters reefs or on oysters farms. Recently, a study showed that a new species of bait worms, *Marphysa victori* Lavesque, Daffe, Bonifácio & Hutchings, 2017 (Lavesque *et al.* 2017b), described from Arcachon Bay was actually an exotic undescribed species, which originated from either Japan or China and assumed to have been imported into the Arcachon Bay via oyster transfers (Lavesque *et al.* 2020c). The morphology of the Asiatic species of *Terebella* has therefore been verified to confirm that *T. banksyi* **n. sp.** is not an exotic species. Three species belonging to this genus were described from Asia: *Terebella copia* Hutchings, 1990 from Hong-Kong; *Terebella punctata* Hessle, 1917, from Japan; and *Terebella sarsii* Grube, 1878 from Philippines (Hutchings *et al.* 2021a). *Terebella copia* differs from *T. banksyi* **n. sp.** by the consecutive presence of branchiae on SGIII–V, and the presence of one to five nephridial and genital papillae only. *Terebella punctata* differs from *T. banksyi* **n. sp.** by the presence of nephridial and genital papillae until SG XXV and the presence of buccal tentacles covered with rows of small and round brown spots (in specimens preserved in alcohol), but no mention is made concerning the distribution of the branchial segments in the original description. Finally, *T. sarsii* differs from *T. banksyi* **n. sp.** by the presence of 17 pairs of notopodia only (and thus probably does not belong to *Terebella* genus), instead of more than 75. To conclude, *T. banksyi* **n. sp.** differs from all currently described species of *Terebella* from the Asiatic region and we are confident that it is a native species.

***Terebella* cf. *lapidaria* Linnaeus, 1767**

Figures 2A; 25

Terebella lapidaria—Linnaeus 1767 : 1092 ; Saint-Joseph 1894: 202–205, pl. VIII, figs 225–229, pl. IX, figs 230–231; Fauvel 1927: 254–255, fig. 87, f-1.

Synonyms. *Terebella constrictor* Montagu, 1819; *Amphitrite neapolitana* Delle Chiaje, 1828; *Terebella misensis* Costa, 1841; *Terebella corallina* Grube, 1855; *Terebella pectinata* Grube, 1855; *Terebella rosea* Grube, 1860; *Terebella megalonema* Schmarda, 1861; *Heterophyselia bosci* Quatrefages, 1866; *Heteroterebella sanguinea* Claparède, 1869; *Terebella sulcigera* Claparède, 1869.

Material examined. MNHN-IA-PNT 131, complete, English Channel, Plougrescant, Pointe du Chateau, 48°52'11"N 3°13'30"W, intertidal, January 2019. SMA-LR-Tere-02, Northeastern Atlantic, Bay of Biscay, La Rochelle Harbour, 46°09'28"N 1°13'16"W, intertidal, September 2019. SMA-Arc-Eupoly-GdBC, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, Arcachon Bay, Grand Banc, 44°40'27"N 01°11'46"W, intertidal, October 2017, mounted for SEM. SMA-LR-Tere-03, posteriorly incomplete, Northeastern Atlantic, Bay of Biscay, La Rochelle Harbour, 46°09'28"N 1°13'16"W, intertidal, September 2019.

Description. Longest complete specimen 36.7 mm long and 2.1 mm wide, for about 80 segments. Transverse prostomium attached to dorsal surface of upper lip; basal part with red eyespots more concentrated laterally, continuing dorso-laterally as a single band of eyespots, with eyespots progressively becoming more separated; distal part shelf-like. Buccal tentacles numerous, long, filiform, wrinkled and deeply grooved (Fig. 25A–C). Peristomium forming lips, upper lip hood-like convoluted, broader than high; lower lip swollen, cushion-like, broader than high (Fig. 25B).

Segment I narrow, forming low ventral lobe; lateral lobes absent on SG II–IV. Three pairs of dichotomous branchiae, on SG II–IV (Fig. 25A–D), with wide medial gap; second pair situated more laterally than first and third pairs; with numerous short filaments, arising from long stems and branches (Fig. 25A–D). Dorsum of anterior chaetigers tessellated (Fig. 25C). Ventral shields on SG II–XIII, rectangular, well defined; mid-ventral groove from SG XIV (Fig. 25A–B).

Notopodia from SG IV, extending posteriorly until last few chaetigers ($n > 80$); notopodia short, rectangular; first pair slightly shorter than following pairs (Fig. 25A–D). Notochaetae from anterior chaetigers narrowly-winged from mid-length, with blade at an angle of about 45° with the shaft and curled serrated tip (Fig. 25E–F); notochaetae of posterior chaetigers with blade at an angle of about 90° with the shaft and curled serrated tip; presence of a spur at the base of the tip (Fig. 25F).

Neuropodia present from SG V, as low, almost sessile ridges throughout (Fig. 25A–B, D). Neurochaetae as short-handled avicular uncini, arranged in double rows from SG XI to posterior body, in a face-to-face arrangement.

Uncini with triangular heel; long digitiform prow, pointing downwards and prolonged by a thin curved tendon, pointed dorsal button inserted halfway between base of main fang and prow, convex base, and main fang surmounted by crest with four rows of secondary teeth (Figs 2A; 25G–H).

Nephridial and genital papillae on SG III and SG VI–X, globular, at base of branchiae on SG III, small, rounded above neuropodia and slightly displaced posteriorly on SG VI–X.

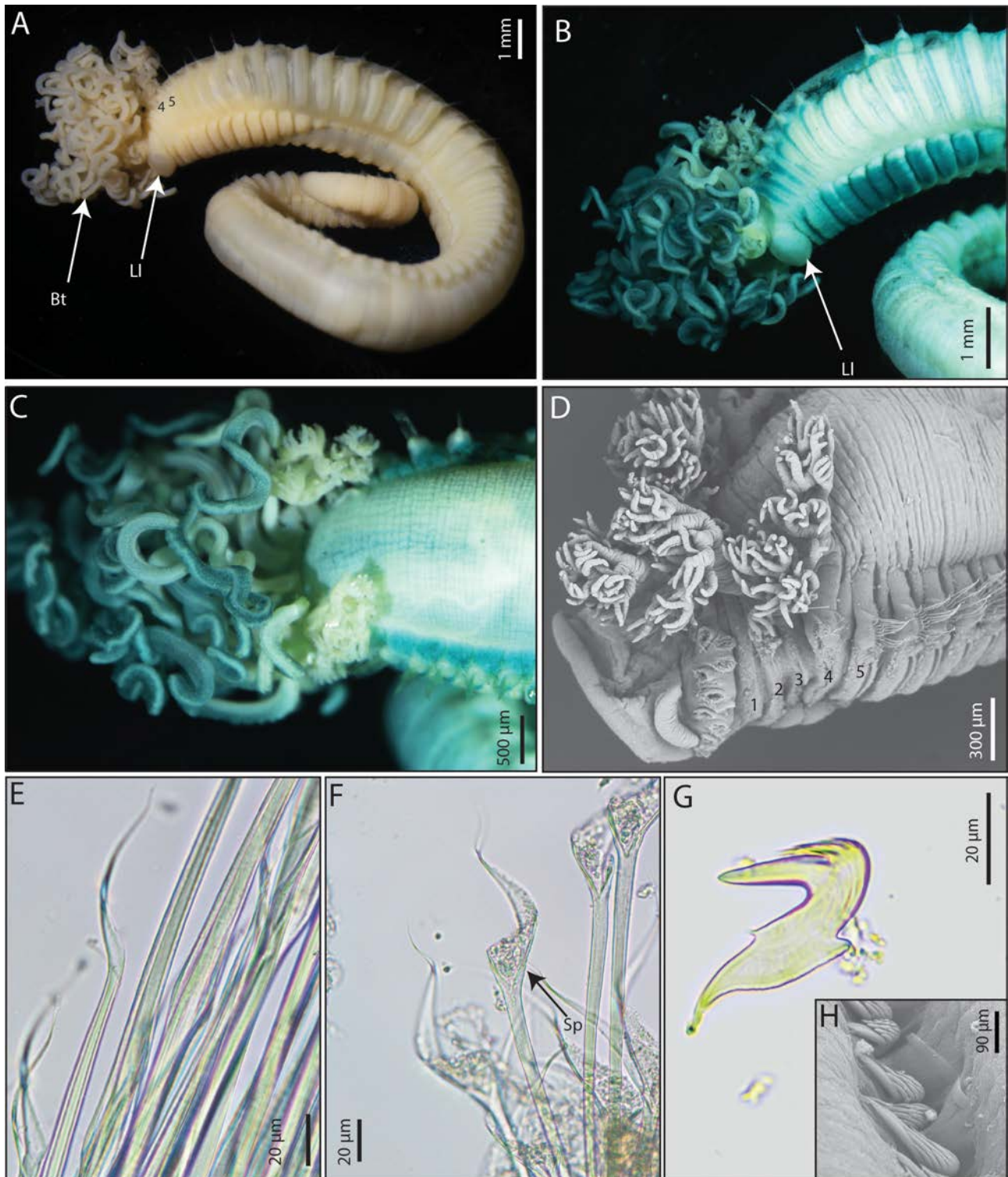


FIGURE 25. *Terebella lapidaria* Linnaeus, 1767 MNHN-IA-PNT 131 (A–C, E–G), SMA-Arc-Eupoly-GdBC (D, H). A. Entire specimen, lateral view; B. Anterior end, lateral view, MG staining; C. Anterior end, dorsal view, MG staining; D. Anterior end, dorso-lateral view; E. Notochaetae, SG IX; F. Notochaetae, posterior segments; G. Uncinus, SG X; H. Uncini, SG V. Abbreviations: Bt, buccal tentacles; LI, lower lip; Sp, spur. Numbers referring to segments.

Pygidium discoidal and crenulated.

Type locality. Mediterranean Sea (Gil 2011).

Type material. Cannot be traced, probably never deposited.

Distribution. Bay of Biscay, English Channel (this study; Fauvel 1927; Gil 2011), Mediterranean Sea (Linnaeus 1767; Fauvel 1927), Adriatic (Fauvel 1927, Gil 2011) and Aegean Sea (Gil 2011).

Habitat. Under rocks, intertidal (this study), in muddy bottoms, shallow waters (Gil 2011).

Remarks. The original description by Linnaeus (1767) is short, with very few taxonomic details and no precise type locality is given, which is not surprising as these taxonomic requirements were developed after Linnaeus. Specimens examined in this study match with descriptions of specimens from the French coasts studied by de Saint-Joseph (1894) and Fauvel (1927). However, all these specimens were sampled from the Atlantic coast while the type locality of this species is situated in the Mediterranean Sea. Until an accurate description, based on Mediterranean specimens, is available, we prefer to identify these specimens as *Terebella* cf. *lapidaria*.

Molecular data

During this study, 10 sequences of COI gene, belonging to eight species and 31 sequences of 16S gene, belonging to 15 species were obtained and deposited in Genbank (Table 1, Figs 26 and 27). For COI, three sequences were attributed to two known species (*A. figulus*, *L. conchilega*), five sequences to three new species described during this study (*E. gili* n. sp., *P. sauriaui* n. sp., *T. banksyi* n. sp.) and two sequences to two (probably) new species that could not be described here because sequences were obtained from a single damaged specimen (*Eupolymnia* sp. C from the Gulf of Lion and *Pista* sp. A from the Bay of Biscay).

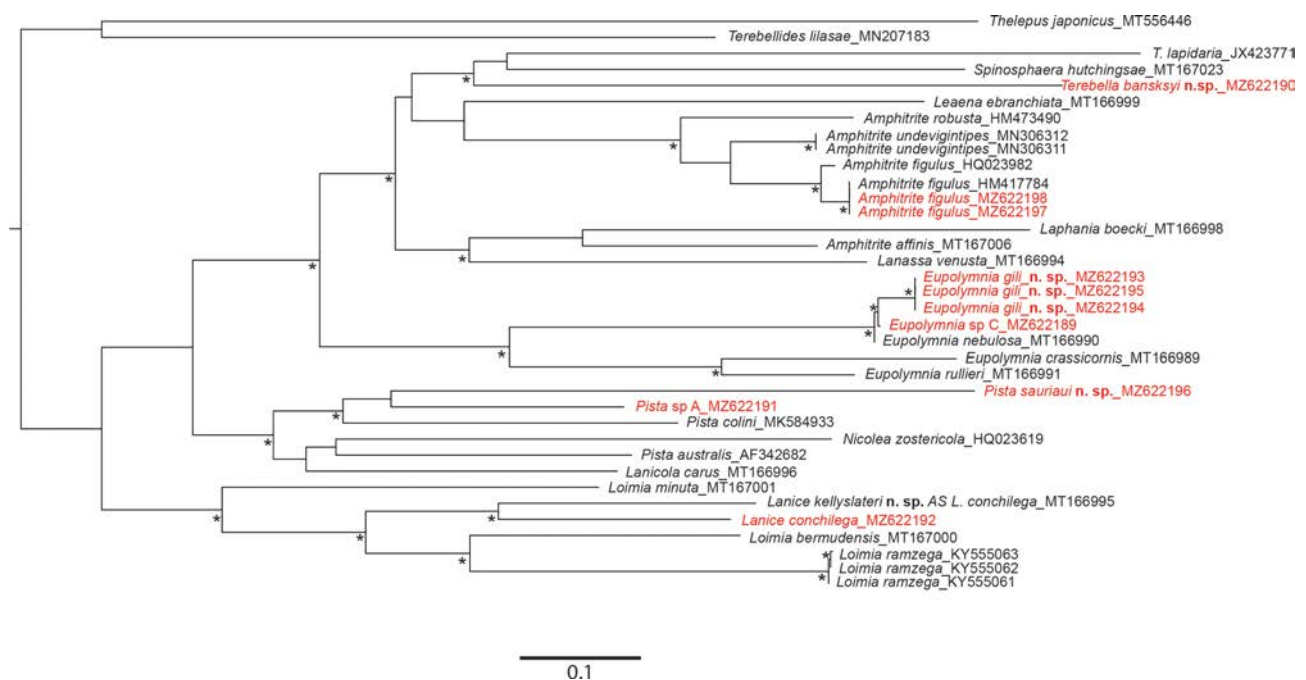


FIGURE 26. Majority-rule consensus tree from Bayesian analysis using COI. Asterisk indicates posterior probability > 80%. Text in red refers to specimens sequenced during this study.

For 16S, eight sequences belonged to three species already known from Europe (*A. figulus*, *L. conchilega*, *T. lapidaria*), 17 sequences to seven new described species (*E. gili* n. sp., *E. lacazei* n. sp., *E. meissnerae* n. sp., *L. kellyslateri* n. sp., *P. miosseci* n. sp., *P. sauriaui* n. sp., and *T. banksyi* n. sp.) and finally, as for COI, six sequences to six (probably) new species impossible to describe in this study (*Eupolymnia* sp. A and *Eupolymnia* sp. D from Corsica, *Eupolymnia* sp. B from the Bay of Biscay, and finally *Eupolymnia* sp. C from the Gulf of Lion; *Pista* sp. A and *Pista* sp. B from the Bay of Biscay and Corsica respectively).

Obtaining these sequences was essential to separate species morphologically very similar. Indeed, several of the new species described here belong to complexes of cryptic or pseudo-cryptic species. Without molecular tools,

it would have been impossible to differentiate and describe species of the *P. cristata*, *L. conchilega* or *E. nebulosa* complexes (Figs 26 and 27). These data also permitted us to highlight that several sequences stored in Genbank do not correspond to the correct species (and probably belong to undescribed species). The first one is *A. figulus*. Based on COI molecular results (Fig. 26), the French specimens differ from the *A. figulus* identified by Carr *et al.* (2011) from Canada, New Brunswick (GenBank accession number: HQ023982). However, as our specimens were sampled much closer to the type locality (East coast of Scotland) and are morphologically similar to the description of the species, we suggest that the Canadian specimens may belong to a different species, probably not new, as several species of *Amphitrite* have been described from that area, such as *A. brunnea* (Stimpson, 1853), *A. ornata* (Leidy, 1855), or *A. attenuata* Moore, 1907. On the other hand, the French specimens match molecularly with specimens from the White Sea, Kandalaksha Bay (GenBank accession: HM417784) (Hardy *et al.* 2011) (Fig. 26). *Lanice conchilega*, identified by Stiller *et al.* (2020) from Scilly Islands (England) is actually *L. kellyslateri* n. sp. and differs molecularly (but also morphologically, see *L. kellyslateri* n. sp. remarks) from specimens of *L. conchilega* sampled close from the type locality. These two species belong to a complex of cryptic species and are visually very difficult to separate. Finally, based on 16S molecular results (Fig. 27), *E. nebulosa* sequenced by Stiller *et al.* (2020) and sampled from Banyuls-sur-Mer Bay is the same one as *E. lacazei* n. sp. described here from the same locality. This species is morphologically different from *E. nebulosa* described from UK (see *E. lacazei* n. sp. Remarks).

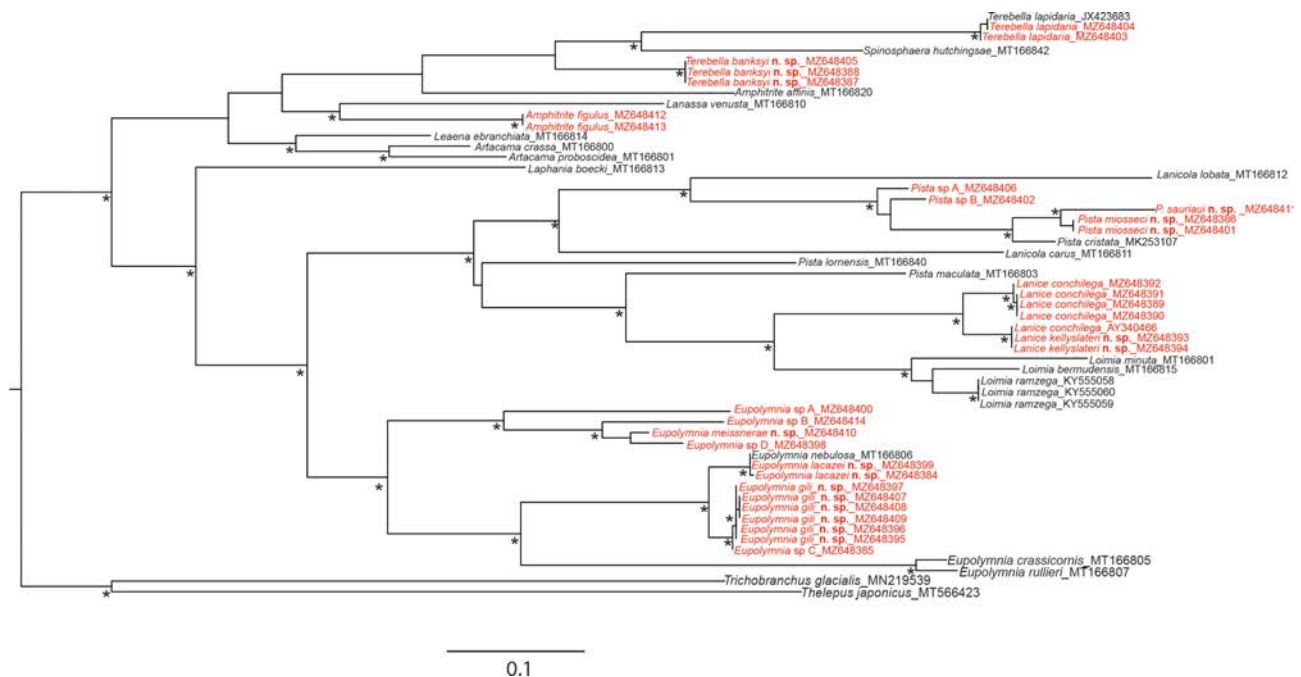


FIGURE 27. Majority-rule consensus tree from Bayesian analysis using 16S. Asterisk indicates posterior probability > 80%. Text in red refers to specimens sequenced during this study.

Key to European species of Terebellidae (*sensu stricto*)

Based on Gil 2011; Jirkov 2020; Hutchings *et al.* 2021b.

- 1A. Peristomiun ventrally forming a larg conical process *Artacama proboscidea* Malmgren, 1866**
- 1B. Absence of peristomial ventral process 2
- 2A (1B). Notochaetae on more than 25 segments, body uniform throughout 3
- 2B. Notochaetae on 25 or fewer segments, thorax and abdomen clearly defined 5
- 3A (2A). Branchiae absent *Baffinia hesslei* (Annenkova, 1924)**
- 3B. Branchiae present 4 (*Terebella*)
- 4A. Branchiae on SG II–IV, five pairs of nephridial and genital papillae *Terebella lapidaria* Linnaeus, 1767
- 4B. Branchiae on SG II–III and V, 12 pairs of nephridial and genital papillae *Terebella banksyi* n. sp.

5A (2B).	Absence of branchiae	6
5B.	Presence of branchiae	12
6A (5A).	Uncini from CH2	7
6B.	Uncini from CH3	11 (<i>Proclea</i>)
6C.	Uncini from CH7	<i>Laphania boeckii</i> Malmgren, 1866**
7A (6A).	Each notopodia with two types of notochaetae	8
7B.	Notopodia with one type of notochaetae only	10 (<i>Lanassa</i>)
8A (7A).	Notochaetae on 10 segments	<i>Leaena ebranchiata</i> (Sars 1865)**
8B.	Notochaetae on more than 13 segments	9 (<i>Phisidia</i>)
9A (8B).	Uncini in double rows on about 24 segments, eyespots present	<i>Phisidia oculata</i> (Langerhans, 1880)**
9B.	Uncini in double rows on 9–10 segments, eyespots absent	<i>Phisidia aurea</i> Southward, 1956**
10A (7B).	Notochaetae on 11 segments	<i>Lanassa venusta</i> (Malm, 1874)**
10B.	Notochaetae on 15 segments	<i>Lanassa nordenskioldi</i> Malmgren, 1866**
11A (6B).	Ventral lobe of SG II smooth and moderately protruding	<i>Proclea graffii</i> (Langerhans, 1884)**
11B.	Ventral lobe of SG II papillose and clearly protruding	<i>Proclea malmgreni</i> (Ssolowiew, 1899)**
12A (5B).	Notochaetae subdistally denticulate	13
12B.	Notochaetae smooth	26
13A (12A).	Lateral lobes absent	14 (<i>Amphitritides</i>)
13B.	Lateral lobes present	15
14A (13A).	Notochaetae on 17–20 segments; 8 segments with nephridial and genital papillae	<i>Amphitritides gracilis</i> (Grube, 1860)
14B.	Notochaetae on 24 segments; 11–13 segments with nephridial and genital papillae	<i>Amphitritides kuehlmanni</i> Arvanitidis & Koukouras, 1995**
15A (13B).	Two pairs of branchiae, on SG II–III	16 (<i>Paramphitrite</i>)
15B.	Three pairs of branchiae, on SG II–IV	17 (<i>Amphitrite</i>)
16A (15A).	Branchiae separated by a wide dorsal gap, developed lateral lobes on SG II–IV, absence of nephridial papillae on SG IV	<i>Paramphitrite dragovabeci</i> n. sp.
16B.	Branchiae without dorsal gap, small lateral lobes on SG II–IV, presence of nephridial papillae on SG IV	<i>Paramphitrite birulai</i> (Ssolowiew, 1899)**
17A (15B).	Notopodia present on first 17 chaetigers	18
17B.	Notopodia present on more than 17 chaetigers	23
18A (17A).	Branchiae with simple filaments	19
18B.	Branchiae dichotomous	21
19A (18A).	Seven pairs of nephridial and genital papillae (SG III and SG VI–XI)	<i>Amphitrite cirrata</i> Müller, 1771**
19B.	Four pairs of nephridial and genital papillae (SG III and SG VI–VIII)	20
20A (19B).	Branchiae arising from short stem or body wall	<i>Amphitrite fauveli</i> Jirkov, Ravara & Cunha, 2018**
20B.	Branchiae arising from large and stout stem	<i>Amphitrite rzhavskiyi</i> Jirkov, 2020**
21A (18B).	Nine pairs of nephridial and genital papillae, on SG III–XI	<i>Amphitrite edwardsi</i> (Quatrefages, 1866)
21B.	Six pairs of nephridial and genital papillae, on SG III–VIII	22
22A (21B).	Branchiae with few ramifications, neuropodia of first abdominal segment less than half size of neuropodia of last thoracic segment	<i>Amphitrite affinis</i> Malmgren, 1866**
22B.	Branchiae with many ramifications, neuropodia of first abdominal segment about same size as neuropodia of last thoracic segment	<i>Amphitrite variabilis</i> (Risso, 1826)**
23A (17B).	Notopodia present on first 19 chaetigers	<i>Amphitrite groenlandica</i> Malmgren, 1866**
23B.	Notopodia present on more than 19 chaetigers	24

24A (23B).	Notopodia present on first 21 chaetigers, 9–10 pairs of nephridial and genital papillae	
		<i>Amphitrite grayi</i> Malmgren, 1866**
24B.	Notopodia present on more than 21 chaetigers, more than 10 pairs of nephridial and genital papillae	25
25A (24B).	Notopodia present on first 23–27 chaetigers, 16 pairs of nephridial and genital papillae, uncini in double rows on SGXI–XXV	<i>Amphitrite figulus</i> (Dalyell, 1853)
25B.	Notopodia present on first 22–24 chaetigers, 13–15 pairs of nephridial and genital papillae, uncini in double rows almost to end of abdomen	<i>Amphitrite rubra</i> (Risso, 1826)**
26A (12B).	Absence of lateral lobes	27 (<i>Nicolea</i>)
26B.	Presence of lateral lobes	28
27A (26A).	Notochaetae on 15 segments, branchiae with short stems	<i>Nicolea zostericola</i> (Ørsted, 1844)**
27B.	Notochaetae on 17–18 segments, branchiae with long stems	<i>Nicolea venustula</i> (Montagu, 1819)**
28A (26B).	Double rows of uncini in a back to back arrangement	29
28B.	Double rows of uncini in a face-to-face arrangement	32
29A (28A).	Uncini pectinate, with teeth in a single vertical row	30 (<i>Loimia</i>)
29B.	Uncini avicular, with several transverse rows of secondary teeth	31 (<i>Lanice</i>)
30A (29A).	Eyespots present, pygidium without distinct papillae, thoracic uncini with 4–5 rows of secondary teeth	<i>Loimia medusa</i> (Savigny, 1822)**
30B.	Eyespots absent, pygidium with 14 distinct papillae, thoracic uncini with 6 rows of secondary teeth	<i>Loimia ramzega</i> Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017
31A (29B).	Ventral shields fused on SG2–4, notopodia inconspicuous, neuropodia as low ridges, upper lip dorsally pigmented	<i>Lanice conchilega</i> (Pallas, 1766)
31B.	Ventral shields well defined on SG3–4, notopodia well developed, neuropodia prominent, upper lip without pigmentation	<i>Lanice kellyslateri</i> n. sp.
32A (28B).	Notopodia on 15–16 segments	33 (<i>Axionice</i>)
32B.	Notopodia on 17 segments	34
33A (32A).	Notopodia on 15 segments	<i>Axionice flexuosa</i> (Grube, 1860)**
33B.	Notopodia on 16 segments	<i>Axionice maculata</i> (Dalyell, 1853)**
34A (32B).	Short-handled avicular uncini	35
34B.	Long-handled avicular uncini, at least on anterior neuropodia	40 (<i>Pista</i>)
35A (34A).	A single pair of branchiae	36 (<i>Pistella</i>)
35B.	Three pairs of branchiae	37 (<i>Eupolymnia</i>)
36A (35A).	Branchial filaments arranged in distinct tiers, ventral shields on SG II–XV, dorsal crest on SG III	<i>Pistella rovigensis</i> Mikac & Hutchings, 2017**
36B.	Branchial filaments arranged in spiral, ventral shields on SG VI–XX, dorsal crests on SG II–IV	<i>Pistella lornensis</i> (Pearson, 1969)**
37A (35B).	Branchiae with long stems	38
37B.	Branchial stems short or absent	39
38A (37A).	Abdominal neuropodia dorsally pointed, lateral lobes translucent	<i>Eupolymnia gili</i> n. sp.
38B.	Abdominal neuropodia rounded, lateral lobes not translucent	<i>Eupolymnia lacazei</i> n. sp.
39A (37B).	First pair of branchiae without stem, lateral lobes on SG III bilobed, lateral lobes of SG II small	<i>Eupolymnia nebulosa</i> (Montagu, 1819)**
39B.	First pair of branchiae with short stem, lateral lobes on SG III spherical, lateral lobes of SG II well-developed	<i>Eupolymnia meissnerae</i> n. sp.
40A (34B).	A single branchia, on SG II	<i>Pista labruneeae</i> n. sp.
40B.	All branchiae paired	41
41A (40B).	One or two pairs of branchiae	42
41B.	Three pairs of branchiae	<i>Pista cretacea</i> (Grube, 1860)**

42A (41A).	One pair of branchiae	43
42B.	Two pairs of branchiae	46
43A (42A).	Absence of lateral lobes on SG II	<i>Pista mirabilis</i> McIntosh, 1885*
43B.	Presence of lateral lobes on SG II	44
44 (43B).	Lateral lobes present on SG I–III, small on SG I and III	<i>Pista bansei</i> Saphronova, 1988**
44B.	Lateral lobes present on SG II–III, well developed on SG III	45
45A (44B).	Lateral lobes well developed on SG II, asymmetrical on SG III	<i>Pista colini</i> Labrune, Lavesque, Bonifácio & Hutchings, 2019
45B.	Lateral lobes narrow on SG II, rectangular on SG III	<i>Pista adriatica</i> Mikac & Hutchings, 2017**
46A. (42B).	Uncini of SG V very high, with a vertical prow	<i>Pista mediterranea</i> Gaillande, 1970
46B.	Uncini of SG V with regular size	47
47A (46B).	Absence of long-handled uncini on SG X (CH5)	48
47B.	Presence of long-handled uncini on SG X	49
48A (47A).	Lateral lobes on SGI short, on SGIV long	<i>Pista cristata</i> (Müller, 1776)**
48B.	Lateral lobes on SGI large, on SGIV very small	<i>Pista sauriauxi</i> n. sp.
49A (47B).	Lateral lobes on SG I small, on SG IV well developed, eyespots absent	<i>Pista wui</i> Saphronova, 1988*
49B.	Lateral lobes on SG I absent, on SG IV small, almost inconspicuous, eyespots present	<i>Pista miossecai</i> n. sp.

(*) doubtful record, probably a misidentification

(**) species not observed during this study, based on literature.

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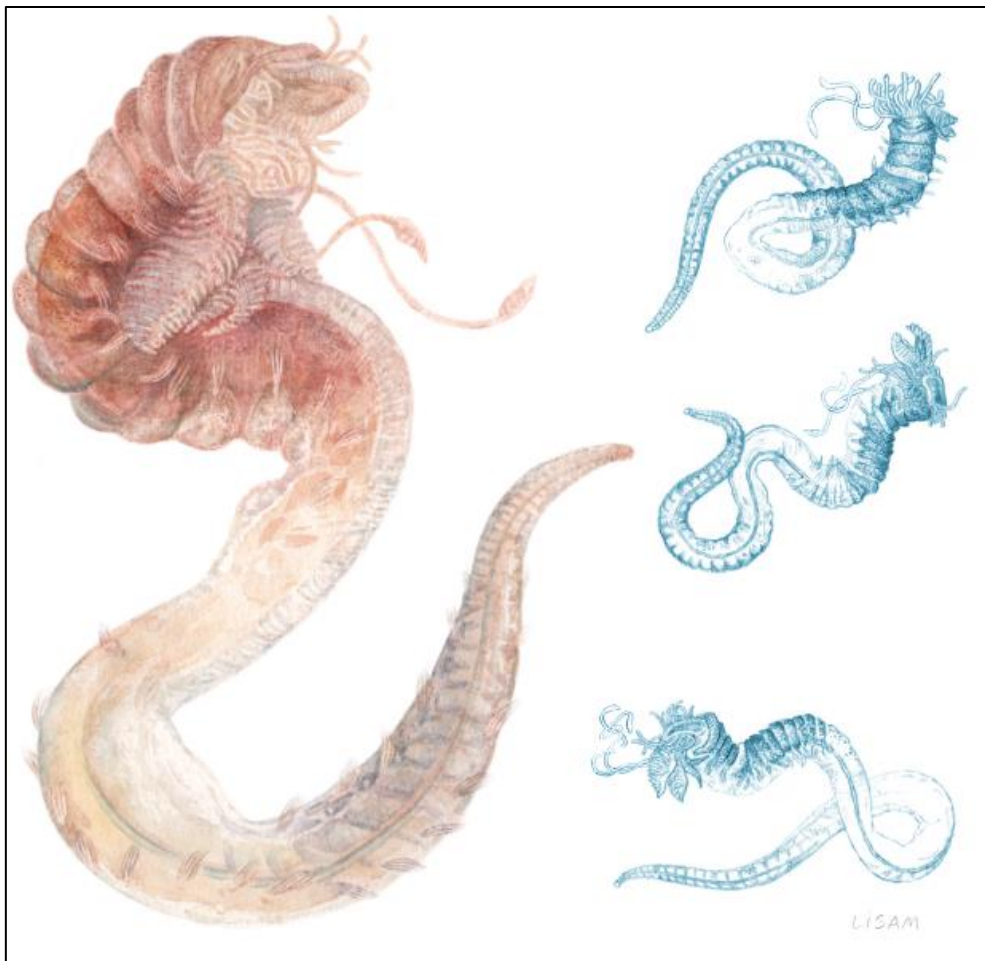
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DISCUSSION & PERSPECTIVES

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Terebellides ceneresi Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019

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Research article

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The “Spaghetti Project”: the final identification guide to European Terebellidae (sensu lato) (Annelida, Terebelliformia)

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Abstract. This paper is the conclusion of the “Spaghetti Project” aiming to revise French species of Terebellidae sensu lato (s.l.) belonging to the five families: Polycirridae, Telothelepodidae, Terebellidae sensu stricto (s.s.), Thelepodidae and Trichobranchidae. During this project, 41 species were observed, 31 of them new for science: eight species of Polycirridae, eleven species of Terebellidae s.s., three species of Thelepodidae and nine species of Trichobranchidae. We provide a comprehensive key for all European species of terebellids with a focus on the important diagnostic characters for each family. Finally, we discuss issues on taxonomy, biodiversity and cryptic and pseudo-cryptic species of polychaetes in European waters, based on results obtained during this project.

Keywords. Taxonomy, terebellids, spaghetti worms, cryptic species, identification key.

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Introduction

This is the concluding paper of the series devoted to the “Spaghetti Project” which aims to revise the French species of Terebellidae sensu lato (s.l.), referring to the original taxa previously considered as subfamilies of the family Terebellidae Johnston, 1846, namely Polycirrinae Malmgren, 1866 (now referred to Polycirridae), Terebellinae Johnston, 1846 (now referred to Terebellidae sensu stricto (s.s.)) and Thelepodidae Hessle, 1917, together with the closely related family Trichobranchidae Malmgren, 1866 and the recently described family Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 (Johnston 1846; Malmgren 1866; Hessle 1917; Nogueira *et al.* 2013; Hutchings *et al.* 2021a).

These tubicolous polychaetes are characterised by the presence of numerous grooved buccal tentacles used for selective deposit feeding, rendering these animals the name of “Spaghetti worms” (Hutchings *et al.* 2021b). These tentacles are of prostomial origin and not retractable into the mouth. They are generally smooth, except for in some polycirrids where they are papillose. Most of the terebellids are sedentary worms found in all marine environments, from the intertidal to the abyss and are common worldwide, distributed from polar to tropical regions (Hutchings *et al.* 2021b). The five families belonging to Terebellidae (s.l.) can be separated from each other by the morphology of the upper lip, the shape and number of branchiae, the glandular areas of ventral segments, the neuropodia and the arrangement of the uncini of anterior segments (i.e., in single or double rows) (Hutchings *et al.* 2021b).

The “Spaghetti Project” was initiated when the first author realized that the taxonomy of these worms in France, but also in Europe, was poorly documented. Indeed, the lack of accurate literature and the absence of useful and up-to-date keys of identification for this part of the world has led to their misidentifications for decades. In 2016, after observations of several specimens of Terebelliformia during a national workshop (at Arcachon, conducted by Mario Londoño-Mesa) and a national taxonomic course (at Caen, conducted by Pat Hutchings), we realized that many of the species required in-depth investigations. This collaborative project involved all benthic taxonomists at all French marine stations (RESOMAR network) who sent us fresh material as well as specimens stored in local collections. The first part of the project, devoted to the Trichobranchidae, allowed us to describe nine new species along the French coasts (Lavesque *et al.* 2019a). The second paper, focused on Telothelepodidae and Thelepodidae, described three new species (Lavesque *et al.* 2020a) and the third one on Polycirridae described eight new species (Lavesque *et al.* 2020b). Finally, the fourth paper dealt with the Terebellidae sensu stricto (s.s.) and included the description of nine species (Lavesque *et al.* 2021). With the previous descriptions

of *Lomia ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017 from Brittany and *Pista colini* Labrune, Lavesque, Bonifácio & Hutchings, 2019 from the Gulf of Lion (Lavesque *et al.* 2017a; Labrune *et al.* 2019), a total of 31 new species have been described from French waters in the past five years, combining both morphological and molecular data. This “Spaghetti Project” is thus an excellent example of what can be done by working in a network, with limited funding but enthusiastic people.

The main objectives of this last paper are (1) to provide a comprehensive key for all European species of terebellids (s.l.) with a focus on important diagnostic characters for each family and (2) to discuss the main results obtained during this project.

Material and methods

During the “Spaghetti Project”, morphological observations were conducted on specimens stored in the MNHN collection and specimens collected during different research programs and specific samplings along the French coasts (see previous papers).

Specimens were fixed in 4% formaldehyde in filtered seawater solution, washed and then, transferred to 70% ethanol for preservation. Methyl green, which can be washed out, was used to reveal the abundant glandular areas and to highlight the ornamentation of these areas, which are difficult to observe otherwise. For the molecular studies, several parapodia were removed from several fresh specimens, or from specimens fixed in 96% ethanol.

Preserved specimens were examined under a Nikon SMZ25 stereo microscope and a Nikon Eclipse *Ci* microscope, and photographed with a Nikon DS-Ri 2 digital camera. Dehydrated specimens used for examination by scanning electron microscopy (SEM) were prepared by critical point drying, coated with gold and examined and photographed with JEOL JSM 6480LA at Macquarie University, Sydney and Hitachi TM3030 at Arcachon Marine Station.

Morphological terminology follows Nogueira *et al.* (2010) and Hutchings *et al.* (2021a), especially concerning the anterior end and the general structure of the uncini (Fig. 1), Glasby & Hutchings (2014) for the types of uncini present in *Polycirrus* species and Parapar *et al.* (2020a, 2020b) for those found in *Terebellides* species.

Authorities of each species are given in the different keys and cited in the references.

Abbreviations

CH = Chaetiger
 MG = Methyl green
 SEM = Scanning Electron Microscope
 SG = Segment

Repositories

AM = Australian Museum, Sydney, Australia
 CEMUA = Colección Estuarina y Marina, Universidad de Antioquia in Medellín, Colombia
 GNM = Göteborg Natural History Museum, Sweden
 KGB = Department of Hydrobiology, Moscow Lomonosov State University, Russia
 LACM = Natural History Museum of Los Angeles County, Los Angeles, USA
 MNHB = Museum der Naturkunde für Humboldt Universität zu Berlin, Germany
 MNHN = Muséum national d’histoire naturelle, Paris, France

MZDAUT	=	Museum of the Department of Zoology, Aristoteleion University of Thessaloniki, Greece
NHMUK	=	Natural History Museum, London, UK
NMSE	=	National Museum of Scotland, Edinburgh
NMW-Z	=	National Museum Wales, Cardiff
NTNU	=	Norwegian University of Science and Technology, University Museum, Trondheim, Norway
PMR	=	Natural History Museum Rijeka, Croatia
SMF	=	Senckenberg Museum Frankfurt, Germany
SMNH	=	Swedish Museum of Natural History, Stockholm, Sweden
USNM	=	National Museum of Natural History, Smithsonian Institution, Washington, USA
UZMO	=	Universitetet i Oslo, Zoologisk Museum, Norway
ZIN	=	Zoological Institute of Russian Academy of Science, St. Petersburg, Russia
ZMUB	=	Zoological Museum, University of Bergen, Norway
ZMUU	=	Zoologiska Museet Uppsala Universitets, Sweden

Results

Phylum Annelida Lamarck, 1809
Class Polychaeta Grube, 1850
Order Terebellida Rouse & Fauchald, 1997

Key to the families of Terebellidae sensu lato

1. Notopodia, if present, elongate, roughly cylindrical, distally bilobed; branchiae absent; ventrum of anterior segments with paired glandular pads (Fig. 2B, D) **Polycirridae** Malmgren, 1866
– Notopodia always present, short, conical, distally bi- or single lobed; branchiae usually present; development and shape of ventral glandular areas of anterior segments variable between families, but never as paired mid-ventral pads 2
2. Thoracic uncini acicular (Figs 1A, 7D) **Trichobranchidae** Malmgren, 1866
– Thoracic uncini avicular (Fig. 1B–F) 3
3. Neuropodia with uncini in double rows on some segments (Fig. 6E); branchiae, if present, cirriform, arborescent or spiralled **Terebellidae** Johnston, 1846 sensu stricto
– Neuropodia with uncini in single rows throughout; branchiae rarely absent, always cirriform 4
4. Upper lip expanded, distinctly longer than wide (Figs 3F, 4A); neuropodia poorly developed throughout, as nearly sessile ridges and distinctly low pinnules on thoracic and abdominal segments, respectively **Telothelepodidae** Nogueira, Fitzhugh & Hutchings, 2013
– Upper lip short, hood-like, about as wide as long, frequently circular (Figs 3D–E, 4B–C); well-developed neuropodia throughout, as fleshy ridges and elongate pinnules on thoracic and abdominal segments, respectively **Thelepodidae** Hessle, 1917

Family **Polycirridae** Malmgren, 1866
Figs 1B, 2

Diagnosis (after Hutchings *et al.* 2021a; most important diagnostic characters highlighted in bold)

Transverse prostomium attached to dorsal surface of upper lip; basal part usually as thick horse-shoe shaped crest, eye spots absent; distal part either as another thick crest, with flaring distal lobes, with or without mid-dorsal process, or extending along upper lip until near anterior margin of lip; prostomium

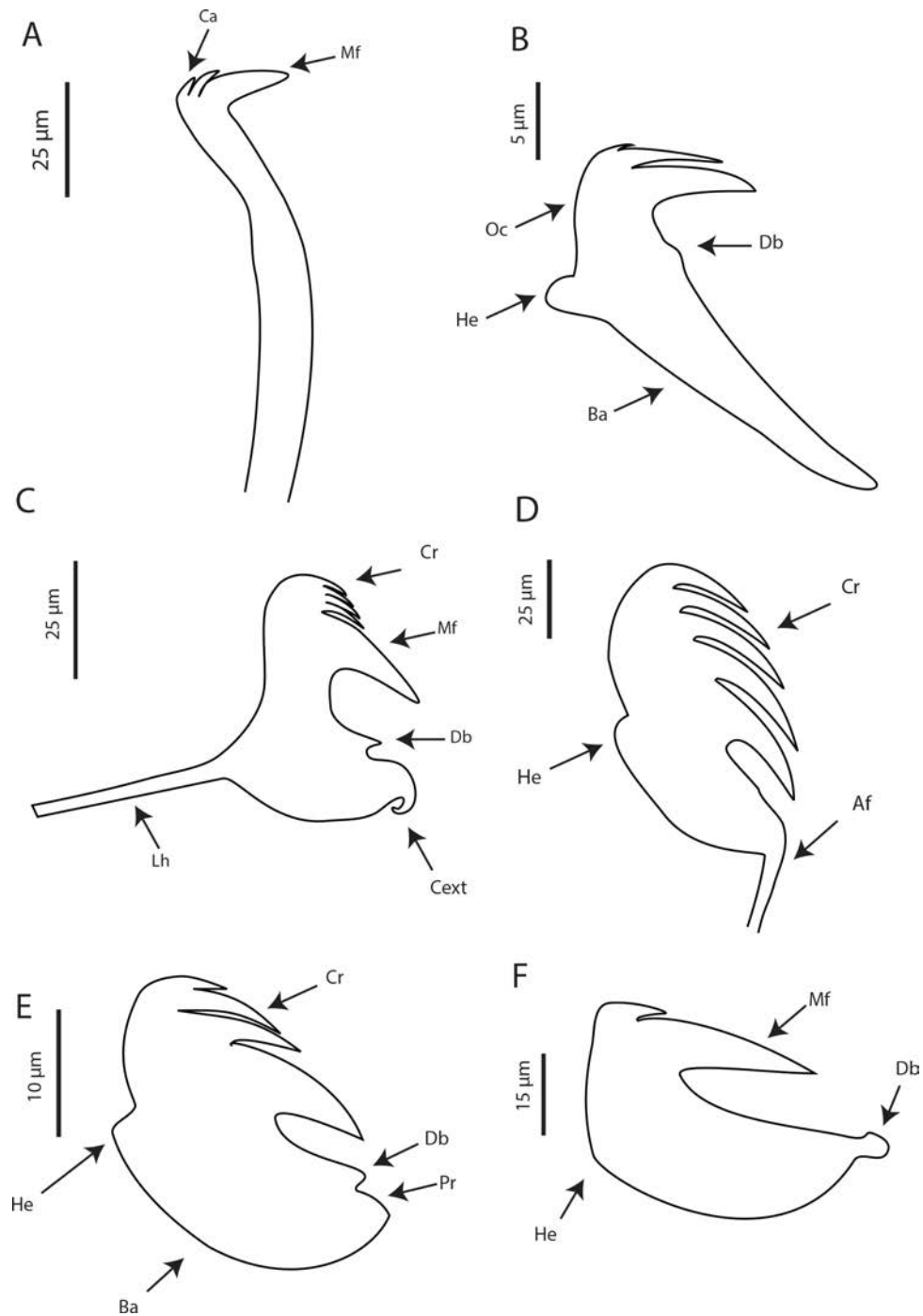


Fig. 1. Schematic illustrations of different uncini morphologies, in lateral view (following Nogueira *et al.* 2010). **A.** *Terebellides* sp., SG IX (SMA-BR-Terebellides-KER1). **B.** *Polycirrus catalanensis* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, SG XX (holotype MNHN-IA-TYPE 2007). **C.** *Pista sauriaui* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, SG V (paratype MNHN-IA-TYPE 2036). **D.** *Lomia ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017, SG XII (paratype MNHN-IA-TYPE 1791). **E.** *Streblosoma cabiochi* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020, SG VI (holotype MNHN-IA-TYPE 2000). **F.** *Thelepus japonicus* Marenzeller, 1884, SG XVII (MNHN-IA-PNT 117). Abbreviations: Af = anterior filament; Ba = base; Ca = capitiium; Cext = coma-shape extension; Cr = crest; Db = dorsal button; He = heel; Lh = long handle; Mf = main fang; Oc = occipitium; Pr = prow.

frequently extending ventrally, terminating laterally to mouth (Fig. 2A–D). Buccal tentacles of two types at least, short ones thin, uniformly cylindrical, long tentacles stouter, expanded at tips to variable degrees, distally spatulate (Fig. 2B, D) or more specialised. Peristomium forming lips; lips expanded, upper lip large, frequently circular and convoluted, folded into three lobes; swollen lower lip, only mid-ventral or cushion-like across ventrum, sometimes extending posteriorly for a few segments (Fig. 2A–D). Segment I reduced, frequently only visible ventrally, sometimes completely hidden. Segment II distinctly narrower than following segments, constricting body posteriorly to “lips head”; **SG II usually with rectangular or pentagonal mid-ventral shield at beginning of mid-ventral groove**, sometimes extending anteriorly through SG I until near posterior margin of lower lip (Fig. 2C). Anterior segments highly glandular ventrally, frequently papillose or tessellated, **with paired ventro-lateral pads** separated from each other within pairs by mid-ventral groove extending from SG II–IV to posterior body (Fig. 2A–D). **Branchiae absent**. Notopodia, if present, from SG III (Fig. 2A–D), extending for variable number of segments, usually few; bilobed, elongate notopodia, post-chaetal lobes sometimes longer, notochaetae originating between lobes along all extension of notopodia, separating lobes from base on ventral side of notopodia (Fig. 2A–D); notochaetae winged (Fig. 2E) and/or pinnate, wings of variable width. **Neuropodia, if present, located posteriorly to notopodia, frequently from posterior thoracic segments or only on abdomen; neurochaetae as acicular spines or avicular uncini, of two types, and arranged in a single row** (Figs 1C, 2F–G). Nephridial and genital papillae usually present, at anterior bases of all notopodia, or only at anteriormost notopodia (Fig. 2A). Pygidium smooth or with rounded ventral papilla.

Remarks

This family was previously considered as a subfamily of Terebellidae (Polycirrinae Malmgren, 1866), but was recently raised to familial level after a comprehensive phylogenetic analysis showed the monophyly of this group (Nogueira *et al.* 2013). Polycirridae is represented by six genera (*Amaeana* Hartman, 1959; *Biremis* Polloni, Rowe & Teal, 1973; *Enoplobranchus* Verrill, 1879; *Hauchiella* Levinsen, 1893; *Lysilla* Malmgren, 1866 and *Polycirrus* Grube, 1850), distinguished from each other by the presence/absence of noto- and neuropodia, and if present, the type of neurochaetae. Only *Amaeana* (Fig. 2A, C), *Hauchiella*, *Lysilla* and *Polycirrus* (Fig. 2B, D–G) are represented in European waters (Lavesque *et al.* 2020b) (Table 1).

Main morphological characters of European species

PARAPODIA. The parapodia of the members of this family are extremely important to separate the different genera. The genus *Hauchiella* is characterised by the absence of parapodia and *Lysilla* by the absence of neuropodia only. The neuropodia of members of *Amaeana* are characterised by the presence of spines, while those of *Polycirrus* bear avicular uncini (Figs 1B, 2F–G). Within the genus *Polycirrus*, the number and location of segments with notopodia and/or neuropodia are of important taxonomic value. Particularly, some species have uncini present only on abdominal segments, i.e., on segments without notopodia, and others have uncini starting before the end of the thorax, on segments bearing also notopodia.

SHAPE OF THE LIPS. As for other terebellids, polycirrids have a peristomium with well-defined upper and lower lips. The upper lip is large and can be trilobed (Fig. 2B) or with a single medial lobe (Fig. 2D). Generally, the upper lip is trilobed but the lobes differ in size and shape and lateral lobes can be reduced or well developed. The shape and the size of the lower lip is also highly variable between species. This lip can be rectangular, squared, rounded or subtriangular, swollen or not, longer than wide or wider than long (Fig. 2B–D).

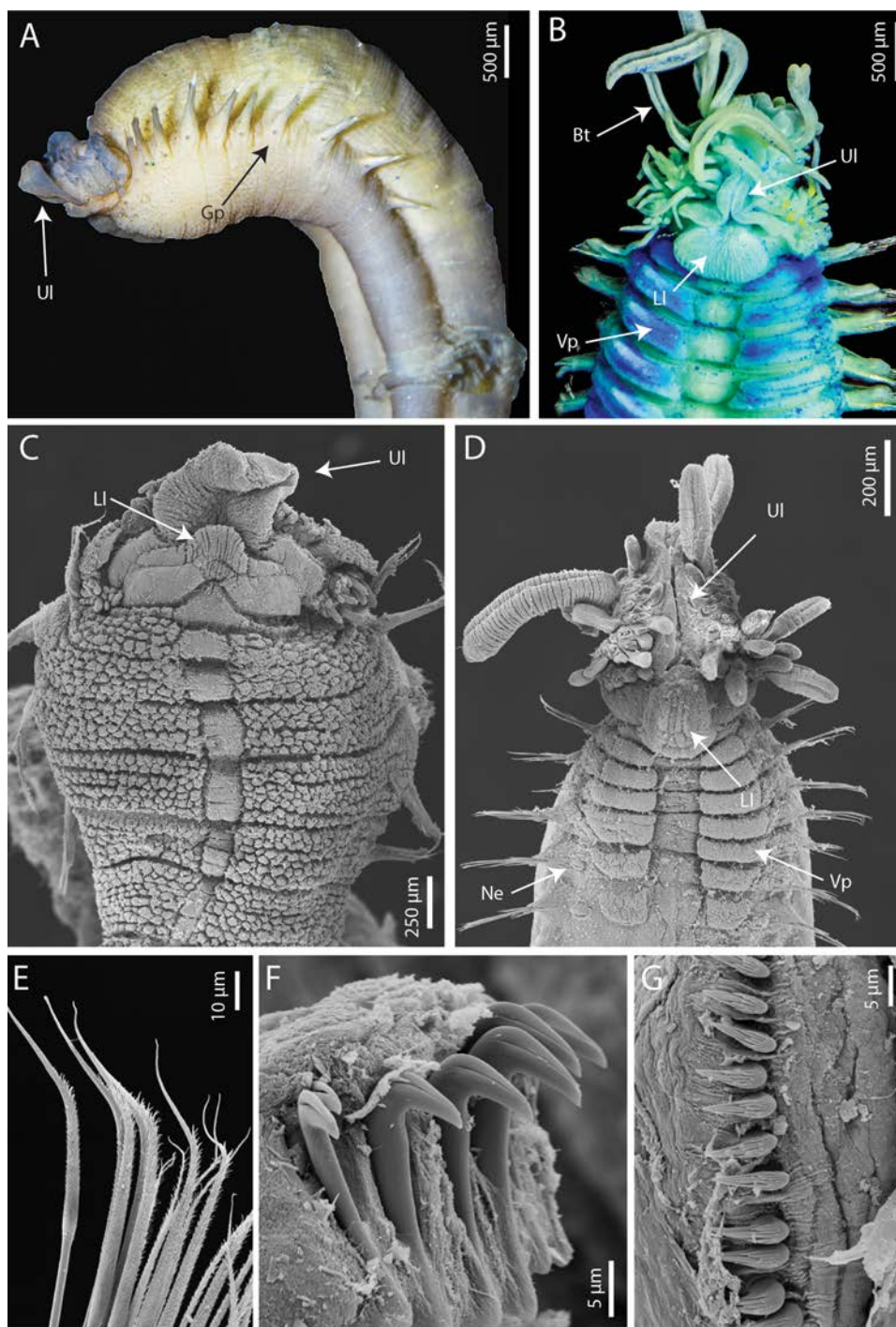


Fig. 2. Diversity of Polycirridae Malmgren, 1866. **A.** *Amaeana gremarei* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, anterior end, lateral view (MNHN-IA-TYPE 2006). **B.** *Polycirrus gujanensis* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, anterior end, ventral view (MNHN-IA-TYPE 2013). **C.** *Amaeana gremarei*, anterior end, ventral view (AM W.53111). **D.** *Polycirrus idex* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, anterior end, ventral view (AM W.53127). **E.** *Polycirrus glasbyi* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, notochaetae SG V (AM W.53118). **F.** *Polycirrus catalanensis* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, abdominal uncini (AM W.53113). **G.** *Polycirrus glasbyi*, thoracic uncini (AM W.53118). Abbreviations: Bt = buccal tentacles; Gp = genital papilla; Ll = lower lip; Ne = neuropodia; Ul = upper lip; Vp = ventral pads.

Table 1 (continued on next five pages). European species of Terebellidae s.l., by family, with authorities, if species are type species of the genus, type locality and collections where type specimens are lodged. In red, doubtful records in Europe, probably representing misidentification.

Family	Species	Authority	Type species	Type locality	Type specimen collections
Polycirridae	<i>Amaeana gremarei</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Gulf of Lion, France	MNHN / AM
	<i>Amaeana trilobata</i>	(Sars, 1863)	yes	Lofoten Islands, Norway	UZMO
	<i>Hauchiella tribullata</i>	(McIntosh, 1869)	yes	England, UK	NHMOUK
	<i>Lysilla loveni</i>	Malmgren, 1866	yes	Bohuslän, Sweden	Probably lost or never designated
	<i>Lysilla nivea</i>	Langerhans, 1884		Madeira, Portugal	Cannot be traced
	<i>Polycirrus arcticus</i>	Sars, 1865		Barents Sea, Spitsbergen	UZMO
	<i>Polycirrus arenivorus</i>	(Caullery, 1915)		Normandy, France	Cannot be traced
	<i>Polycirrus asturiensis</i>	Cepeda & Lattig, 2016		Asturias, Spain	MNCN
	<i>Polycirrus aurantiacus</i>	Grube, 1860		Adriatic Sea, Croatia	MNHB
	<i>Polycirrus catalanensis</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Gulf of Lion, France	MNHN / AM
	<i>Polycirrus denticulatus</i>	Saint-Joseph, 1894		Normandy France	MNHN, doubtful
	<i>Polycirrus elisabethae</i>	McIntosh, 1915		Scotland, UK	NHMOUK
	<i>Polycirrus fedorovi</i>	Jirkov & Leontovich in Jirkov, 2001		Arctic Ocean	KGB
	<i>Polycirrus glasbyi</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Arcachon Bay, France	MNHN / AM
	<i>Polycirrus gujanensis</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Arcachon Bay, France	MNHN / AM
	<i>Polycirrus idex</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Corsica Cape, France	MNHN / AM
	<i>Polycirrus latidens</i>	Eliason, 1962		Skagerrak, North Sea	ZMUU / GNM
	<i>Polycirrus medusa</i>	Grube, 1850	yes	Mediterranean Sea, France	MNHN
	<i>Polycirrus nogueirai</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Arcachon Bay, France	MNHN / AM
	<i>Polycirrus norvegicus</i>	Wolfebaek, 1912		Drobak, Norway	UZMO
<i>Polycirrus pennarbedae</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Southern Brittany, France	MNHN / AM	
<i>Polycirrus plumosus</i>	(Wolfebaek, 1912)		Norway	UZMO	
<i>Polycirrus readi</i>	Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020		Corsica Cape, France	MNHN / AM	

Table 1 (continued). European species of Terebellidae s.l.

Family	Species	Authority	Type species	Type locality	Type specimen collections
Telothelpepodidae	<i>Parathelpepus collaris</i>	(Southern, 1914)	yes	Clew Bay, Ireland	Not designated in original description
Terebellidae	<i>Amphitrite affinis</i>	Malmgren, 1866		Saguenay Fjord, Canada	SMNH
	<i>Amphitrite cirrata</i>	Müller, 1776	yes	Not stated, but probably Norway or Denmark	Probably lost or never designated
	<i>Amphitrite edwardsii</i>	(Quatrefages, 1866)		Normandy, France	Lost
	<i>Amphitrite fauveli</i>	Jirkov, Ravara & Cunha, 2018		Capbreton Canyon, Spain	NHMUK
	<i>Amphitrite figulus</i>	(Dalyell, 1853)		Scotland, UK	Cannot be traced
	<i>Amphitrite grayi</i>	Malmgren, 1866		Bohuslän, Sweden	SMNH
	<i>Amphitrite groenlandica</i>	Malmgren, 1866		Greenland	SMNH
	<i>Amphitrite rubra</i>	Risso, 1826		Mediterranean Sea, France	Cannot be traced
	<i>Amphitrite rzhavskiyi</i>	Jirkov, 2020		Melilla, Morocco	MNCN
	<i>Amphitrite variabilis</i>	(Risso, 1826)		Mediterranean Sea, France	Cannot be traced
	<i>Amphitritides gracilis</i>	(Grube, 1860)		Scilly Isles, UK	MNHB
	<i>Amphitritides kuehlmanni</i>	Arvanitidis & Koukouras, 1995		Euboea Gulf, Greece	MZDAUT
	<i>Artacama proboscidea</i>	Malmgren, 1866		Spitzbergen, Norway	Probably lost or never designated
	<i>Axionice maculata</i>	(Dalyell, 1853)		Scotland, UK	Cannot be traced
	<i>Axionice flexuosa</i>	(Grube, 1860)		Greenland	MNHB
<i>Baffinia hesslei</i>	(Annenkova, 1924)		Barents Sea	ZIN	
<i>Eupolyommia gili</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Normandy, France	MNHN / AM	
<i>Eupolyommia lacazei</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Gulf of Lion, France	MNHN / AM	
<i>Eupolyommia meissnerae</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Bay of Brest, France	MNHN / AM	
<i>Eupolyommia nebulosa</i>	(Montagu, 1819)		Devon, England, UK	Cannot be traced	
<i>Eupolyommia nesidensis</i>	(Delle Chiaje, 1828)		Gulf of Naples, Italy	Cannot be traced	
<i>Lanassa nordenskiöldi</i>	Malmgren, 1866		Spitzbergen, Norway	Probably lost or never designated	

Table 1 (continued). European species of Terebellidae s.l.

Family	Species	Authority	Type species	Type locality	Type specimen collections
	<i>Lanassa venusta</i>	(Malm, 1874)		Sweden	GNM
	<i>Lanice conchilega</i>	(Pallas, 1766)	yes	Netherlands	Probably lost or never designated
	<i>Lanice kellylateri</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Arcachon Bay, France	MNHN / AM
	<i>Laphania boeckii</i>	Malmgren, 1866	yes	Finmark, Norway	SMNH
	<i>Leaena ebranchiata</i>	(M. Sars, 1865)	yes	Norway	UZMO
	<i>Loimia medusa</i>	(Savigny, 1822)	yes	Red Sea	LACM
	<i>Loimia ramzega</i>	Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017		Northern Brittany, France	MNHN / NMW-Z / CEMUA
	<i>Nicolea venustula</i>	(Montagu, 1819)		Devon, England, UK	Cannot be traced
	<i>Nicolea zostericola</i>	(Ørsted, 1844)	yes	Denmark	Probably lost or never designated
	<i>Paramphitrite birulai</i>	Ssolowiew, 1899	yes	White Sea	ZMUB
	<i>Paramphitrite dragovabeci</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Bay of Brest, France	MNHN
	<i>Phisidia aurea</i>	Southward, 1956		Ireland	NHMUK
	<i>Phisidia oculata</i>	(Langerhans, 1880)	yes	Madeira, Portugal	Cannot be traced
	<i>Pista adriatica</i>	Mikac & Hutchings, 2017		Istrian Peninsula, Croatia	AM
	<i>Pista banssei</i>	Saphronova, 1988		NW Pacific	ZIN
	<i>Pista colini</i>	Labrune, Lavesque, Bonifácio & Hutchings, 2019		Gulf of Lion, France	MNHN / AM
	<i>Pista cretacea</i>	(Grube, 1860)		Cres Island, Croatia	Cannot be traced
	<i>Pista cristata</i>	(Müller, 1776)	yes	Kristiansand Fjord, Norway	Probably lost or never designated
	<i>Pista labruneeae</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Gulf of Lion, France	MNHN / AM
	<i>Pista mediterranea</i>	Gaillande, 1970		Mediterranean Sea, France	MNHN / USNM
	<i>Pista miossecci</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Bay of Brest, France	MNHN / AM
	<i>Pista mirabilis</i>	McIntosh, 1885		Rio de la Plata, Argentina	Not stated in original description
	<i>Pista sauriaui</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Bay of Brest, France	MNHN / AM

Table 1 (continued). European species of Terebellidae s.l.

Family	Species	Authority	Type species	Type locality	Type specimen collections
	<i>Pista wui</i>	Saphronova, 1988		Pacific Ocean	Cannot be traced
	<i>Pistella lornensis</i>	(Pearson, 1969)	yes	Scotland, UK	NHIMUK
	<i>Pistella rovigignensis</i>	Mikac & Hutchings, 2017		Istrian peninsula, Croatia	AM
	<i>Proclea graffii</i>	(Langerhans, 1884)	yes	Madeira, Portugal	Cannot be traced
	<i>Proclea malmgreni</i>	(Ssolowiew, 1899)		White Sea	Probably lost
	<i>Sischapovella tatjanae</i>	Levenstein, 1957		Arctic Ocean, Bering Sea	Cannot be traced
	<i>Terebella banksyi</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Arcachon Bay, France	MNHN / AM
	<i>Terebella lapidaria</i>	Linnaeus, 1767	yes	Mediterranean Sea	Cannot be traced
	<i>Euthelepus setubalensis</i>	McIntosh, 1885	yes	Setúbal, Portugal	NHIMUK
	<i>Streblosoma bairdi</i>	(Malmgren, 1866)	yes	Sweden	Probably lost
	<i>Streblosoma cabiochi</i>	Lavesque, Londoño-Mesa, Daffé & Hutchings, 2020		Northern Brittany, France	MNHN / AM
	<i>Streblosoma hutchingsae</i>	Lezzi & Giangrande, 2019		Torre Insserraglio, Italy	MNCN
	<i>Streblosoma intestinalis</i>	M. Sars in G.O. Sars, 1872		Oslo Fjord, Norway	UZMO
	<i>Streblosoma lindsayae</i>	Lavesque, Londoño-Mesa, Daffé & Hutchings, 2020		Bay of Biscay, France	MNHN
	<i>Streblosoma nogueirai</i>	Lezzi & Giangrande, 2019		Torre Guaceto, Italy	MNCN
	<i>Streblosoma pseudocomatus</i>	Lezzi & Giangrande, 2019		Mar Grande of Taranto, Italy,	MNCN
	<i>Thelepus cincinnatus</i>	(Fabricius, 1780)	yes	Greenland	Probably lost
	<i>Thelepus corsicanus</i>	Lavesque, Londoño-Mesa, Daffé & Hutchings, 2020		Corsica Cape, France	MNHN / AM
	<i>Thelepus davehalli</i>	Jirkov, 2018		Faroe Islands	KGB / MNCN
	<i>Thelepus japonicus</i>	Marenzeller, 1884		Japan	Cannot be traced
	<i>Thelepus marthae</i>	Jirkov, 2018		Norwegian Sea	KGB / MNCN / ZIN
	<i>Thelepus nucleolata</i>	(Claparède, 1869)		Gulf of Naples, Italy	Cannot be traced
	<i>Thelepus parapari</i>	Jirkov, 2018		Almeria, Spain	KGB / MNCN
	<i>Thelepus setosus</i>	(Quatrefages, 1866)		Normandy, France	MNHN
	<i>Thelepus triseriatis</i>	(Grube, 1855)		Mediterranean Sea	Cannot be traced

Table 1 (continued). European species of Terebellidae s.l.

Family	Species	Authority	Authority	Type locality	Type specimen collections
Trichobranchidae	<i>Octobranchus floriceps</i>	Kingston & Mackie, 1980		Northern North Sea	NHMUK / NMSE
	<i>Octobranchus lingulatus</i>	(Grube, 1863)	yes	Adriatic Sea, Croatia	MNHB
	<i>Terebellides atlantis</i>	Williams, 1984		New England, USA	AM / USNM
	<i>Terebellides bakkeni</i>	Parapar, Capa, Nygren & Moreira, 2020		Lofoten Islands, Norway	ZMBN / NTNU
	<i>Terebellides bigeniculatus</i>	Parapar, Moreira & Helgason, 2011		Iceland	NMSE / NHMUK / MNCN
	<i>Terebellides bonif</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Gulf of Lion, France	MNHN
	<i>Terebellides ceneresi</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Bay of Biscay, France	MNHN
	<i>Terebellides europaea</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Bay of Brest, France	MNHN
	<i>Terebellides gentili</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Northern Brittany, France	MNHN / AM
	<i>Terebellides gracilis</i>	Malm, 1874		Norway	GNM
	<i>Terebellides gralli</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Bay of Brest, France	MNHN / AM
	<i>Terebellides kongsrudi</i>	Parapar, Capa, Nygren & Moreira, 2020		Skagerrak	GNM / ZMBN / NTNU
	<i>Terebellides lilasae</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Bay of Biscay, France	MNHN / AM
	<i>Terebellides mediterranea</i>	Parapar, Mikac & Fiege, 2013		North Adriatic Sea	PMR / MNCN
	<i>Terebellides norvegica</i>	Parapar, Capa, Nygren & Moreira, 2020		Roagland, Norway	ZMBN / NTNU / GNM
	<i>Terebellides parapari</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Bay of Biscay, France	MNHN / AM
	<i>Terebellides resomari</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		North Sea, France	MNHN / AM
<i>Terebellides ronningae</i>	Parapar, Capa, Nygren & Moreira, 2020		Norway	ZMBN	

Table 1 (continued). European species of Terebellidae s.l.

Family	Species	Authority	Type species	Type locality	Type specimen collections
	<i>Terebellides scotica</i>	Parapar, Capa, Nygren & Moreira, 2020		Scotland, UK	ZMBN
	<i>Terebellides shetlandica</i>	Parapar, Moreira & O'Reilly, 2016		between Shetland Islands and Norway	NMSE / NHMUK / MNCN
	<i>Terebellides stroemii</i>	Sars, 1835	yes	Bergensfjord, Norway	UZMO
	<i>Trichobranchus demontaudouini</i>	Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019		Bay of Biscay, France	MNHN
	<i>Trichobranchus glacialis</i>	Malmgren, 1866	yes	Norway	Probably lost
	<i>Trichobranchus roseus</i>	(Malm, 1874)		Sweden	GNM

NOTOCHAETAE. Two types of notochaetae can be present: winged chaetae as for *P. glasbyi* (Fig. 2E) and/or pinnate as for *P. plumosus*. The winged notochaetae have wings of different width which are often conspicuous under light microscope but appear hirsute under SEM (Fig. 2E).

UNCINI SHAPE AND DENTICULATION. In *Polycirrus* two types of uncini are present: Type 1 with a short occipitum (back) and a straight to slightly convex base (Fig. 1B); and Type 2 with a long occipitum and a concave base (Glasby & Hutchings 2014). To date, all described European species have Type 1 uncini. The denticulation of uncini is also helpful in separating species, with the presence (as for *P. catalanensis*) (Fig. 2F) or the absence (as for *P. arenivorus*) of a main tooth above the main fang, and the number of rows of secondary teeth.

Key to European species of Polycirridae (after Lavesque *et al.* 2020b)

1. Parapodia absent (no chaetae) *Hauchiella tribullata* (McIntosh, 1869)
- Parapodia present 2
2. Only notopodia present 3 (*Lysilla*)
- Notopodia and neuropodia present 4
3. Notochaetae with smooth tips, 6 pairs of thoracic papillae *Lysilla loveni* Malmgren, 1866
- Notochaetae with plumose tips, 9 pairs of thoracic papillae *Lysilla nivea* Langerhans, 1884
4. Neuropodia with spines 5 (*Amaeana*)
- Neuropodia with avicular uncini 6 (*Polycirrus*)
5. Upper lip without lobe, lower lip rounded, long achaetous region
- *A. gremarei* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020
- Upper lip with trilobed, lower lip rectangular, short achaetous region
- *Amaeana trilobata* (Sars, 1863)
6. With 28 or more segments with notochaetae 7
- With 22 or fewer segments with notochaetae 8
7. With 29 segments with notopodia, neuropodia from SG XII, lower lip longer than wide, uncini without a main tooth above the main fang
- *Polycirrus arenivorus* (Caullery, 1915)
- With 46 segments with notopodia, neuropodia from SG XIV, lower lip longer than wide, uncini with a main tooth above the main fang
- *Polycirrus aurantiacus* Grube, 1860
- With 28 segments with notopodia, neuropodia from SG XV, lower lip wider than long, uncini with a main tooth above the main fang
- *Polycirrus gujanensis* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020
8. Neuropodia beginning before SG VIII 9
- Neuropodia beginning between SG IX and SG XII 10
- Neuropodia beginning after SG XIII 14
9. Upper lip trilobed, lower lip wider than long, uncini with 2 rows of teeth above the main tooth
- *Polycirrus asturiensis* Cepeda & Lattig, 2016
- Upper lip with single medial lobe, lower lip longer than wide, uncini with 1 row of teeth above the main tooth
- *Polycirrus idex* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020b

-
10. Uncini without a main tooth about the main fang *Polycirrus norvegicus* Wollebaek, 1912
 – Uncini with a main tooth about the main fang 11
11. Lower lip subtriangular, pointed towards mouth 12
 – Lower lip oval or oblong 13
12. With 12 or 13 segments with notopodia, lower lip longer than wide
 *Polycirrus denticulatus* Saint-Joseph, 1894
 – With 16 segments with notopodia, lower lip wider than long
 *Polycirrus elisabethae* McIntosh, 1915
13. With 18 or more segments with notopodia, lower lip oval, ventro-lateral pads not separated by a
 large mid-ventral groove
 *Polycirrus glasbyi* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020
 – Fewer than 18 segments with notopodia, lower lip oblong, ventro-lateral pads separated by a large
 midventral groove *Polycirrus readi* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020
14. With 16 or more segments with notopodia 15
 – Fewer than 16 segments with notopodia 17
15. Neuropodia beginning from SG XIV–XVI 16
 – Neuropodia beginning from SG XVIII–XX *Polycirrus plumosus* (Wollebaek, 1912)
16. Upper lip elongated, uncini with a main tooth above the main fang, ventro-lateral pads well
 developed *Polycirrus nogueirai* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020
 – Upper lip semicircular, uncini without a main tooth above the main fang, ventro-lateral pads poorly
 defined *Polycirrus arcticus* Sars, 1865
17. Neuropodia beginning from SG XIV, uncini with four teeth above the main fang arranged in single
 vertical series; lower lip large, shield-like, wider than long *Polycirrus latidens* Eliason, 1962
 – Neuropodia beginning from SG XV or after, secondary teeth of uncini not as above 18
18. Upper lip trilobed, lower lip subtriangular pointed toward mouth
 *Polycirrus medusa* Grube, 1850
 – Upper lip with a single median lobe, lower lip not subtriangular 19
19. Upper lip with thick medial lobe, uncini with two small lateral teeth above the main tooth, lower lip
 rectangular longer than wide
 *Polycirrus catalanensis* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020
 – Upper lip with elongated triangular medial lobe, uncini with two rows of teeth above the main tooth,
 lower lip oval and wider than long
 *P. pennarbedae* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020

Family **Telothelepodidae** Nogueira, Fitzhugh & Hutchings, 2013
Figs 3–4

Diagnosis (after Nogueira *et al.* 2018; Hutchings *et al.* 2021a, most important diagnostic characters highlighted in bold)

Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eyespots frequently present in one pair of dorso-lateral clusters, each with several rows of eyespots (Fig. 3A); distal part at base of upper lip, frequently **with low or erect mid-dorsal tongue-like process**, fused to upper lip at variable degrees, with free distal lobe(s), or free from the base. Buccal tentacles of two types, short ones thin, uniformly cylindrical, long tentacles stouter and expanded at tips, slightly spatulate (Figs 3A–B, F, 4A). Peristomium forming lips and continuing dorsally at least for short extension, with dorso-lateral nuchal organs at margin with prostomium; lips expanded, **upper lip distinctly elongate and narrow, undulated to convoluted**; swollen lower lip extending across ventrum, cushion-like or segment-like, frequently deeply grooved (Figs 3A–B, 4A). Either SG I or SG II reduced, not forming complete ring in many species. Anterior segments glandular ventrally, smooth, discrete shields absent and frequently with glandular regions poorly developed in comparison to other families of Terebellidae s.l.; mid-ventral groove frequently extending from anterior segments. **Two pairs of cirriform branchiae on SG II–III**, each pair with simple thin, curled and relatively short filaments progressively tapering to tips (Figs 3A, 4A), originating from raised crests on anterior margins of SG II and III, or from specialised, apparently glandular, dorso-lateral cushion-like pads occupying from anterior margins to level of posterior bases of notopodia of those segments. Notopodia beginning from SG II or III, usually SG III, extending for at least 15 segments; notopodia as short cones, notochaetae originating from central core on top, distal lobes absent; notochaetae winged, sometimes with bulbous head and alimbate tips (bayonet-like chaetae), at least in anterior row of anterior thoracic segments. **Neuropodia beginning posteriorly to notopodia, usually around SG VIII–XII**; neuropodia in conjunction with **notopodia as sessile tori, as distinctly low pinnules after notopodia terminate; neurochaetae in single row, as avicular uncini** about as long as high, with short triangular heel directed posteriorly, wide and slightly curved base, and dorsal button near mid-length of uncini, but closer to anterior margin (Fig. 4E). Nephridial and genital papillae, if conspicuous, on SG V–VII, posterior to bases of notopodia.

Remarks

This recent family was described by Nogueira *et al.* (2013) after conducting a comprehensive phylogenetic analysis. The members of this family were previously considered as Thelepodidae but differ in having a narrow and elongate upper lip, poorly developed neuropodia and anterior segments less glandular ventrally than in other thelepodids. In European waters, this family is represented by a single species, *Parathelepus collaris* (Figs 3A–B, 4A, E; Table 1), characterised by an expanded, tongue-like upper lip, by neuropodia poorly developed and beginning from SG XI.

Family **Thelepodidae** Hessle, 1917
Figs 1F, 3–4

Diagnosis (after Hutchings *et al.* 2021a, most important diagnostic characters highlighted in bold)

Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eyespots frequently present, in short lateral rows, or extending transversely across basal part of prostomium, usually progressively more spaced towards dorsal mid-line, with mid-dorsal gap or not; distal part of base of upper lip short, from nearly indistinct to shelf-like. Buccal tentacles all uniformly thin and cylindrical, to slightly spatulate distally (Figs 3D, F, 4B). Peristomium forming lips, sometimes also complete annulation, with dorso-lateral nuchal organs as ciliated grooves; lips expanded, relatively short

upper lip, hood-like, about as long as wide; swollen, button-like, mid-ventral lower lip (Figs 3D, F, 4B–C). Segment 1 usually present all around, frequently with ventral lobe marginal to mouth (Figs 3D, F, 4B–C); **SG II typically with anterior margin as protruding crest**, at least ventrally (Figs 3D–E, 4B–C); lobes on following anterior segments sometimes present. Anterior segments highly glandular ventrally, smooth to highly corrugated between neuropodia within pairs, discrete shields absent (Figs 3D, F, 4B); mid-ventral groove frequently extending from anterior segments with notopodia. **Two to three pairs of branchiae**, on SG II–III or II–IV, each pair with **simple thin, curled and relatively short filaments** progressively tapering to tips (Figs 3C, E, 4C), leaving mid-dorsal gap or not between filaments within pairs; branchial filaments originating directly from the body wall or from specialised dorso-lateral cushion-like pads. **Notopodia beginning on SG II–III**, usually extending to mid-body, at least, sometimes until near posterior end; cylindrical to rectangular, distally bilobed notopodia, notochaetae originating between lobes; most taxa with winged notochaetae only, with wings of variable width (Fig. 4D), distally serrated notochaetae sometimes also present; bayonet-like and pinnate chaetae both absent. Neuropodia beginning posteriorly to notopodia, on SG IV–VI, typically on SG V; neuropodia in conjunction with notopodia as fleshy, swollen ridges, as raised rectangular to cylindrical pinnules after notopodia terminate; neurochaetae as avicular uncini frequently longer than high, with short triangular heel directed posteriorly, distinctly **curved and wide base**, and dorsal button near anterior margin of uncini, or within anterior third of distance between anterior margin of uncini and base of main fang (Fig. 4F). Nephridial and genital papillae usually present, on SG IV–VII, posterior to bases of notopodia or between parapodial lobes (Fig. 3C).

Remarks

A comprehensive phylogenetic analysis conducted by Nogueira *et al.* (2013) permitted the elevation of the previous Thelepodinae subfamily to Thelepodidae family level, as they represented a separate clade from other terebellids. This family is represented in European waters by three genera *Euthelepus* McIntosh, 1885 (a single species), *Streblosoma* Sars, 1872 (seven species) and *Thelepus* Leuckart, 1849 (nine species) (Table 1). Among these species, *Thelepus japonicus* Marenzeller, 1884, native from Japan, is considered as a non-indigenous species in French waters, probably introduced with oyster transfers (Lavesque *et al.* 2020a) (Fig. 3C).

Main morphological characters of European species

BRANCHIAE. Both in *Thelepus* and *Streblosoma* genera, the number of pairs of branchiae varies between two (e.g., *Streblosoma lindsayae* or *Thelepus nucleolata*) and three (e.g., *Streblosoma hutchingsae* or *Thelepus setosus*). Branchiae in Thelepodidae are always cirriform (Figs 3C, E, 4C) but the number of branchial filaments varies among the species with for example 5–10 filaments on the second and third pairs of branchiae for *Streblosoma cabiochi* (Fig. 3E) and only three or less filaments for *Streblosoma intestinale*. Finally, the size of the medial dorsal gap separating the pairs of branchiae is a good diagnostic character. This gap is for example inconspicuous for *T. parapari* and wide for *Thelepus cincinnatus* (Nogueira 2019).

PRESENCE OF EYESPOTS. The eyespots are very useful in differentiating species of *Streblosoma* and *Thelepus* for which they can be absent (e.g., *Thelepus davehalli* or *Streblosoma hutchingsae*) or present (e.g.m *Thelepus corsicanus* or *Streblosoma nogueirai*). Also, the arrangement of the eyespots, if in a continuous line, or leaving a medial gap is of taxonomic importance (Nogueira *et al.* 2010).

START AND EXTENSION OF NOTOPODIA. The segment with the first appearance of notopodia permits the discrimination between the genus *Streblosoma*, for which notopodia begin on the second segment, and *Euthelepus* and *Thelepus* for which it begins on the third segment. These notopodia also extend for a variable number of segments, sometimes present only on the anterior half of the body (e.g., *T. corsicanus*) or present until the end of the body (*T. japonicus*).

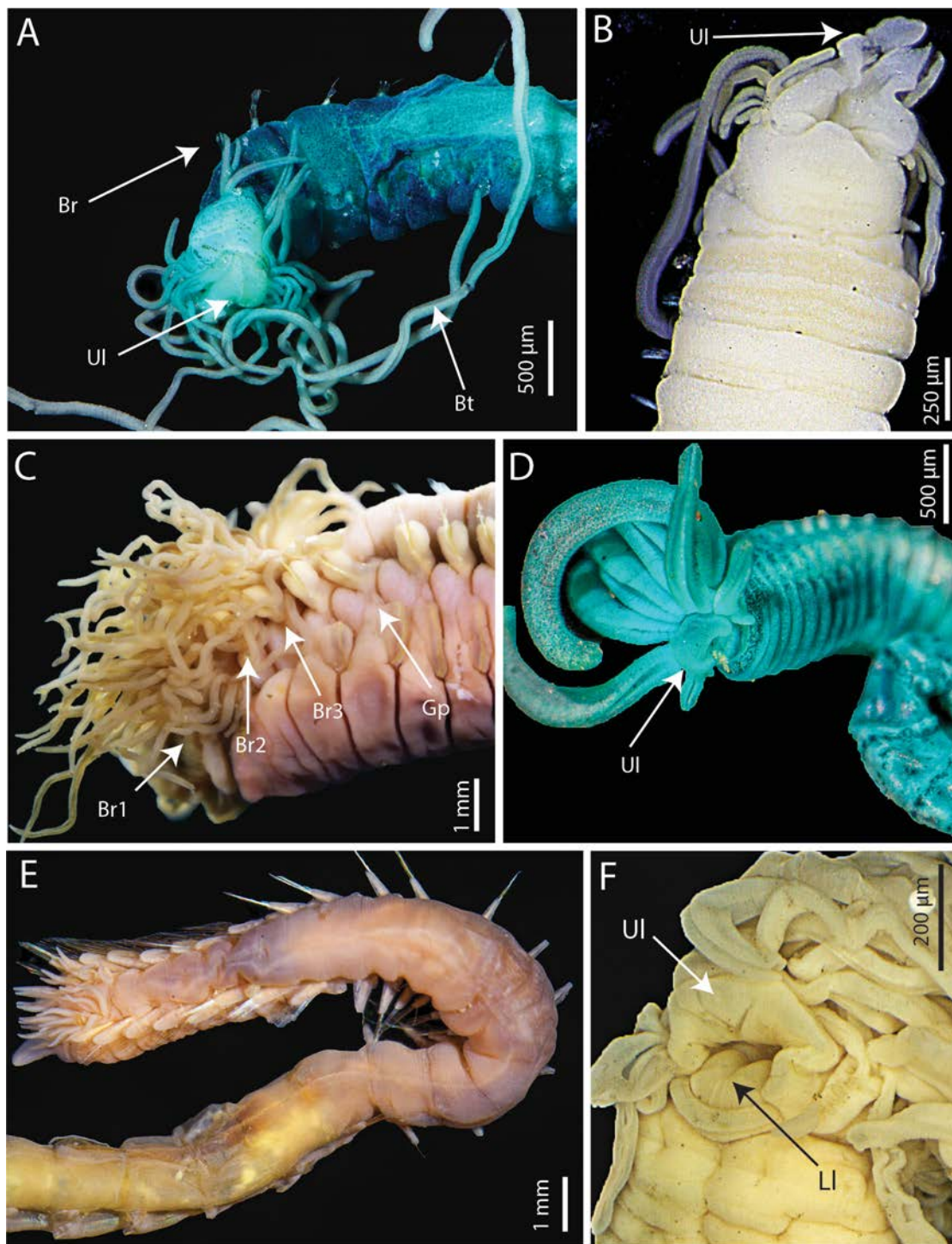


Fig. 3. Diversity of Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 and Thelepodidae Hessle, 1917. **A.** *Parathelepus collaris* (Southern, 1914), anterior end, frontal view (AM W.53063). **B.** *Parathelepus collaris*, anterior end, ventral view (NHMUK ANEA 1983.1696). **C.** *Thelepus japonicus* Marenzeller, 1884, anterior end, lateral view (AM W.53073). **D.** *Thelepus corsicanus* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020, anterior end, frontal view (AM W.53068). **E.** *Streblosoma cabiochi* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020, anterior end, dorsal view (MNHN-IA-TYPE 2000). **F.** *Thelepus japonicus*, anterior end, ventral view (MNHN-IA-PNT 117). Abbreviations: Br = Branchiae; Bt = Buccal tentacles; Gp = genital papillae; LI = Lower lip; UI = Upper lip.

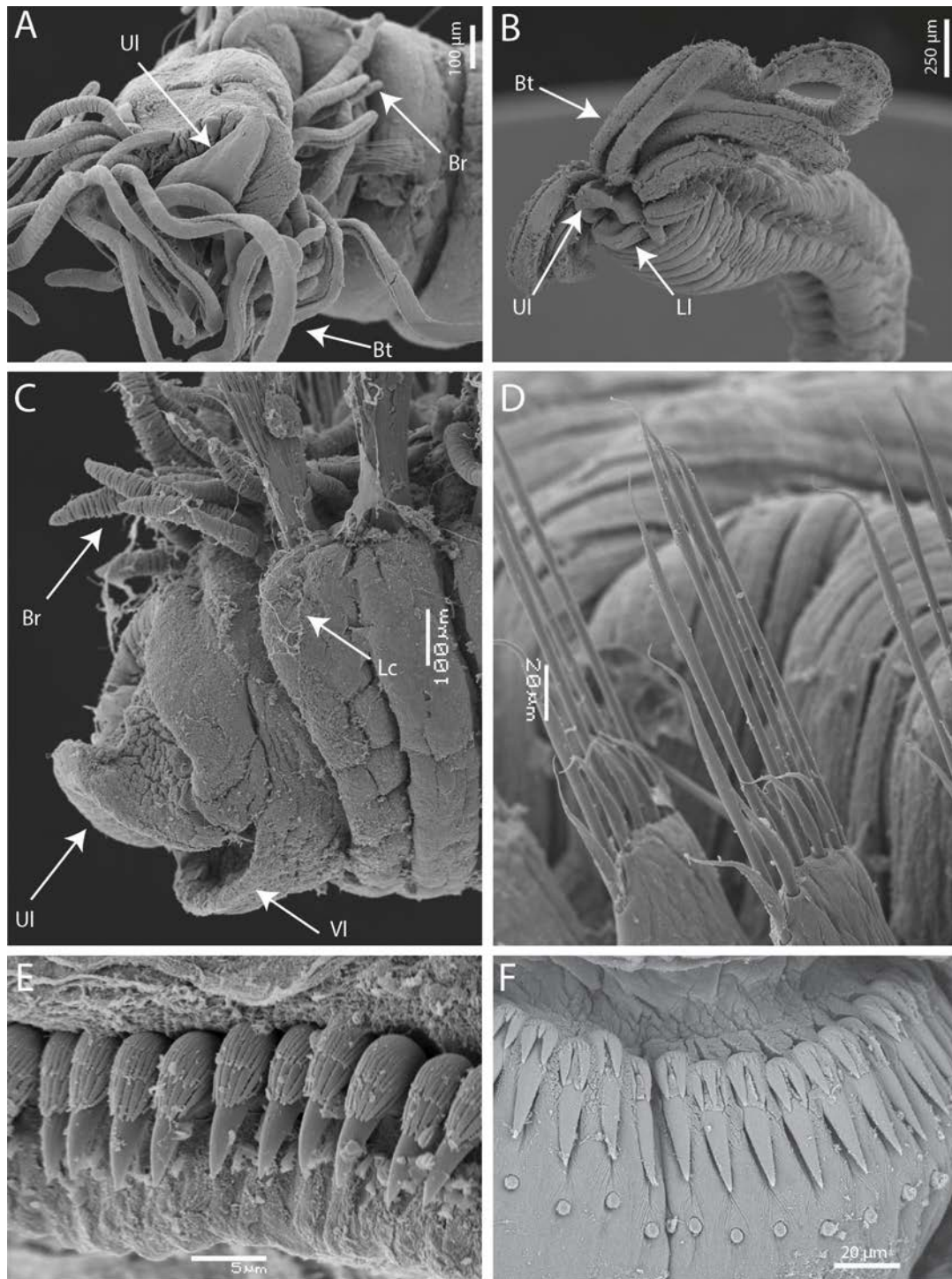


Fig. 4. Diversity of Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 and Thelepodidae Hesse, 1917, SEM. **A.** *Parathelepus collaris* (Southern, 1914), anterior end, frontal view (AM W.53063). **B.** *Thelepus corsicanus* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020, anterior end, latero-frontal view (AM W.53069). **C.** *Streblosoma cabiochi* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020, anterior end, lateral view (AM W.53066). **D.** *Thelepus corsicanus*, thoracic notochaetae (AM W.53069). **E.** *Parathelepus collaris*, abdominal uncini, (AM W.53063). **F.** *Thelepus japonicus* Marenzeller, 1884, abdominal uncini, SG48. (SMA-NL-Thele08). Abbreviations: Br = Branchiae; Bt = Buccal tentacles; Lc = lateral crest; LI = Lower lip; VI = Ventral lobe of SG I.

SHAPE OF NEUROPODIA AND UNCINI. In most of the species, the uncini start on SGV which could correspond to CH3 (as in *Thelepus*) or CH4 (as in *Streblosoma*). The uncini are arranged habitually in single rows but some have uncini forming loops (C-shaped arrangement) from mid thorax onwards. This last character is found for example in *S. nogueirai*. Between species, the uncini differ in the development of the prow (e.g., well developed in *T. triserialis*), the shape of the base (e.g., strongly curved in *S. cabiochi*), the position of the dorsal button (e.g., far from anterior margin in *S. bairdi* or in a terminal position for *T. japonicus* (Fig. 1F) and number of secondary of teeth.

CREST AND LATERAL LOBES. The presence of lateral lobes on SG II–IV allows the separation of the genus *Euthelepus* from other genera of the family. The presence of lateral crests on SG II (= thick anterior margin) is an important character within the *Streblosoma* genus. For example, *S. cabiochi* has a very low crest on SG II (Fig. 4C) while *S. bairdi* has a protruding crest (Nogueira 2019).

Key to European species of Thelepodidae (after Lavesque *et al.* 2020a)

1. Notopodia from SG II (i.e., first branchiferous segment), start of uncini from CH4 2 (*Streblosoma*)
 - Notopodia from SG III (i.e., second branchiferous segment), start of uncini from CH3 8
2. Two pairs of branchiae *Streblosoma lindsayae* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020
 - Three pairs of branchiae 3
3. Uncini arranged in C-shaped loops from mid thorax 4
 - Uncini always in straight rows 6
4. Notopodia not extending to posterior body 5
 - Notopodia until posterior body *Streblosoma pseudocomatus* Lezzi & Giangrande, 2019
5. Eyespots absent *Streblosoma hutchingsae* Lezzi & Giangrande, 2019
 - Eyespots present *Streblosoma nogueirai* Lezzi & Giangrande, 2019
- 6- Branchiae on SG III and SG IV with 3 or less filaments on each side *Streblosoma intestinale* M. Sars in G.O. Sars, 1872
 - Branchiae on SG III and SG IV with 5–10 filaments on each side 7
7. Absence of prostomial process, presence of lateral crest on SG II, absence of branchial cushion *Streblosoma cabiochi* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020
 - Presence of prostomial process, absence of lateral crest on SG II, presence of branchial cushion *Streblosoma bairdi* (Malmgren, 1866)
8. Lateral lobes on SG II–IV *Euthelepus setubalensis* McIntosh, 1885
 - Lateral lobes on SG I only 9 (*Thelepus*)
9. Two pairs of branchiae 10
 - Three pairs of branchiae 15
10. Uncini in a single row throughout 11
 - Uncini in loops from SG XIV *Thelepus nucleolata* (Claparède, 1870)
11. Notopodia present on 50–66% of body length 12
 - Notopodia present on at least 90% of body length 13

12. Eyespots absent*Thelepus davehalli* Jirkov, 2018
 – Eyespots present*Thelepus corsicanus* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020
13. Uncini of CH 1 with one tooth above main fang 14
 – Uncini of CH 1 with two teeth above main fang *Thelepus parapari* Jirkov, 2018
14. Eyespots present *Thelepus cincinnatus* (Fabricius, 1780)
 – Eyespots absent*Thelepus marthae* Jirkov, 2018
15. Prow of uncini well developed; notch between the prow and dorsal button of the uncini well marked *Thelepus triserialis* (Grube, 1855)
 – Prow of uncini poorly developed; notch between the prow and dorsal button of the uncini poorly marked 16
16. Notopodia present on about 60% of the body length*Thelepus setosus* (Quatrefages, 1866)
 – Notopodia present until end of the body length *Thelepus japonicus* Marenzeller, 1884

Family **Terebellidae** Johnston, 1846 (sensu stricto)

Figs 1C–D, 5–6

Diagnosis (after Hutchings *et al.* 2021a, most important diagnostic characters highlighted in bold)

Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eyespots frequently present (Fig. 5B), in short rows at each lateral sides, or extending transversely across basal part of prostomium. Buccal tentacles all usually uniformly cylindrical. Peristomium usually forming lips only; lips expanded, relatively short upper lip, hood-like, about as long as wide; swollen, usually button-like and mid-ventral lower lip. Segment I terminating laterally to ventro-laterally, partially fused to expanded lower lip, or developed, forming lobes of variable extension and position. Lobes on anterior segments frequently present, of variable length, sometimes extending to SGV–VII (Figs 5B–D, 6A–D). Anterior segments highly glandular ventrally, with discrete, smooth to corrugated, rectangular to trapezoidal mid-ventral shields extending from anterior segments until termination of notopodia, or near it; mid-ventral groove extending from termination of mid-ventral shields. **Two to three pairs of branchiae usually present** (Figs 5A–D, 6A–D), but three genera have a single pair and several are abranchiate; branchial filaments originating all together from single point on body wall, on either side of branchiferous segments, unbranched, or, more frequently, originating from conspicuous main stalk on either side of pair, branching from one to several levels, in plumose (spiraled), dichotomous, pectinate or arborescent arrangement. Notopodia beginning on SGII–V, SGIV in most genera, usually extending to mid-body, around SGXX, but sometimes present on fewer segments or extending more posteriorly for variable extension, rarely until near posterior end; first pairs of notopodia inserted dorso-laterally, progressively more laterally, then vertically aligned; cylindrical to rectangular notopodia. Notochaetae originating from central core on top, distal lobes absent; notochaetae distally winged, wings of variable length and width, or serrate, sometimes with wings at midlength, basally to a serrated blade; some more specialised types of notochaetae may be present (Fig. 5E–G). Neuropodia beginning posteriorly to notopodia, on SGV–IX, usually on SGV; neuropodia in conjunction with notopodia as low, sessile ridges, sometimes continuing posteriorly until pygidium, but most taxa with rectangular to cylindrical or foliaceous neuropodial pinnules after notopodia terminate; neurochaetae as avicular uncini usually as long as high, with short triangular heel directed posteriorly, slightly curved and wide base, and dorsal button (Figs 1C–D, 6E–F); **uncini arranged in double rows** (Fig. 6E) from around SGXI usually until termination of notopodia, but several genera with double rows.

Remarks

In European waters, the Terebellidae s.s. are represented by 19 genera and 44 species (Table 1). Four genera are represented only by a single species: *Artacama* Malmgren, 1866; *Baffinia* Wesenberg-Lund, 1950; *Laphania* Malmgren, 1866; *Leaena* Malmgren, 1866 and *Stschapovella* Levenstein, 1957. Eleven of them are represented by two European species each: *Amphitritides* Augener, 1922; *Axionice* Malmgren, 1866; *Lanassa* Malmgren, 1866; *Lanice* Malmgren, 1866; *Loimia* Malmgren, 1866; *Nicolea* Malmgren, 1866; *Paramphitrite* Holthe, 1976; *Phisidia* Saint-Joseph, 1894; *Pistella* Hartmann-Schröder, 1996; *Proclea* Saint-Joseph, 1894 and *Terebella* Linnaeus, 1767 (Lavesque *et al.* 2021). The genus *Eupolymnia* Verrill, 1900 is represented by four species and the two most diverse European genera are *Amphitrite* Müller, 1771, with ten species, and *Pista* Malmgren, 1866 with eleven (Lavesque *et al.* 2021). In our recent paper focusing on French Terebellidae s.s. we have confirmed the synonymy of *Neoamphitrite* with *Amphitrite*, as suggested by several authors (Jirkov 2020; Hutchings *et al.* 2021a). In contrast, we consider that *Amphitritides*, *Lanice* *Loimia* and *Paramphitrite* are still valid genera (Read & Fauchald 2021), contrary to what was proposed by Jirkov (2020) (see details in Lavesque *et al.* 2021).

Main morphological characters of European species

BRANCHIAE. The number and shape of branchiae are very important to separate species of Terebellidae s.s. Typically, species 2–3 pairs of branchiae are present on SG II–III or II–IV, but members of some genera, as for Polycirridae, completely lack branchiae: *Baffinia*, *Lanassa*, *Laphania*, *Leaena*, *Phisidia* and *Proclea*. *Terebella banksyi* is characterised by having branchiae on discontinuous segments: SG II–III and V (Fig. 5D). Generally branchiae are branching (dichotomous or arborescent), originating dorso-laterally from a main stalk (Figs 5A–D, 6A–D) or a single point on body wall, but some species have multiple unbranching branchial filaments, like *Amphitrite cirrata* or *A. rzhavskyi*. The presence or absence and the size of the branchial stem is important, like in *Eupolymnia* (Figs 5A–B, 6D).

LOBES. Genera of Terebellidae s.s. are distinguished from each other by the presence (or absence) and morphology of anterior lobes, usually positioned laterally. These structures are flaps of tissues covering at least part of the preceding segment (Nogueira *et al.* 2010) (Figs 5B–C, 6A–D). They can be absent, as in *Nicolea* or *Terebella*, narrow, as in *Paramphitrite birulai* or large, as in *Lanice* and *Eupolymnia* (Fig. 5 A–C) and they also vary significantly in morphology and position, from ventral to dorso-lateral (Figs 5B–C, 6A–D).

NEPHRIDIAL AND GENITAL PAPILLAE. Terebellids are characterised by the presence of papillae situated close to the notopodia or between parapodial lobes. The nephridial papillae occur from SG III–V, while genital papillae are present from SG VI onwards and are prominent only when the animals are mature (Fig. 5C–D, 6C). When they are visible, the morphology and the number of these papillae and their number permit the discrimination of species, as for *Amphitrite* or *Terebella* for example.

NOTOPODIA AND NEUROPODIA. Terebellidae s.s. differ by the number of pairs of notopodia, the segment on which notopodia and neuropodia start and the morphology of both noto- and neurochaetae. Usually, notochoetae are present on 17 segments, beginning from SG IV, but several exceptions exist as for example for *Lanassa* ($n < 15$) or *Terebella* ($n > 25$, often present to the pygidium). Notochaetae of Terebellidae are divided in two types: distally smooth as in *Pista*, *Eupolymnia* or *Lanice*, or distally serrated as in *Amphitritides* or *Paramphitrite* (Fig. 5E), and each type is sub-divided in sub groups (Nogueira *et al.* 2010: table 4). Concerning the neurochaetae, each part of the uncinus (Fig. 1C–D) differ greatly among the genera of Terebellidae and their morphology should be examined in detail. For example, members of the genus *Pista* have long-handled uncini, with the handle originating from the heel (Fig. 1C), while uncini in most of the other genera have short-handles. Contrary to tendons which are soft and thin structures attached to uncini, handles are chitinous structures extended from the heel. Members of the genus *Loimia* are unique due to the presence of pectinate uncini, with teeth arranged

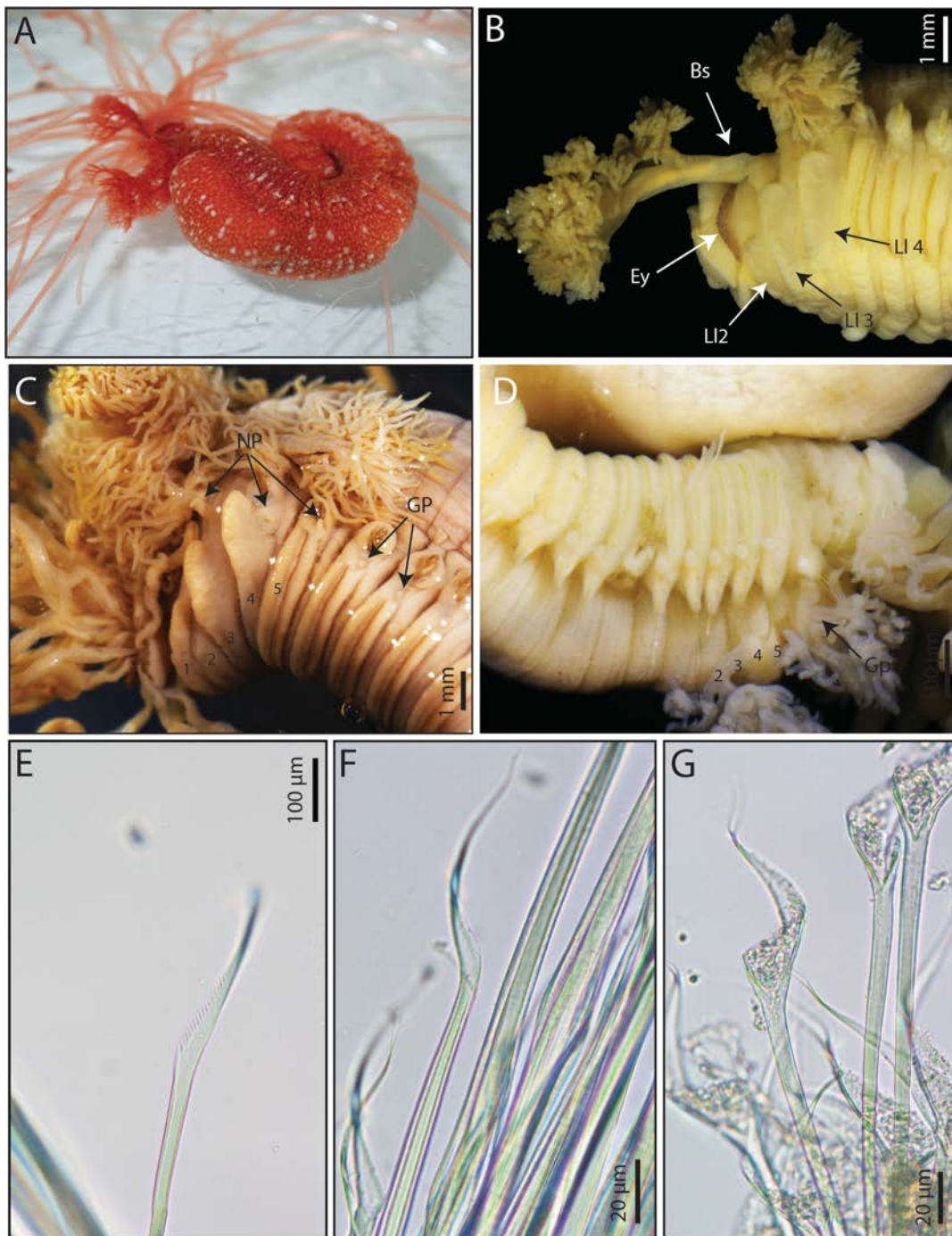


Fig. 5. Diversity of Terebellidae Johnston, 1846 (s.s.). **A.** *Eupolymnia lacazei* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, live specimen (paratype MNHN-IA-TYPE 2023). **B.** *Eupolymnia gili* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (holotype MNHN-IA-TYPE 2020). **C.** *Amphitrite edwardsii* (Quatrefages, 1866), anterior end, lateral view (MNHN-IA-PNT 126). **D.** *Terebella banksyi* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (holotype MNHN-IA-TYPE 2037). **E.** *Paramphitrite dragovabeci* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, notochaeta, SG XI (paratype MNHN-IA-TYPE 2030). **F.** *Terebella* cf. *lapidaria* Linnaeus, 1767, notochaetae, SG IX (MNHN-IA-PNT 131). **G.** *Terebella lapidaria*, notochaetae, posterior segments (MNHN-IA-PNT 131). Abbreviations: Bs = branchial stem; Ey = eyes; Gp = genital papillae; Ll = lateral lobes; Np = nephridial papillae. Numbers referring to segments.

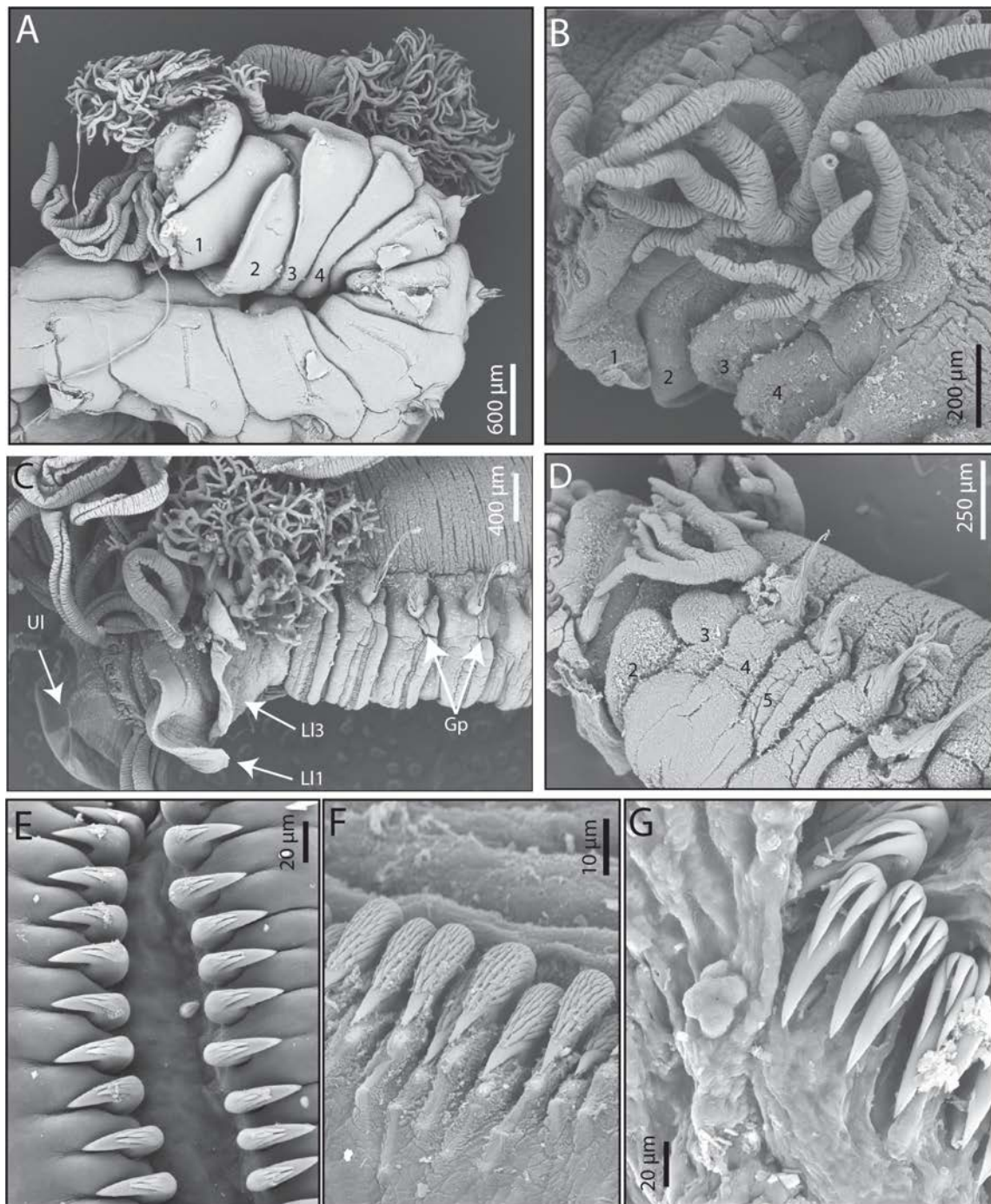


Fig. 6. Diversity of Terebellidae Johnston, 1846 (s.s.), SEM. **A.** *Pista sauriaui* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (paratype MNHN-IA-TYPE 2036). **B.** *Paramphitrite dragovabeci* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (paratype MNHN-IA-TYPE 2030). **C.** *Lanice kellyslateri* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (paratype MNHN-IA-TYPE 2028). **D.** *Eupolymnia meissnerae* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, anterior end, ventro-lateral view (paratype MNHN-IA-TYPE 2025). **E.** *Lanice kellyslateri*, thoracic uncini (paratype MNHN-IA-TYPE 2028). **F.** *Paramphitrite dragovabeci*, uncini SG XIV (paratype MNHN-IA-TYPE 2030). **G.** *Eupolymnia meissnerae*, uncini SG VIII (paratype MNHN-IA-TYPE 2025). Abbreviations: Gp = genital papillae; Ll = lateral lobes; Ul = upper lip. Numbers referring to segments.

vertically in a single row (Fig. 1D), while other species have multiple transverse rows of secondary teeth above the main fang (Fig. 6E–G). The dorsal button is generally well developed and situated about midway between the base of the main fang and the tip of the prow, but is inconspicuous in specimens of *Lanice* and can be closer to the tip of the prow, as in *Eupolymnia gili* or the base of the main fang, as for *Artacama proboscidea*. Finally, the prow and the heel vary in shape and can be distally rounded or pointed.

Key to European species of Terebellidae (sensu stricto) (after Lavesque *et al.* 2021).

1. Peristomium ventrally forming a large conical process *Artacama proboscidea* Malmgren, 1866
– Absence of peristomial ventral process 2
2. Notochaetae on more than 25 segments, body uniform throughout 3
– Notochaetae on 25 or fewer segments, thorax and abdomen clearly defined 5
3. Branchiae absent *Baffinia hesslei* (Annenkova, 1924)
– Branchiae present 4 (*Terebella*)
4. Branchiae on SG II–IV, five pairs of nephridial and genital papillae
..... *Terebella lapidaria* Linnaeus, 1767
– Branchiae on SG II–III and V, 12 pairs of nephridial and genital papillae
..... *Terebella banksyi* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
5. Absence of branchiae 6
– Presence of branchiae 12
6. Uncini from CH2 7
– Uncini from CH3 11 (*Proclea*)
– Uncini from CH7 *Laphania boeckii* Malmgren, 1866
7. Notopodia with two types of notochaetae 8
– Notopodia with one type of notochaetae only 10
8. Notochaetae on 10 segments *Leaena ebranchiata* (Sars, 1865)
– Notochaetae on more than 13 segments 9 (*Phisidia*)
9. Uncini in double rows on about 24 segments, eyespots present
..... *Phisidia oculata* (Langerhans, 1880)
– Uncini in double rows on 9–10 segments, eyespots absent *Phisidia aurea* Southward, 1956
10. Notochaetae on 11 segments *Lanassa venusta* (Malm, 1874)
– Notochaetae on 15 segments *Lanassa nordenskioldi* Malmgren, 1866
– Notochaetae on 16 segments *Stschapovella tatjanae* Levenstein, 1957
11. Ventral lobe of SG II smooth and moderately protruding *Proclea graffii* (Langerhans, 1884)
– Ventral lobe of SG II papillose and clearly protruding *Proclea malmgreni* (Ssolowiew, 1899)
12. All notochaetae subdistally denticulate 13
– Notochaetae smooth 26
13. Lateral lobes absent 14 (*Amphitritides*)
– Lateral lobes present 15

14. Notochaetae on 17–20 segments; 8 segments with nephridial and genital papillae *Amphitritides gracilis* (Grube, 1860)
 – Notochaetae on 24 segments; 11–13 segments with nephridial and genital papillae *Amphitritides kuehlmanni* Arvanitidis & Koukouras, 1995
15. Two pairs of arborescent branchiae, on SG II–III 16 (*Paramphitrite*)
 – Three pairs of unbranched branchiae, on SG II–IV 17 (*Amphitrite*)
16. Branchiae separated by a wide dorsal gap, developed lateral lobes on SG II–IV, absence of nephridial papillae on SG IV *Paramphitrite dragovabeci* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
 – Branchiae without dorsal gap, small lateral lobes on SG II–IV, presence of nephridial papillae on SG IV *Paramphitrite birulai* (Ssolowiew, 1899)
17. Notopodia present on 17 chaetigers 18
 – Notopodia present on more than 17 chaetigers 23
18. Branchiae with simple filaments 19
 – Branchiae dichotomous 21
19. Seven pairs of nephridial and genital papillae (SG III and SG VI–XI) *Amphitrite cirrata* Müller, 1771
 – Four pairs of nephridial and genital papillae (SG III and SG VI–VIII) 20
20. Branchiae arising from short stem or directly from body wall *Amphitrite fauveli* Jirkov, Ravara & Cunha, 2018
 – Branchiae arising from large and stout stem *Amphitrite rzhavskiyi* Jirkov, 2020
21. Nine pairs of nephridial and genital papillae, on SG III–XI *Amphitrite edwardsi* (Quatrefages, 1866)
 – Six pairs of nephridial and genital papillae, on SG III–VIII 22
22. Branchiae with few ramifications, neuropodia of first abdominal segment less than half size of neuropodia of last thoracic segment *Amphitrite affinis* Malmgren, 1866
 – Branchiae with many ramifications, neuropodia of first abdominal segment about same size as neuropodia of last thoracic segment *Amphitrite variabilis* (Risso, 1826)
23. Notopodia present on 19 chaetigers *Amphitrite groenlandica* Malmgren, 1866
 – Notopodia present on more than 19 chaetigers 24
24. Notopodia present on 21 chaetigers, 9–10 pairs of nephridial and genital papillae *Amphitrite grayi* Malmgren, 1866
 – Notopodia present on more than 21 chaetigers, more than 10 pairs of nephridial and genital papillae 25
25. Notopodia present on first 23–27 chaetigers, 16 pairs of nephridial and genital papillae, uncini in double rows on SGXI–XXV *Amphitrite figulus* (Dalyell, 1853)
 – Notopodia present on first 22–24 chaetigers, 13–15 pairs of nephridial and genital papillae, uncini in double rows almost to end of abdomen *Amphitrite rubra* (Risso, 1826)
26. Absence of lateral lobes 27 (*Nicolea*)
 – Presence of lateral lobes 28

-
27. Notochaetae on 15 segments, branchiae with short stems *Nicolea zostericola* (Ørsted, 1844)
 – Notochaetae on 17–18 segments, branchiae with long stems *Nicolea venustula* (Montagu, 1819)
28. Double rows of uncini in a back to back arrangement 29
 – Double rows of uncini in a face-to-face or intercalated arrangement 32
29. Uncini pectinate, with teeth in a single vertical row 30 (*Loimia*)
 – Uncini avicular, with several transverse rows of secondary teeth 31 (*Lanice*)
30. Eyespots present, pygidium without distinct papillae, thoracic uncini with 4–5 rows of secondary teeth *Loimia medusa* (Savigny, 1822)
 – Eyespots absent, pygidium with 14 distinct papillae, thoracic uncini with 6 rows of secondary teeth *Loimia ramzega* Lavesque, Bonifácio, Londoño-Mesa, Le Garrec & Grall, 2017
31. Ventral shields fused on SGII–IV, notopodia short, neuropodia as low ridges, upper lip dorsally pigmented *Lanice conchilega* (Pallas, 1766)
 – Ventral shields well defined on SGIII–IV, notopodia well developed, neuropodia prominent, upper lip without pigmentation
 *Lanice kellyslateri* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
32. Notopodia on 15–16 segments, a single pair of short dichotomously branchiae 33 (*Axionice*)
 – Notopodia on 17 segments 34
33. Notopodia on 15 segments *Axionice flexuosa* (Grube, 1860)
 – Notopodia on 16 segments *Axionice maculata* (Dalyell, 1853)
34. Short-handled avicular uncini throughout 35
 – Long-handled avicular uncini, at least on anterior neuropodia (i.e., SGV–VII) 40 (*Pista*)
35. A single pair of plumose branchiae 36 (*Pistella*)
 – Three pairs of branching branchiae 37 (*Eupolymnia*)
36. Branchial filaments arranged in distinct tiers, ventral shields on SG II–XV, dorsal crest on SG III ..
 *Pistella rovigensis* Mikac & Hutchings, 2017
 – Branchial filaments arranged in spiral, ventral shields on SG VI–XX, dorsal crests on SG II–IV
 *Pistella lornensis* (Pearson, 1969)
37. Branchiae with long stems 38
 – Branchial stems short or absent 39
38. Abdominal neuropodia dorsally pointed, lateral lobes translucent
 *Eupolymnia gili* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
 – Abdominal neuropodia rounded, lateral lobes not translucent
 *Eupolymnia lacazei* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
39. First pair of branchiae without stem, lateral lobes on SG III bilobed, lateral lobes of SG II small ...
 *Eupolymnia nebulosa* (Montagu, 1819)
 – First pair of branchiae with short stem, lateral lobes on SG III spherical, lateral lobes of SG II well-developed *Eupolymnia meissnerae* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
40. A single branchia inserted mid-dorsally on SG II
 *Pista labrunae* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
 – All branchiae paired 41

41. One or two pairs of branchiae 42
– Three pairs of branchiae *Pista cretacea* (Grube, 1860)
42. One pair of branchiae 43
– Two pairs of branchiae 46
43. Absence of lateral lobes on SG II *Pista mirabilis* McIntosh, 1885*
– Presence of lateral lobes on SG II 44
44. Lateral lobes present on SG I–III, small on SG I and III
..... *Pista bansei* Saphronova, 1988*
– Lateral lobes present on SG II–III, well developed on SG III 45
45. Lateral lobes well developed on SG II, asymmetrical on SG III
..... *Pista colini* Labruno, Lavesque, Bonifácio & Hutchings, 2019
– Lateral lobes narrow on SG II, rectangular on SG III
..... *Pista adriatica* Mikac & Hutchings, 2017
46. Uncini of SG V very high, with a vertical prow *Pista mediterranea* Gaillande, 1970
– Uncini of SG V with regular size 47
47. Absence of long-handled uncini on SG X (CH5) 48
– Presence of long-handled uncini on SG X 49
48. Lateral lobes on SGI short, on SGIV long *Pista cristata* (Müller, 1776)
– Lateral lobes on SGI large, on SGIV very small
..... *Pista sauriaui* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
49. Lateral lobes on SG I small, on SG IV well developed, eyespots absent
..... *Pista wui* Saphronova, 1988*
– Lateral lobes on SG I absent, on SG IV small, almost inconspicuous, eyespots present
..... *Pista miosseci* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
- * doubtful record, probably a misidentification.

Family **Trichobranchidae** Malmgren, 1866

Figs 1A, 7–8

Diagnosis (after Hutchings *et al.* 2021a, most important diagnostic characters highlighted in bold)

Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eyespots sometimes present; distal part at base of upper lip or extending along lip. Buccal tentacles of two types, uniformly cylindrical and expanded at tips, spatulate. Peristomium forming lips, sometimes also a ventral lobe, as an extension of the lower lip; lips expanded, circular upper lip, distal margin folded or convoluted; lower lip button-like, usually continuing by ventral lobe, or expanded, forming large scoop-shaped process (Figs 7A–C, 8A, C–D). Segment I usually short, frequently only visible ventrally; anterior margin of anterior segments with lobes as low, even-length collars covering posterior margins of preceding segments, at least ventrally; ventro-lateral or lateral lobes on anterior segments sometimes present. Anterior segments poorly glandular ventrally, smooth, discrete shields absent; mid-ventral groove extending from posterior segments with notopodia. **Two to four pairs of branchiae**, beginning from SGII, each pair with single, thick and elongate, tapered or foliaceous filament, or two pairs fused in single four lobed structure originating mid-dorsally between SGII–III or II–IV (Figs 7C,

8C–D). Notopodia beginning from SGIII–VI, typically terminating at SGXX; short, conical notopodia, chaetae emerging from central core on top, distal lobes absent; narrowly-winged notochoetae in both rows throughout. Neuropodia beginning on same segment as notopodia or slightly posteriorly, rarely beginning before notopodia; sessile neuropodia until termination of notopodia, neurochaetae emerging directly from body wall, as rectangular to foliaceous pinnules after termination of notopodia; thoracic **neurochaetae as acicular uncini** (Figs 1A, 7D, 8F), sometimes with small hood or beard below main fang; avicular abdominal uncini, with secondary teeth in rows on top and laterally to main fang. Nephridial papillae on SGIII usually present, other papillae sometimes present on SGVI and SGVII, but reduced to inconspicuous in most taxa. Pygidium smooth to slightly crenulate, sometimes bilobed.

Remarks

In the past, the Trichobranchidae family was considered to be a subfamily of Terebellidae (Fauvel 1927; Day 1967; Garraffoni & Lana 2004), but recent phylogenetic analyses support the hypothesis of a valid family (Glasby *et al.* 2004; Nogueira *et al.* 2013). The family includes only three genera, i.e., *Octobranchus* Marion & Bobretzky, 1875, *Terebellides* Sars, 1835, and *Trichobranchus* Malmgren, 1866. For *Trichobranchus* and *Octobranchus*, only three species of each occur in Europe. The genus *Terebellides* is very speciose and is represented in Europe by 19 species, 13 of them described in the last two years (Lavesque *et al.* 2019b; Parapar *et al.* 2020a) (Table 1).

Main morphological characters for European species

The number of branchiae is the best character to discriminate the different genera, with *Terebellides* having a single large branchia, *Trichobranchus* with two or three pairs of branchiae and finally *Octobranchus* with four pairs.

Trichobranchus species are easy to differentiate based on the number of branchiae (two vs three) (Figs 7C, 8C) and the absence or presence of eyespots. In *Octobranchus*, the species differ by the shape of the branchiae (Fig. 8D) and the number of secondary teeth above the main fang of the uncini. Regarding *Terebellides* species, recent studies highlighted that several characters are very important for identification to the species level (Lavesque *et al.* 2019a; Parapar *et al.* 2020a, 2020b). However, as many cryptic species occur at a small geographical scale (Nygren *et al.* 2018), which currently are confirmed only by molecular analyses (Parapar *et al.* 2020a) much more work needs to be done to resolve all the species present.

BRANCHIAE. Even if *Terebellides* branchiae seem to be very similar within the genus (Figs 7A–B, 8A–B), several morphological characters permit the discrimination of species, such as the presence of a fifth anterior branchial lobe (e.g., *T. europaea*), the degree of fusion of both upper and lower lobes (e.g., not fused on *T. ceneresi*), the presence of long terminal filaments (e.g., in *T. shetlandica*) or short posterior processes (Fig. 7B), and finally the presence and the shape of papillae situated on the margins of the branchial lamellae (Fig. 8B) (e.g., *T. lilasae*).

NOTOCHAETAE FROM FIRST CHAETIGER. The size of notochoetae of the first chaetiger varies between species. For most of the species, these chaetae are of a similar size compared to those of the following chaetigers. However, they can be absent or much shorter (e.g., *T. ceneresi*) or much longer (e.g., *T. mediterranea*).

PRESENCE OF GENICULATE CHAETAE ON ONE OR TWO CHAETIGERS. The geniculate chaetae are exclusive to members of *Terebellides* and they are typically present on CH6 (SG VIII) only (Fig. 8E), but in some species they are present on two chaetigers, as for example in *T. bigeniculatus*.

UNCINI DENTICULATION. The different types of uncini follow the classifications provided by Parapar *et al.* (2020b) for thoracic uncini (Fig. 8F) and Parapar *et al.* (2020a) for abdominal uncini. These

classifications are based on the ratio between the length of the main fang (rostrum) and the crest of secondary teeth (capitium), and the size and number of the secondary teeth.

THORACIC CILIATED PAPILLAE. Following the recent study of Parapar *et al.* (2020a), the absence or the presence of thoracic ciliated papillae allow for the discrimination of *Terebellides* species. These papillae are situated dorsally to the thoracic notopodia (see for example Parapar *et al.* 2020a; Fig. 7B).

METHYL GREEN PATTERN. The colouration of *Terebellides* specimens prior to identification is essential. Indeed, MG staining highlights the presence and the shape of the glandular region of the third thoracic chaetiger (e.g., undulating glandular region present and in members of *T. gentili*, oval for *T. lilasae*

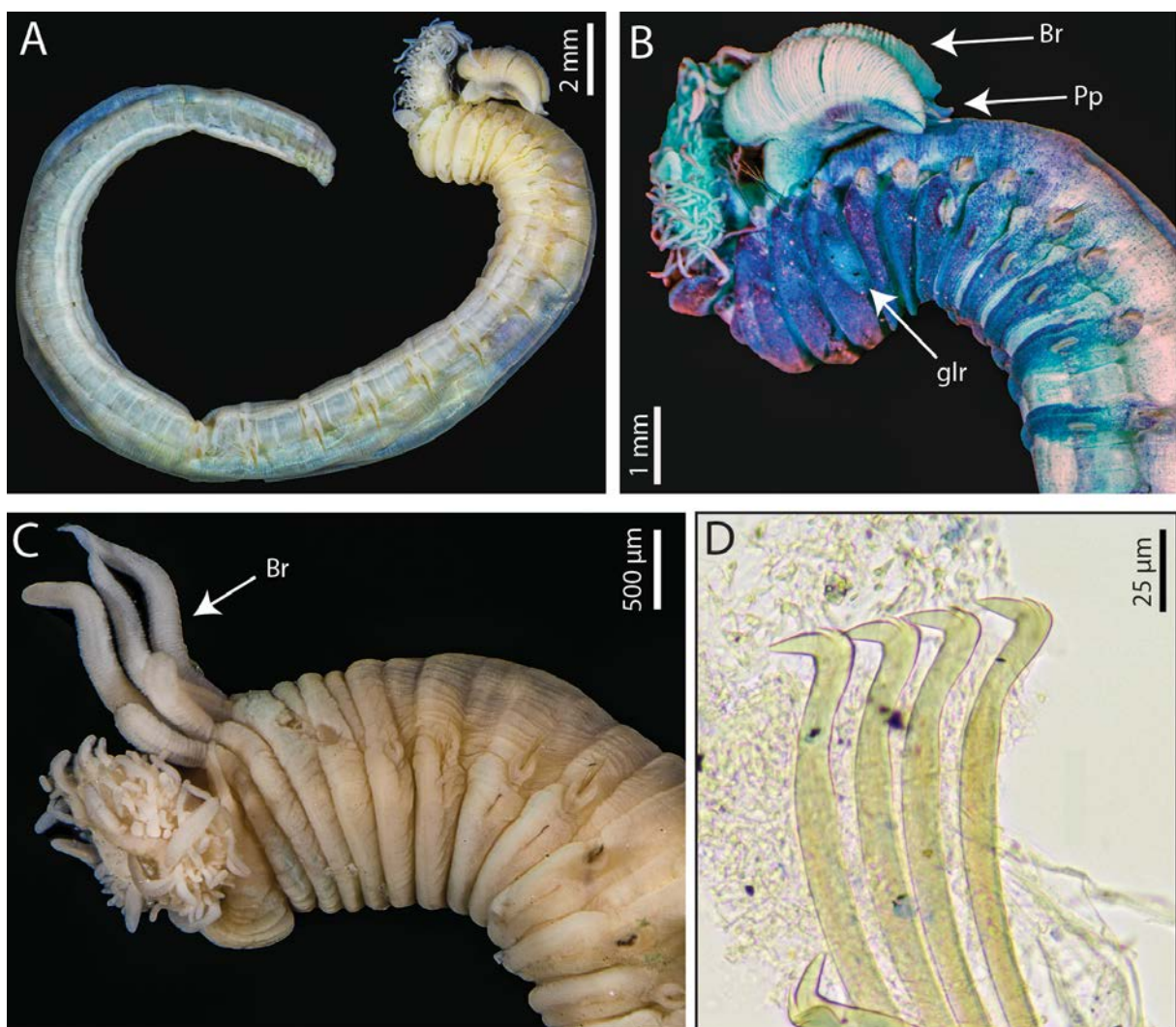


Fig. 7. Diversity of Trichobranchidae. **A.** *Terebellides lilasae* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019, entire specimen, lateral view (MNHN-IA-TYPE 1879). **B.** *Terebellides lilasae*, anterior end, lateral view, methyl green staining (MNHN-IA-TYPE 1879). **C.** *Trichobranchus glacialis* Malmgren, 1866, anterior end, lateral view (MNHN-IA-PNT 96). **D.** *Terebellides* sp., thoracic acicular uncini (SMA-BR-Terebellides-KER1). Abbreviations: Br = Branchiae; glr = glandular region; Pp = Posterior process.

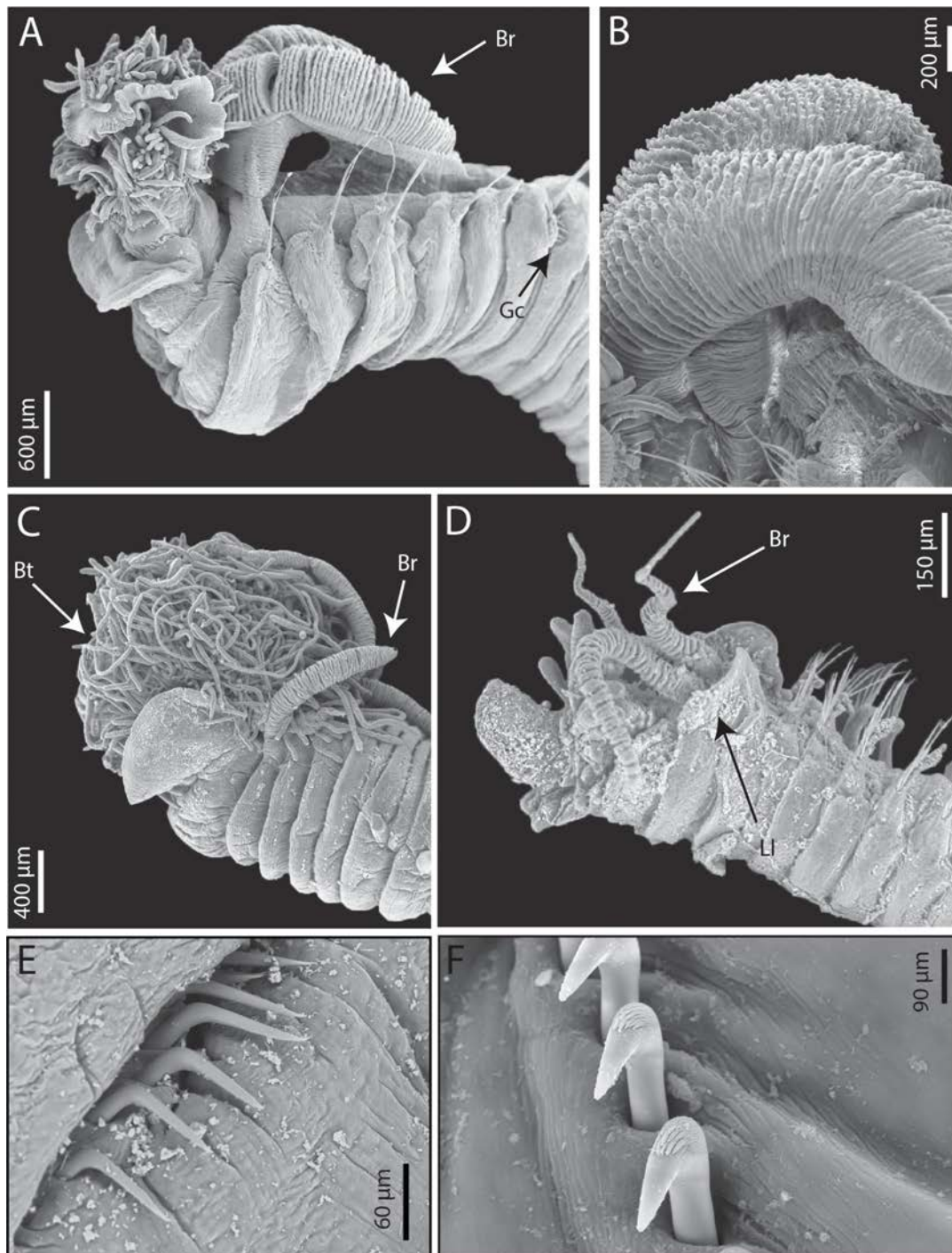


Fig. 8. Diversity of Trichobranchidae, SEM. **A.** *Terebellides gentili* Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019, anterior end, lateral view (MNHN-IA-TYPE 1873). **B.** *Terebellides lilasae* Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019, branchia, lateral view (MNHN-IA-TYPE 1881). **C.** *Trichobranchus glacialis* Malmgren, 1866, anterior end, lateral view (SMA-BR-Tricho-05). **D.** *Octobranchus lingulatus* (Grube, 1863), anterior end, lateral view (MNHN-IA-PNT 94). **E.** *Terebellides resomari* Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019, geniculate chaetae (paratype MNHN-IA-TYPE 1892). **F.** *Terebellides lilasae*, thoracic uncini (SMA-ARC-Terebellides-VOG8-1). Abbreviations: Br = Branchiae; Bt = Buccal tentacles; Gc = Geniculate chaetae; Ll = Lateral lobes.

Fig. 7B) and the compact/striped pattern of the ventral part of anterior chaetigers (e.g., CH4 (SG VI) white in *T. ceneresi*).

Key to European species of Trichobranchidae (after Lavesque *et al.* 2019a and Parapar *et al.* 2020a)

1. One large branchia consisting of a stem and four lobes with transverse lamellae5 (*Terebellides*)
 - Two or three pairs of branchiae 2 (*Trichobranchus*)
 - Four pairs of branchiae 4 (*Octobranchus*)
2. Two pairs of branchiae 3
 - Three pairs of branchiae, eyespots present
..... *Trichobranchus glacialis* Malmgren, 1866
3. Eyespots absent*Trichobranchus roseus* Malm, 1874
 - Eyespots present
... *Trichobranchus demontaudouini* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
4. Pairs of branchiae of different shapes; abdominal uncini with three rows of secondary teeth above the main fang *Octobranchus floriceps* Kingston & Mackie, 1980
 - All pairs of branchiae similar; abdominal uncini with two rows of secondary teeth above the main fang*Octobranchus lingulatus* (Grube, 1863)
 - Bases of branchiae covered by dorso-lateral lobes, abdominal uncini with two rows of secondary teeth above the main fang *Octobranchus sikorskii* (Leontovich & Jirkov. 2001)
5. Genuiculate acicular chaetae on CH5 (SG VII) and CH6 (SG VIII)
.....*Terebellides bigeniculatus* Parapar, Moreira & Helgason, 2011
 - Genuiculate acicular chaetae on CH6 (SG VI) only 6
6. Branchial lamellae without marginal papillae 7
 - Branchial lamellae with marginal papillae 15
7. Lower branchial lobes with long filaments 8
 - Lower branchial lobes with or without short projections 9
8. Glandular region on CH3 (SG V) present; branchial lamellae pointed; notochaetae from CH1 longer than following ones; dorsal papillae absent
..... *Terebellides parapari* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
 - Glandular region on CH3 (SG V) absent; branchial lamellae rounded; all notochaetae equal-sized; dorsal papillae present *Terebellides shetlandica* Parapar, Moreira & O'Reilly, 2016
9. Ventral white band present on CH4 (SG VI) after MG staining 10
 - No distinct pattern on CH4 (SG VI) after MG staining 11
10. Large species (> 30 mm); 5th branchial lobe present; notochaetae of CH1 (SG III) similar to following ones; main fang of thoracic uncini straight*Terebellides gracilis* Malm, 1874
 - Small species (<20 mm); 5th branchial lobe absent; notochaetae of CH1 (SG III) absent or shorter than following ones; main fang of thoracic uncini ‘eagle head’ (= curved) shaped
..... *Terebellides ceneresi* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
11. First notopodia and notochaetae longer than following ones
.....*Terebellides mediterranea* Parapar, Mikac & Fiege, 2013
 - First notopodia and notochaetae similar or shorter than following ones 12

12. Large-sized species (>50 mm); dorsal rounded projections on CH1–CH5 conspicuous 13
 – Small-sized species (<20 mm); dorsal rounded projections on CH1–CH5 absent; main fang of thoracic uncini straight 14
13. Abdominal uncini of type 1 (length of capitium about 0.7 length of the main fang, capitium simple consisting of a few, wide denticles)
 *Terebellides kongsrudi* Parapar, Capa, Nygren & Moreira, 2020 and
 *Terebellides bakkeni* Parapar, Capa, Nygren & Moreira, 2020 complex
 – Abdominal uncini of type 2 (capitium of about same length as main fang, capitium complex composed of a first row of 4(5) denticles and a variable number of teeth in two more rows)
 *Terebellides stroemii* Sars, 1835
14. Glandular region on CH3 (SG V) and 5th branchial lobe both absent
 *Terebellides atlantis* Williams, 1984
 – Glandular region on CH3 (SG V) and 5th branchial lobe both present
 *Terebellides gralli* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
15. Glandular region on CH3 (SG V) rounded or oval 16
 – Glandular region on CH3 (SG V) otherwise 17
16. Glandular region on CH3 (SG V) staining in white, branchial lamellae with rounded papillae, CH1–3 without conspicuous dorsal projection
 *Terebellides lilasae* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
 – Glandular region on CH3 (SG V) staining in blue, branchial lamellae with conical papillae, CH1–3 with conspicuous dorsal projection
 *Terebellides bonifi* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
17. Most branchial lamellae with marginal papillae 18
 – Only anterior branchial lamellae with marginal papillae 19
18. Branchial lamellae with digitiform papillae, upper lip elongated; MG staining pattern as compact bands from CH 1–5
 *Terebellides resomari* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
 – Branchial lamellae with widely spaced, small and elongated digitiform papillae; MG staining pattern leaving white stripes from CH 1–5
 *Terebellides gentili* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019
19. Thoracic uncini type 1 (main fang vs capitium length ratio 2(3)/1; capitium with 2(3) large teeth, following ones much smaller)
 *Terebellides ronningae* Parapar, Capa, Nygren & Moreira, 2020
 – Thoracic uncini type 3 (main fang vs. capitium length ratio 1/1; capitium with 4(5) mid-sized teeth, following ones slightly smaller) 20
20. Deep-water species, mostly found below 200 m deep
 *Terebellides norvegica* Parapar, Capa, Nygren & Moreira, 2020
 – Shallow-water species, mostly found above 100 m deep
 *Terebellides europaea* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019 and
 *Terebellides scotica* Parapar, Capa, Nygren & Moreira, 2020 complex

Discussion

Why have so many new species been discovered in such well-known waters?

In Europe (Greenland included), 109 valid species had been described since the first description of *Lanice conchilega* by Pallas (1766). Most of these species (i.e., 44) were described by early European taxonomists in the 18th and 19th centuries, and only a few during the 20th century (12 species). However, only five species were described before the start of this project from French waters: *Amphitrite edwardsii*, *Pista mediterranea*, *Polycirrus arenivorus*, *Polycirrus denticulatus* and *Thelepus setosus*. In addition, four species described from French waters are now considered as nomen dubium: *Lanassa proecox* (Saint-Joseph, 1899) which could be a postlarval stage of a known species (Fauvel 1927; Gil 2011), *Polycirrus haematodes* (Claparède, 1864) and *Polycirrus pallidus* (Claparède, 1864) for which no type material exists and the original descriptions are very brief (Glasby & Hutchings 2014), and finally *Amphitrite ramosa* Risso, 1826, stated to be indeterminable based on the original description (Jirkov 2020). Since the start of the “Spaghetti Project” in 2018, more than 400 specimens were carefully examined and more than 100 molecular sequences obtained. In French coastal waters, 58 species occur, 31 of them described as new during this project. The first question we can ask ourselves is: why? Why have so many new species been discovered in such well-known waters?

How can we explain the quasi-absence of discovery of new species in France for over a century? The first reason is the difficulty to identify known European terebellids. Indeed, as commented on by Hutchings & Lavesque (2020), the lack of literature and type material are especially challenging for taxonomists. Most of the European species were described by earlier workers who failed to designate type specimens and to deposit them in an official collection, or when they did, material is often damaged and unusable (Lavesque *et al.* 2021). Moreover, they provided only approximate type localities and few details on habitat preferences. Thus, comparison between new material and type material is difficult. Referring to original descriptions is not helpful either; they are usually very brief with inadequate figures, and could correspond to several species because of the lack taxonomic details (Hutchings *et al.* 2021a, 2021b).

The second reason, without any mystical connotation, is linked to the spectre of the priest Pierre Fauvel. Actually, the main reference work in polychaete taxonomic literature is, without any doubt, his “Faune de France” (Fauvel 1923, 1927). These two books are widely used by taxonomists, ecologists, students and private companies in France but also worldwide (Hutchings & Kupriyanova 2018; Hutchings & Lavesque 2020; Capa & Hutchings 2021). Fauvel was one of the most prolific authors in the history of polychaete taxonomy with 141 accepted species described, ranking 16th polychaetologist in the world (Pamungkas *et al.* 2019). Surprisingly, he described only four species from French coastal waters as most of his works were focused on the fauna from India (e.g., Fauvel 1932) or Africa (e.g., Fauvel 1918). He also described many deep sea species which are stored in the Musée Océanographique de Monaco and were sampled in the European Atlantic Ocean during the “Hirondelle” (1885–1888) and the “Princesse-Alice” (1894–1897) cruises by the Prince Albert 1st (e.g., Fauvel 1913). The specimens examined by Fauvel for his “Faune de France” were collected mainly at low tides or during dredging campaigns, while only some were received from a few colleagues (Fauvel 1923). In comparison, we had the opportunity to examine specimens from a greater variety of habitats, thanks to our RESOMAR colleagues working in eight coastal laboratories along the French coasts. With their help, we were able to compare material from a wide range of habitats, depths, and ecosystems. For example, 12 species were described from maerl (rhodolith) beds in Brittany (Lavesque *et al.* 2019a, 2020a, 2020b, 2021), confirming that this habitat is an important hotspot of biodiversity (Grall & Hall-Spencer 2003; Barbera *et al.* 2003). Moreover, our colleagues also undertook new sampling excursions to obtain fresh material so that we could undertake molecular analyses. These analyses, coupled with morphological observations, permitted us to confirm the existence of many cryptic species belonging to several species complexes such as the “*Terebellides stroemii* complex”, “*Pista cristata* complex” or “*Eupolyornia nebulosa* complex”

(Lavesque *et al.* 2019a, 2021). Even if, as taxonomists, we work in a similar way to Grube, Malmgren, McIntosh and other early scientists spending hours behind a stereo microscope, we are fortunate to have access to advanced technologies like high resolution cameras, scanning electron microscopes, molecular laboratories and internet facilities. These technologies help us to find differences or characters that early taxonomists would have missed and easy access to all the available literature.

The third reason is the lack of accurate literature for European waters, which is intimately linked to Fauvel's work. His two volumes of the "Faune de France" were of an excellent standard for his time. But publication was time consuming and costly, and resources were lacking to update his work in subsequent decades. For a long time, to 'correctly' identify a terebellid worm from French waters meant using either Fauvel's or Holthe's books. The latter, more recent work (Holthe 1986) is based on accurate observations (type material when possible), but the diagnoses are very short and do not take into account recent valuable taxonomic characters. Moreover, this work was focused on Scandinavian waters, from Greenland to Great Britain, a large region which differs from French waters and other countries from southern Europe especially with regard to water temperatures. Fauvel's books were widely used for nearly a century in France, in Europe and also in the rest of the world. This wide use was not a major issue for decades as scientists, polychaete taxonomists in particular, were convinced by the cosmopolitanism of marine worms (Hutchings & Kupriyanova 2018). Kristian Fauchald was the first one to suggest that polychaetes can show interesting biogeographical patterns when properly identified (Fauchald 1984). Recent studies clearly confirmed that species of polychaetes have restricted distributions and this is particularly true for terebellids. Focusing on the genus *Terebellides* in Northern European waters, Nygren *et al.* (2018) identified more than 25 species hidden within the so-called "cosmopolitan" species *Terebellides stroemii*. Most of these species occur only in a restricted area and specific habitat, and two species from Northern Europe are confirmed for French waters: *T. europaea* and *T. scotica* (Lavesque *et al.* 2019a; Parapar *et al.* 2020a).

The final explanation comes from the lack of taxonomic positions in France. This country is known for its famous early taxonomists such as Audouin, Gravier, Quatrefages, Saint-Joseph and Savigny, followed by few more recent ones like Bellan, Bhaud, Gillet, Laubier or Rullier. However, as many parts of the world, the number of taxonomists has dramatically declined in recent years, because taxonomy was not 'sexy' or technology-focused enough to attract policy makers attention. As a result, French scientists were almost absent from the international worm community for the last few decades. Indeed, prior to 2016, almost no French taxonomists participated in the different International Polychaete Conferences, with the exception of the conference organized in Angers in 1992. The absence of French representatives on the council of the International Polychaetology Association meetings was also a reality for several years. Fortunately, French marine biologists are now included in the RESOMAR network, allowing for a new dynamic and the recruitment of several technicians and researchers specialised in identification of benthic fauna. The lack of experienced taxonomists acting as mentors in France was compensated by the motivation of these young scientists. During the past decade, they have published numerous papers on French polychaete taxonomy (e.g., Bonifácio *et al.* 2015; Jourde *et al.* 2015; Lavesque *et al.* 2015, 2020c; Blake & Lavesque 2017; Le Garrec *et al.* 2017) with the fundamental help of international experts such as Barnich, Blake, Glasby, Hutchings, Meißner, Londoño-Mesa and Parapar among others.

What are the consequences of this hidden biodiversity?

So what difference does it make to know that not only one, but two extremely similar species of *Lanice* exist? Does this hidden diversity really matter? Of course the answer is yes! Of course, it is essential to use the appropriate name when identifying a species (Lavesque *et al.* 2019b; Hutchings & Lavesque 2020; Hutchings 2021). Specimens belonging to cryptic or pseudo-cryptic species are very similar and thus difficult for people, even for taxonomists, to distinguish. However, as most of these species evolve differently from a common ancestor, their life-traits and their ecological function may be different, or in

the process of becoming different. Indeed, in his review on cryptic polychaete diversity, Nygren (2014) shows that many cryptic species can be distinguished by a number of biological characteristics, such as reproductive biology, life history, feeding biology, salinity, habitat and depth preferences or anoxia and temperature tolerances. Each species has a unique set of micro-habitat requirements and functions with important ecological consequences. Misidentification or an underestimation of the diversity thus have a strong impact on ecological studies.

The sand mason worm, *Lanice conchilega*, is a perfect example to illustrate this point. By aggregating sand particles on its tube, this species acts as ecosystem engineer for forming reef-like structures (Rabaut *et al.* 2009; Hutchings *et al.* 2021b). The presence of these biogenic structures increases habitat quality and enhances local biodiversity by changing hydrodynamics and nature of the shore, increasing habitat stability and oxygen supply, and finally creating heterogeneity in a uniform environment (Van Hoey *et al.* 2008). This habitat is thus very attractive for predators like fishes and foraging waders, and thanks to its high functional value, this habitat also has high conservation value (Godet *et al.* 2008). By contrast, in Arcachon Bay, the very similar species *L. kellyslateri* has a scattered distribution with worms appearing solitary. Maybe this absence of a “reef structure” could be linked to a specificity of this new species or to the particular environment occurring in this lagoon. These worms from Arcachon Bay may not be attractive for birds and perhaps policy makers would be unlikely to protect this species and its habitat. As we can see, the stakes can be high when considering cryptic species individually.

Another example worth considering is the strawberry worm *Eupolymnia nebulosa*. Experiments conducted on specimens sampled in the Gulf of Lion (Mediterranean Sea) allowed for insights into its feeding mode and tube building (Grémare 1988; Grémare *et al.* 1989; Grémare & Amouroux 1990), its bioturbation activity (Maire *et al.* 2007) and development (Bhaud 1988; Bhaud & Grémare 1988). Another study by Grémare (1986) highlighted that two populations, one from Banyuls-sur-Mer (Gulf of Lion), the second from Dinard (English Channel) had different reproductive modes. However, Lavesque *et al.* (2021) have shown that specimens sampled from Banyuls-sur-Mer belonged to two new species: *E. lacazei* and *Eupolymnia* sp. C. Additionally, specimens from Normandy and Brittany (English Channel) belonged to a third new species: *E. gili*. All these specimens were previously identified as *E. nebulosa*, but clearly belong to three cryptic species. We can therefore observe that these differences in reproductive modes can be linked to different species rather than different populations, as previously suggested by Martin *et al.* (1996). Discovery of multiple species with restricted distributions has implications for conservation. For example, it may be assumed that isolated populations can easily recover from local disasters (oil spill for example) by recruitment from nearby populations. But if it turns out that a species previously thought to be widespread is really several different species, this may have implications for recovery from local perturbations.

Regarding non-indigenous species (NIS), misidentifications can have a significant impact on the understanding of ecosystems, and cascading consequences for environmental management if they are detected too late. Frequently, exotic species are often morphologically very similar to native species. As they are not reported from European waters, they are absent from identification keys restricted to the local area. It is therefore essential that the most up-to-date and relevant literature is used to identify species for ecological monitoring studies. Even if this is time consuming and expensive, the species which are typically found in an ecosystem should be regularly checked in detail by using a complete diagnosis, and not just by means of outdated keys that will of course give a poor result. Particular attention should be paid to sensitive areas, where NIS are known to occur, such as harbours, marinas and oyster farms. For example to illustrate this problem, using the blood-worm *Marphysa sanguinea* (Montagu, 1813) which was largely reported from Arcachon Bay for decades. However, after a thorough morphological and molecular analysis, a second species, new for science was found, i.e., *Marphysa victori* Lavesque, Daffe, Bonifácio & Hutchings, 2017. This discovery may seem anecdotal, but after extensive investigations,

we could confirm that this species native to South East Asia was probably introduced into the bay via oyster transfers in the 1970's, after mass mortalities of Portuguese oysters (Lavesque *et al.* 2020c). Moreover, *M. victori* is an important economic resource as bait and collected both by recreational and professional fishermen, with about 1 million worms traded per year (Lavesque *et al.* 2017b), most of them shipped live and sold in Western Mediterranean fishing shops in France (Lavesque *et al.* 2020c). Similarly, the presence of the Asiatic terebellid *Thelepus japonicus* was recently reported for the first time in Europe. Again, its presence in Arcachon Bay and in Normandy is linked to oyster farming with a probable introduction from Japan to Arcachon Bay via oyster transfers and a secondary introduction from Arcachon to Normandy by local transfers (Lavesque *et al.* 2020a). Prior to the “Spaghetti Project”, this species was confused with *Thelepus setosus*, originally described from France, and therefore absent from European identification keys.

Finally, knowing the exact number of species within a region, or at least the number as close to reality as possible, is fundamental to understanding biodiversity issues. In the context of the extent of the biodiversity crisis, ignoring cryptic species leads to an underestimation of the species richness in the oceans (Bickford *et al.* 2007; Nygren 2014). Describing this cryptic diversity is absolutely fundamental in the context of the biodiversity crisis (Bickford *et al.* 2007). We cannot assess the loss of biodiversity in an anthropogenic context if we do not know how many species really occupy an area. Similarly, we cannot identify areas of endemism or areas of biological interest, without knowledge of cryptic species. If we just take into account the results of this “Spaghetti Project”, the biodiversity of terebellids has exploded recently, with 31 new species for French waters. Of course, we know that all these new species are not really new but have just been overlooked for ages, representing a hidden biodiversity. The alarming message of how much biodiversity has been underestimated must be clearly conveyed to the public, the politicians and the managers. In the same way, we need to know exactly which species live in an ecosystem to evaluate the effects of global change. For example, recent studies tend to prove a “tropicalization” of the Bay of Biscay, with several species belonging to different biological groups (algae, fishes, decapods, molluscs or worms) shifting their northern distribution limit from tropical regions north to the southern part of the Bay of Biscay (Portugal, Spain and South of France) (Lima *et al.* 2007; Arias & Crocetta 2016; Encarnaç o *et al.* 2019; Sch afer *et al.* 2019). Among these species, at least one of them could become problematic. Indeed, the bearded fireworm *Hermodice carunculata* (Pallas, 1766), originated from the West Indies and recently observed in southwestern Iberian Peninsula (Encarnaç o *et al.* 2019), can cause severe pain if its stinging chaetae come into contact with human skin.

What remains to be done with these Spaghetti worms?

We, as taxonomists, have the responsibility to share our studies and make sure that our work reaches a wide audience. Scientific papers and international conferences are not sufficient and we should use a variety of media (TV, newspapers, social media and blogs) to communicate our findings (Hutchings 2020). Biodiversity is not restricted to geeks of taxonomy and our mission is to help students, ecologists and other professionals to put the right name on the right animal (Hutchings & Lavesque 2020). We also have to explain to politicians why taxonomy is important to the economy and biodiversity conservation, especially with regards to zoning plans for marine parks or management of marine pests (Hutchings 2020, 2021). We have to produce easy to use identification keys, which allows people to differentiate species from cryptic complexes if possible. Our keys should be web-based and thus widely available to the wider biological community (Hutchings *et al.* 2021b). We, as experts, should be available to help people to identify or confirm their identifications, especially if those seeking for help come from countries lacking taxonomists and/or accurate literature.

Even if our “Spaghetti Project” permitted the improvement of the knowledge of terebellids from French waters, there is still a lot to be done. Firstly, most of the specimens examined were collected in French

coastal waters, with the exception of some worms sampled from the deep Capbreton canyon (Lavesque *et al.* 2019a). The exploration of off-shore deep sea areas should be enhanced in order to have a better understanding of the distribution of these species. Some regions, like the eastern part of the French Mediterranean Sea, were poorly surveyed due to absence of benthic ecologists and samples (i.e., Marseille and Villefranche-sur-mer). This project has highlighted the presence of at least another eight undescribed species in France, based on molecular results. These “orphan” sequences belonged to small or damaged specimens, which were not in good enough condition to be described morphologically. Nygren *et al.* (2018) obtained similar results while working on *Terebellides* from Northern Europe; they obtained sequences belonging to 14 still undescribed species (Parapar *et al.* 2020a). Many more new species probably occur in other parts of Europe where this group was not really studied in detail before, for example in the UK or Italy to name but a few. As discussed before, due to species having restricted distributions (Nygren *et al.* 2018), more local studies are needed to give us a better picture of the true biodiversity of the region. Globally, some regions like Australia and Brazil are relatively well studied, leading to descriptions of tens of species (Hutchings *et al.* 2021b), but several regions in the world represent a “taxonomic desert” for terebellids like African, Indian and polar regions (Hutchings *et al.* 2021b; Capa & Hutchings 2021). So this “Spaghetti Project” could provide a blue print for what is needed in other parts of the world.

For the stability of taxonomic nomenclature, it is important to erect neotypes for old European species described by early naturalists. Indeed, most of these species were only subsequently designated as type species of genera, and very often type specimens were not designated or do not exist anymore and original descriptions are very brief according to current standards. During this project, we highlighted this need for several species like *Trichobranchus glacialis* and *Octobranchus lingulatus*, both type species of their genera (Lavesque *et al.* 2019a), *Polycirrus denticulatus* (Lavesque *et al.* 2020b), *Amphitrite edwardsii* and *A. figulus*, *Eupolymnia nebulosa* and *E. nesidenis* (the type species of the genus), *Lanice conchilega* (the type species of the genus), and finally *Pista cristata* (the type species of the genus) which is currently being redescribed (Londoño-Mesa *et al.* in prep.; Lavesque *et al.* 2021) (Fig. 9; Table 1). Obtaining molecular sequences from neotypes is also crucial for future comparison and integrative taxonomy. This ensures that every species will have a modern description based on morphological and molecular tools. Undoubtedly, fixing neotypes will allow taxonomists to describe new species, as they will have a reference point for comparison. When Parapar & Hutchings (2014) designated a neotype for *T. stroemii*, they opened the door to the description of 13 new species of *Terebellides* from Europe, with most of these new species identified in the past as *T. stroemii* (Lavesque *et al.* 2019a; Parapar *et al.* 2020a).

To conclude, the collaborative “Spaghetti Project”, supported by numerous enthusiastic people was a real success story. We are aware that some areas and habitats along the French coast are under-represented in this study but nonetheless, we are sure that it will facilitate the discovery of additional undescribed species not only in our region, but also in the rest of Europe. This focus on the hidden biodiversity of terebellids can be translated to other parts of the world and also to other families, the estimated number of remaining new polychaetes species being greater than 20 000 (Pamungkas *et al.* 2019; Capa & Hutchings 2021; Magalhães *et al.* 2021). An interesting challenge will now be to develop online user-friendly tools, like the Delta (Coleman *et al.* 2010) or Xper (Ung *et al.* 2010) identification keys. A new volume of the *Fauna Iberica* collection with a focus on terebellids is also in preparation and coordinated by Julio Parapar. Finally, a “European Terebellids Tour” to sample and erect neotypes of old species should be planned (Fig. 9)!

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Fig. 9. Type localities of European species for which a neotype is required.

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ANNEXES

Lavesque N., Bonifácio P., Londoño-Mesa M.H., Le Garrec V., Grall J. (2017). *Loimia ramzega* sp. nov., a new giant species of Terebellidae (Polychaeta) from French waters (Brittany, English Channel). *Journal of the Marine Biological Association of the United Kingdom* 97(5) 935-942 *

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Loimia ramzega sp. nov., a new giant species of Terebellidae (Polychaeta) from French waters (Brittany, English Channel)

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A new species of Terebellidae, Loimia ramzega sp. nov., has been identified from North Brittany beaches (English Channel). This new species is characterized by its gigantic size (max 650 mm, live), two pairs of lateral lappets on segments 1 and 3; first pair more ventral, second pair more developed and lateral but oblique, with wavy edge. Nine ventral pads from segment 2 (fused on segments 2 and 3), first three pads swollen, next ones subsequently decreasing in size. Three types of notochaetae, asymmetrically bilimbate, symmetrically bilimbate and capillary. Uncini pectinate with 6 teeth (some with 5 teeth) slightly decreasing in size, in one vertical row. Pygidium with about 14 long conical marginal papillae surrounding anus.

Keywords: Terebellinae, morphology, molecular, taxonomy, DNA COI 16S, North-east Atlantic, France

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INTRODUCTION

Terebellids belong to a very species-rich group of sedentary polychaetes, widely distributed in most marine benthic substrates, from shallow waters to deep-sea environments (Rouse & Pleijel, 2001). Terebellidae Johnston, 1846 is currently subdivided into three subfamilies: Polycirrinae Malmgren, 1867, Terebellinae Johnston, 1846 (frequently referred to as Amphitritinae) and Thelepodinae Hesse, 1917 (as Thelepinae) (Londoño-Mesa & Carrera-Parra, 2005). However, Nogueira *et al.* (2013) carried out a large phylogenetic analysis which resulted in splitting the family Terebellidae into four families: Polycirridae, Terebellidae (=previous Terebellinae), Telothelepodidae and Thelepodidae. Herein, the former proposal will be followed (Read, 2016).

According to Carrerette & Nogueira (2015), this family includes around 300 species belonging to 50 genera. Among the subfamily Terebellinae, the genus *Loimia* Malmgren, 1865 currently comprises 28 valid species, of which seven have been recently described from Brazilian and Australian coasts (Carrerette & Nogueira, 2015; Nogueira *et al.*, 2015). This genus can be found worldwide, especially occurring in tropical waters (Read & Bellan, 2011), with only two species known from European waters. *Loimia arborea* Moore, 1903a was recorded from the Mediterranean Sea (RESOMAR –

French marine stations and observatories network – database, <http://resomar.cnrs.fr/bases/index.php>; Faulwetter, 2010) and from the Irish Sea (Guiry & Guiry, 2011). However, these records are doubtful since this species originated from Japan. According to the World Register of Marine Species, validation of these occurrences and species presence beyond Japanese waters is needed (WoRMS, 2008). *Loimia medusa* (Savigny in Lamarck, 1818) was previously believed to occur from the Mediterranean to Norway but this species was redescribed by Hutchings & Glasby (1995) who suggested that its distribution may be restricted to the Arabian Sea Region. Due to the lack of accurate literature, many European studies have identified their specimens as *Loimia* sp. (e.g. Mackie *et al.*, 1995 in the south-eastern Irish Sea; RESOMAR database along the French coasts). Since 2011, one of the authors (JG) regularly found specimens of a giant species of *Loimia* within Northern Brittany beaches that could not be related to any described species. The present paper provides the description of this new species based on morphological characters and supplemented by molecular data. The geographic origin of the species, perhaps not originating from Europe, is discussed.

MATERIALS AND METHODS

Sampling and morphological analyses

The first specimens of this new *Loimia* species were sampled in 2011 from intertidal sandy beaches of the English Channel

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(Brittany, France) (Figure 1) after notification of strange large annelid tubes (Figure 2A) by Michel Glémarec (senior French benthic ecologist from Brest University). Specimens examined in this study were collected in 2011, 2012 and 2016 by hand, using a shovel-fork and a technique called ‘finger tube tracking’ allowing the monitoring of the tube position and changes in direction at any moment (Figure 2B). Live specimens were anaesthetized with 7% magnesium chloride ($MgCl_2$) and photographed using a Canon EOS 600D camera. A small piece of body was removed from several specimens and fixed in 96% ethanol for molecular studies. The main material was fixed in 4% formaldehyde seawater solution, then transferred to ethanol 70% solution for morphological analysis. Preserved specimens were examined under a Nikon SMZ25 stereomicroscope and a Nikon Eclipse E400 microscope, and photographed with a Nikon DS-Ri 2 camera. Total length, length of thorax and width of thorax (10th chaetiger) were measured with the NIS-Elements Analysis software. Drawings were made from pictures using Inkscape software and a Wacom Intuos 5 tablet. Holotype and most paratypes were deposited at the Muséum National d’Histoire Naturelle, Paris (MNHN), other paratypes were deposited in the National Museum Wales, Cardiff (NMW-Z) and in the Colección Estuarina y Marina, Universidad de Antioquia (CEMUA) in Medellín, Colombia. Additional material was

lodged in collections of the Arcachon and Brest Marine Stations, in France.

DNA isolation, amplification and sequencing

Sub-samples for DNA analysis were removed from live specimens, placed in ethanol 96% and frozen at $-20^{\circ}C$. Extraction of DNA was done with a NucleoSpin Tissue (Macherey–Nagel) kit following the manufacturer’s protocol. About 450 bp of 16S and 700 bp of COI (cytochrome c oxidase subunit I) genes were amplified using primers Ann16SF and 16SbrH for 16S (Palumbi, 1996; Sjölin *et al.*, 2005), and polyLCO and polyHCO for COI (Carr *et al.*, 2011). The PCR (Polymerase Chain Reaction), with 25 μ l mixtures contained: 5 μ l of Green GoTaq® Flexi Buffer (final concentration of $1\times$), 2.5 μ l of $MgCl_2$ solution (final concentration of 2.5 mM), 0.5 μ l of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 9.875 μ l of nuclease-free water, 2.5 μ l of each primer (final concentration of 1 μ M), 2 μ l template DNA and 0.125 of GoTaq® G2 Flexi DNA Polymerase (Promega). The temperature profile was as follows: $95^{\circ}C/240$ s – ($94^{\circ}C/30$ s – $52^{\circ}C/60$ s – $72^{\circ}C/75$ s) * 35 cycles (for 16S) or * 40 cycles (for COI) – $72^{\circ}C/480$ s – $4^{\circ}C$. PCR-products, which produced light bands after electrophoresis on 1% agarose gel, were sent to the MacroGen Europe Laboratory in Amsterdam (the Netherlands) to obtain sequences, using the same set of primers as used for the PCR. Overlapping sequence (forward and reverse) fragments were merged into consensus sequences using Geneious Pro 8.1.7 2005–2015 (Biomatters Ltd) and aligned using the plugins: MAAFT (Kato *et al.*, 2002) for 16S and MUSCLE (Edgar, 2004) for COI. For COI, the sequences were translated into amino acid alignment and checked for stop codons to avoid pseudogenes. The minimum length coverage was around 450 bp for 16S and 610 bp for COI. All sequences obtained in this study have been deposited in GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>).

RESULTS

SYSTEMATICS

Family TEREBELLIDAE Johnston, 1846

Subfamily TEREBELLINAE Johnston, 1846

Genus *Loimia* Malmgren, 1865

Type species: *Terebella medusa* Savigny in Lamarck, 1818

GENERIC DIAGNOSIS

Malmgren (1865: 380). Hesse (1917: 170). Hutchings and Glasby (1995: 149–150).

Branchiae on segments 2–4; lateral lappets on segments 1 and 3, 1 and 2/3 (in combination of segments 2 and 3) or 1, 3 and 4; ventral shields from segment 2 or 3; nephridial papillae on segments 3–4 and 6–8; 17 pairs of thoracic notopodia from segment 4; chaetae alimbate, unilimbate, symmetrical or asymmetrically bilimbate, smooth tipped; neuropodia from segment 5, uncini avicular or pectinate with a single vertical series of teeth, arranged in single rows on segment 5–10, in double rows, back to back, up to segment 20, and in single rows along the abdomen; pygidium sometimes with anal cirri or papillae.

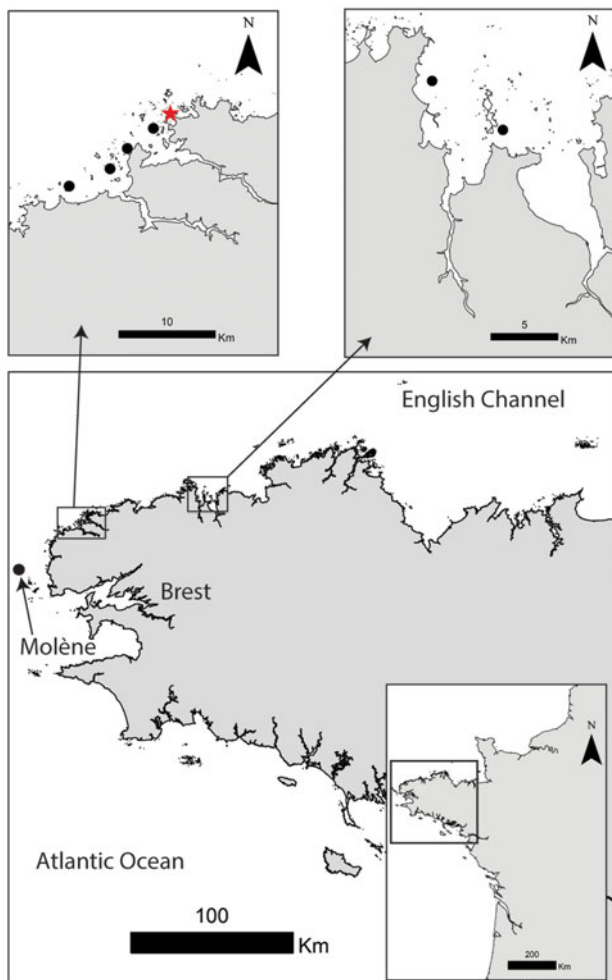


Fig. 1. Sampling sites of *Loimia ramzega* sp. nov. on the Brittany coasts (English Channel, Western France). Dots: presence; star: type locality.



Fig. 2. *Loimia ramzega* sp. nov. (A) Tube opening; (B) Trench required to collect a single specimen; (C) Live specimen in its tube, antero-ventral view; (D) Entire live specimen. Scale bars: A, 2 cm; B, 50 cm; D, 10 cm.

Loimia ramzega sp. nov.
(Figures 2–5)

TYPE MATERIAL

Holotype: anterior fragment, 139 segments, 254.2 mm long; thorax 58.6 mm long and 15.84 mm wide (MNHN-IA-TYPE 1788); France, English Channel, Brittany, Plouguerneau, Lilia beach (48°37'37.2"N 4°34'08.5"W), intertidal, 23 February 2016.

Measured Paratypes: complete specimen, broken, 165 segments, 241.13 mm long; thorax 65.56 mm long and 13.23 mm wide (MNHN-IA-TYPE 1789), anterior fragment, 41 segments, 68.5 mm long; thorax 63.29 mm long and 13.11 mm wide (MNHN-IA-TYPE 1790); France, location and sampling as for holotype. Anterior fragment, 47 segments, 154.37 mm long; thorax 74.64 mm long and 13.22 mm wide (MNHN-IA-TYPE 1791), anterior fragment, 46 segments, 130.91 mm long; thorax 64.52 mm long and 13.44 mm wide

(MNHN-IA-TYPE 1792); France, English Channel, Brittany, Landéda beach (48°36'37.7"N 04°36'24.5"W), intertidal, 25 January 2012.

Other Paratypes: 6 anterior fragments, 6 abdominal fragments, 3 posterior fragments (NMW.Z.2017.002.0001); France, English Channel, Brittany, Landéda beach (48°36'37.7"N 04°36'24.5"W), intertidal, 27 December 2011; one complete specimen (NMW.Z.2017.002.0002), one anterior fragment (CEMUA-POLY-TERE-0100); France, English Channel, Brittany, Landéda beach (48°36'37.7"N 04°36'24.5"W), intertidal, 25 January 2012.

ADDITIONAL MATERIAL

Four anterior fragments and 2 posterior fragments (Arcachon Marine Station Collection); France, English Channel, Brittany, Landéda Beach (48°36'37.7"N 04°36'24.5"W), intertidal, 25 January 2012. One anterior fragment (Arcachon Marine Station Collection), 2 anterior fragments (Brest Marine

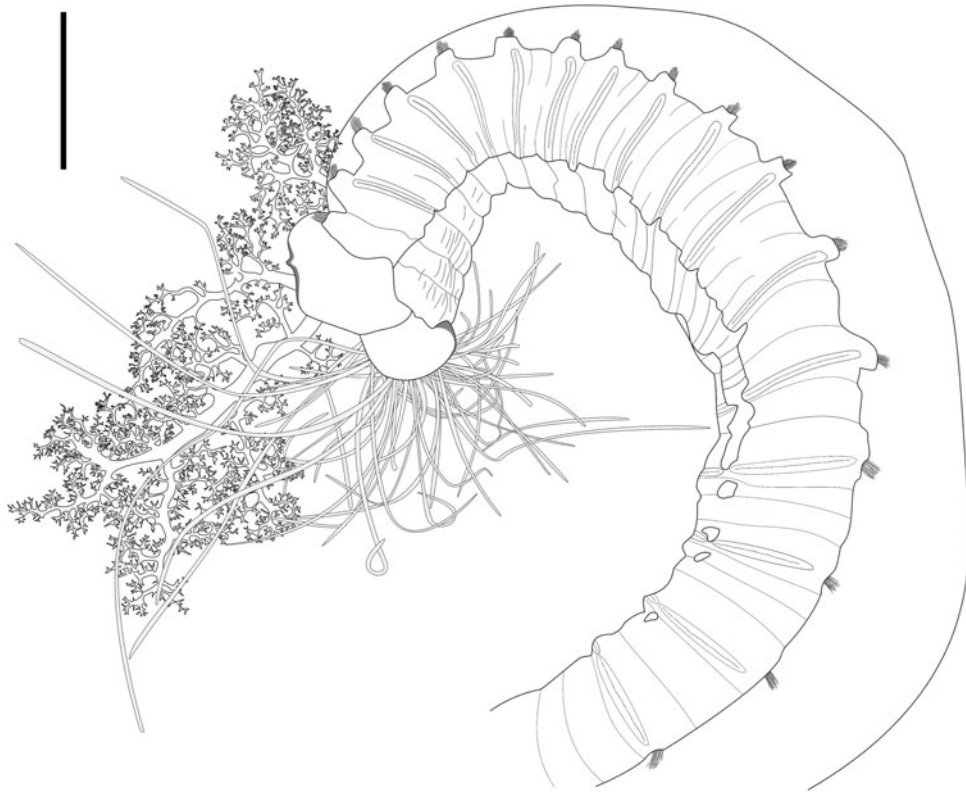


Fig. 3. *Loimia ramzega* sp. nov. anterior part (live specimen), lateral view (holotype MNHN-IA-TYPE 1788). Scale bar: 1 cm.

Station Collection); France, English Channel, Brittany, Plouguerneau, Lilia Beach ($48^{\circ}37'37.2''N$ $4^{\circ}34'08.5''W$), intertidal, 23 February 2016.

DIAGNOSIS

Gigantic size (max. 650 mm, live), two pairs of lateral lappets on segments 1 and 3; first pair more ventral, second pair more developed and lateral but oblique, with wavy edge. Nine ventral pads from segment 2 (fused on segments 2 and 3), first three pads swollen, next ones decreasing in size. Uncini pectinate with 6 teeth (some with 5 teeth) slightly decreasing in size, in one vertical row. Pygidium with about 14 long conical marginal papillae surrounding anus.

DESCRIPTION (BASED ON HOLOTYPE AND PARATYPES, MNHN)

Tube long and only 17 mm in width, made of shells fragments and small gravels, emerging end with fragments of macroalgae attached, inner surface with strong smooth membrane allowing tube to maintain a hard consistency (Figure 2A, C). In life, body colour pinkish to light green (Figure 2C, D); buccal tentacles translucent; upper lip light pink; first pair of lateral lappets white with blood red margins (Figure 2C); second pair blood red; branchiae blood red; first ventral pad whitish, second one whitish anteriorly and blood red posteriorly, ventral pads from segment 5 to 11 (S₅ to S₁₁) blood red and with tiny whitish lateral bands, shields from S₁₂ to end of thorax dark red (Figure 2C). Dorsal posterior part of abdomen with dark spots. Formalin fixed body with brownish lappets, ventral shields from S₄ to S₁₁ light brown, others dark brown, dorsal-posterior margin of thoracic segment light orange. In alcohol, body whitish.

Tentacles abundant and long, reaching end of thorax when projecting backward on live specimens (Figure 3), without ridges, with a deep groove. Eyespots absent from very developed tentacular membrane. Upper lip rounded, with free edge, projecting forward. Lower lip small, completely covered ventrally by membrane connecting lappets of segment 1. Lateral lappets discontinuous, 2 pairs on S₁ and S₃. First pair large, oval, projecting forwards, merged ventrally (originating ventrally), covering upper lip (Figures 3 & 4A). Second pair of lateral lappets the largest, laterally concealing S₂, originating ventro-laterally and connected to first ventral shields, anterior margin wrinkled or wavy, dorsolaterally ear-shaped, covering the base of the first and second pairs of branchiae (Figure 3).

Three pairs of arborescent branchiae, long, starting from S₂, first pair longest, projecting forward, third pair smallest. Branchiae with thick stalks, and many dendritic branches arranged in five levels (Figure 3). Nephridial papillae, tube-like, from S₃–4 and S₆–8. Whitish glandular patches, gradually decreasing in size, surrounding the first 11 notopodia (Figure 4B). Sixteen ventral shields from S₂, fused on S₂–S₃ (Figures 2C & 4C), not subdivided, progressively narrower and more indented posteriorly by neuropodia from S₁₂ to S₁₇. Ventral shields more evident in live specimens, appearing as blood red pigmentation (Figure 2C). Abdomen ventrally smooth.

Notopodia from S₄, extending through S₂₀. Notopodial lobes well developed (Figure 4B), first notopodia button-like. Notochaetae of three types within a fascicle: long serrated, asymmetrically bilimbate; long bilimbate, serrated, with narrow limbs; and slightly shorter alimbate capillaries few in number, around 1:10 relative to long chaetae (Figure 5A). Thoracic neuropodia as ventrolateral belts of uncini, decreasing in width toward the posterior thoracic region. Abdominal

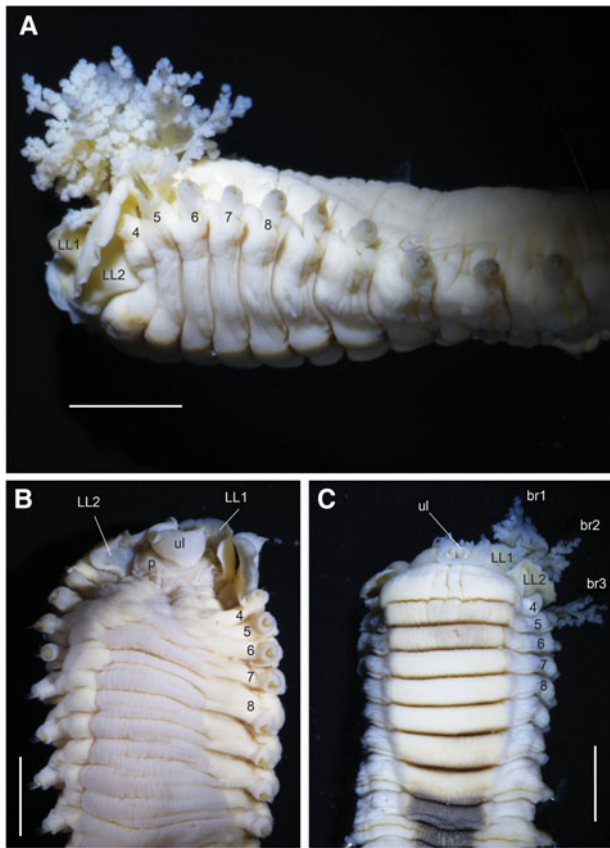


Fig. 4. *Loimia ramzega* sp. nov. (A) Anterior part, lateral view (holotype MNHN-IA-TYPE 1788); (B) Anterior part, dorsal view (paratype MNHN-IA-TYPE 1792); (C) Anterior part, ventral view (holotype MNHN-IA-TYPE 1788). Numbers refer to segments; LL1, first lateral lappet; LL2, second lateral lappet; p, peristomium; ul, upper lip; br1, br2, br3 refer to the three pairs of branchiae. Scale bars: 5 mm.

neuropodia long, projected posteriorly, with narrow belt of uncini along posterior margins. Thoracic ($N = 280-350$) and abdominal ($N = 90-110$) uncini pectinate, arranged in double rows from segment 11, similar in size and shape, with 6 teeth in single vertical row, some uncini with 5 teeth (Figure 5B, C). Uncini long with curved occipitium, posterior process absent, basis concave, anterior process absent, anterior filament long, projected downwards, long and narrow subrostrum, subrostral process absent. Pygidium with terminal rounded anus, surrounded by 14 long, conical papillae (Figure 5D).

VARIATION

One paratype (MNHN-IA-TYPE 1790) with the first pair of lateral lappets showing a deep anterodorsal notch. One posterior part of additional material with only 12 pygidial papillae, but probably two lost. Remaining characters strictly similar to holotype.

DNA

COI and 16S genes were successfully sequenced and published at NCBI GenBank for: holotype MNHN-IA-TYPE 1788 accession number 16S: KY555058 and COI: KY555061; paratypes MNHN-IA-TYPE 1789 accession number 16S: KY555059 and COI: KY555062 and MNHN-IA-TYPE 1790 accession number 16S: KY555060 and COI: KY555063.

ETYMOLOGY

The species name *ramzega* refers to the gigantic size of this species. In Breton 'ramzeg' means titanic, giant.

DISTRIBUTION

Only known from France, English Channel, North Brittany (along 60 km) and from Molène island; on sandy beaches, intertidal (Figure 1).

DISCUSSION

According to Holthe (1986), the genus *Loimia* had 16 valid and described species, one subspecies and four synonymized species. However, Read & Bellan (2011) stating recent newly described species, reported 28 valid species and one *nomen dubium*. This genus shows a tropical distribution, with only a few subtropical species, and no arctic species. *Loimia medusa*, the type species described from the Red Sea, has long been erroneously identified in many distant localities, hiding possible new species identifications (Hutchings & Glasby, 1995). Thus, true cosmopolitan species are now a topical subject for debate by marine taxonomists (Hutchings, 2016). Recently, new species of polychaetes have been identified from supposed well studied localities (Londoño-Mesa, 2009; Carrerette & Nogueira, 2015; Nogueira *et al.*, 2015). Concerning European waters, no species belonging to the genus *Loimia* has been officially described, although some specimens originating from the area may have been erroneously deposited in museums under the name *L. medusa*. Thus, the present description of *L. ramzega* sp. nov. may offer a local solution for those misidentified species but given the presence of *Loimia* sp. in the south-eastern Irish Sea (Mackie *et al.*, 1995), there are probably more undescribed *Loimia* species in Europe (especially small species) and all specimens should be observed carefully. Indeed, a similar exercise has been done by Londoño-Mesa & Carrera-Parra (2005) with specimens initially identified as *L. medusa* from the Caribbean. These authors found that *L. medusa* does not occur in the western tropical Atlantic, and that the material identified as *L. medusa* from the region already belonged to three species; one incorrectly hidden by synonymy, *Loimia minuta* Treadwell, 1929, and one new for science, *Loimia salazari* Londoño-Mesa & Carrera-Parra, 2005.

We report *L. ramzega* sp. nov. for the first time from one of the best known marine ecosystems of the world: the western English Channel. We believe that a species of such size and from an easily accessible habitat could not have been overlooked through 150 years of marine biological study in the area. Indeed, Roscoff and Concarneau Biological stations both founded during the 19th century, and later the Biological Oceanography Laboratory of the University of Western Brittany since the 1960s, have led hundreds of benthic surveys in the area. It is thus very unlikely that the species would not have been noticed before 2011. The main hypothesis for lack of record previous to the 2010s is that *L. ramzega* sp. nov. could be a non-European indigenous species recently introduced to Brittany. The fact that it has been first identified within two areas with extensive oyster farming of the Pacific Oyster *Crassostrea gigas* (Thunberg, 1793) (some spat and juveniles being directly imported from

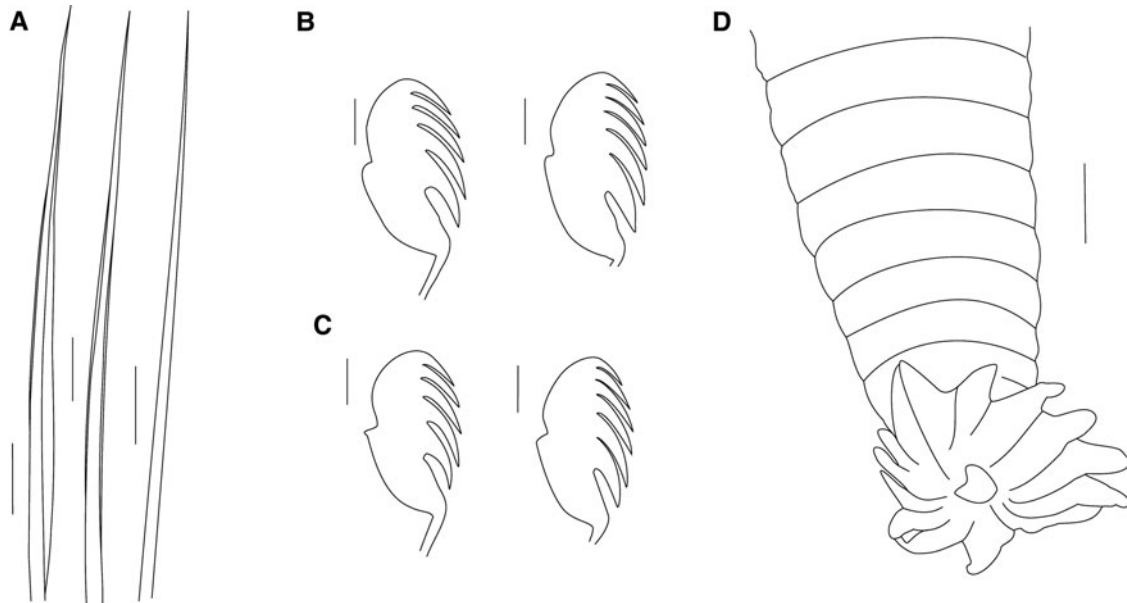


Fig. 5. *Loimia ramzega* sp. nov. (A) Notochaetae from chaetiger 11 (paratype MNHN-IA-TYPE 1790); (B) Thoracic uncini from segment 12, lateral views (paratype MNHN-IA-TYPE 1791); (C) Abdominal uncini from segment 25, lateral views (paratype MNHN-IA-TYPE 1791); (D) Pygidium lateral view (paratype MNHN-IA-TYPE 1789). Scale bars: A 0.1 mm; B, C 25 μ m; D 0.5 mm.

marine areas outside France) would support such hypothesis. The question of its area of origin then arises. Another way could be an immigration from southern Europe or Africa. Warming seas with climate change could have brought the species further north. This hypothesis seems unlikely as 'tropicalization' of the English Channel is not yet documented, especially in the area (Tréguer *et al.*, 2014), at the opposite of Bay of Biscay (Arias & Crocetta, 2016). Indeed, thermal and haline structures in the Iroise Sea hinder dispersal between the Bay of Biscay and English Channel and numerous benthic fauna species find their limit of distribution in Brittany (Le Garrec *et al.*, 2016; Gallon *et al.*, in revision). However, because it is so difficult to catch, we cannot exclude the fact that the species may be native from Europe, and when (if) sampled, would have been misidentified under the name *L. medusa*.

Loimia ramzega sp. nov. is easily identifiable by its very large size, the pigmentation on the ventral shields, and the development of its lateral lappets. Before this record, the largest species within the genus was *L. salazari* from the Mexican Caribbean, at 221 mm length, but it differs from *L. ramzega* by having avicular instead of pectinate uncini.

We do not believe that the very large size of *L. ramzega* represents a reliable example of gigantism. Indeed gigantism is rather known from polar or abyssal environments (Moran & Woods, 2012) and not from intertidal temperate waters. Gigantism that would result from a consequence of a pollution is also dismissed. Indeed, sampling sites are not particularly affected by anthropogenic perturbations. Moreover, no other benthic invertebrate species from these highly diversified benthic communities are oversized in comparison with other sites or adjacent waters.

Species belonging to *Loimia* having pectinate uncini, and from geographically close regions are scarce. *Loimia viridis* Moore, 1903b, from Massachusetts (USA), has similar shape on first ventral shields, but it differs from *L. ramzega* sp. nov., by having pectinate uncini with 7–8 teeth, only one

type of notochaeta, being symmetrically bilimbate, and with the second pair of lateral lappets transverse to the body axis. Other *Loimia* species with pectinate uncini differ by combinations of morphological characters (disposition and number of lateral lappets and number of uncinal teeth) as well as by their geographic distribution. For example, *L. arborea* (from Japan) has lateral lappets on segments 1 and 2/3, and thoracic uncini with 5 (rarely 6) teeth, and abdominal ones with 6 (rarely 7) teeth. *Loimia batilla* Hutchings & Glasby, 1988 (from Queensland, Australia) has lateral lappets on segments 1 and 2/3, and thoracic uncini with 6 teeth, and abdominal ones with 7 teeth. *Loimia bermudensis* Verrill, 1900 (from Bermuda) has lateral lappets on segments 1 and 3, and uncini with 5 teeth (rarely 6 very reduced). *Loimia decora* Pillai, 1961 (from Sri Lanka) has lateral lappets on segments 1 and 2/3, and uncini having 5 teeth. *Loimia grubei* Holthe, 1986 (from the Philippines) has lateral lappets on segments 1 and 2/3, and thoracic uncini with 5 teeth and abdominal uncini with 6–7 teeth. *Loimia triloba* Hutchings & Glasby, 1988 (from Queensland) has three pairs of lateral lappets on segments 1, 3 and 4, and uncini with 5 (rarely 6) teeth. Finally, *Loimia verrucosa* Caullery, 1944 (from Indonesia) has lateral lappets on segments 1 and 3, and uncini with 7 teeth. Thus, none of the species having pectinate uncini have been described from Europe, and *L. ramzega* sp. nov. is the first such species being described from the region.

Finally, a revision of the genus is ongoing, examining the phylogenetic relationship of the species within the genus based on morphology.

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A new species of *Pista* Malmgren, 1866 (Polychaeta, Terebellidae) from the north-western Mediterranean Sea

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Abstract

A new species of Terebellidae, *Pista colini* sp. n., has been identified from the harbour of Banyuls-sur-Mer, north-western Mediterranean Sea. This new species was found in very high densities, exclusively in gravelly sand deposited manually, and was not found in the original source habitat of the gravel. This species is characterized by the colour of the ventral shields with pinkish anterior part and a blood red posterior part in live specimens, a pair of unequal-sized plumose branchiae inserted on segment II and anterior thoracic neuropodia with long-handled uncini. The presence of long-handled uncini even in the smallest specimens constitutes the major difference between *Pista colini* sp. n. and other *Pista* species with a single pair of branchiae such as *P. lornensis* and *P. bansei*.

Keywords

Annelida, gravel deposits, harbour, *Pista colini* sp. n., taxonomy, Terebellida

Introduction

Terebellids belong to a very species-rich group of sedentary polychaetes, widely distributed in most marine benthic substrates, from shallow waters to deep-sea environments (Hutchings 2000, Rouse and Pleijel 2001). A recent review of Terebellidae Johnston, 1846 has been undertaken by Hutchings et al. (2017). The genus *Pista* Malmgren, 1866 currently includes 74 valid species (Hutchings et al. 2017). Difficulties in observing morphological characters and lack of geographically relevant literature have led to misidentifications of specimens belonging to this group. For example, *Pista cristata* (Müller, 1776) has been considered as a cosmopolitan species, but represents a complex of species (Gil 2011, Hutchings and Kupriyanova 2018). Recently, many changes have occurred in the *Pista sensu lato* group (Hutchings et al. 2017, Jirkov and Leontovich 2017) which currently includes seven genera: *Axionice* Malmgren, 1866, *Eupistella* Chamberlin, 1919, *Lanicides* Hesse, 1917, *Paraxionice*, Fauchald, 1972, *Pista* Malmgren, 1866, *Pistella* Hartmann-Schröder, 1996, and *Scionella* Moore 1903. Among these genera, only four have some species with a single pair of branchiae: *Pista*, *Lanicides*, *Pistella*, and *Scionella*. *Pista* and *Lanicides* can be differentiated from each other by the shape of avicular uncini and particularly by the presence of long-handled uncini (Hutchings et al. 2017). Nogueira et al. (2010, 2015) highlighted the presence of distally serrated notochaetae in *Lanicides*, which are absent in *Pista*. Furthermore, according to Nogueira et al. (2010), species of *Scionella* have a single pair of branchiae on segment IV while those of *Pistella* have a single pair of branchiae on segment II. Mikac and Hutchings (2017) provide a generic diagnosis of *Pistella* versus *Pista*. According to them, the main difference between these two genera is that *Pistella*'s neurochaetae are all short-handled avicular uncini while *Pista*'s neurochaetae are long-handled avicular uncini, at least on some anterior neuropodia.

Currently, morphological-based studies on *Pista*-like genera (Saphronova and Jirkov 2001; Gil 2011) consider the number of pairs of branchiae and the presence of long-handled anterior thoracic uncini as size-related characters, and therefore synonymized several genera and suggested some species have very wide distributions. However, it is clear that a detailed revision of all these genera is required using both morphological and molecular techniques. Ontogenetic studies could also clarify if the development of the long-handled uncini present in anterior thoracic neuropodia is a size-related character or is fixed for a species within a genus. Hutchings et al. (2017) and the present study accept them as stable generic characters and therefore reject these synonymies of Saphronova and Jirkov (2001). Currently, only seven species in the genus *Pista* are characterised by possessing a single pair of branchiae: *P. dibranchis* Gibbs, 1971 known from the Solomon Islands, *P. godfroyi* (Gravier, 1911) and *P. spinifera* (Ehlers, 1908) from Antarctica; *P. mirabilis* McIntosh, 1885 from deep water off Argentina; *P. bansei* Saphronova, 1988 described from Northern Pacific Ocean (although no specific type locality is given in the original description, but recently confirmed by Hutchings unpublished data.); *P. lornensis* (Pearson, 1969) from a Scottish loch, and finally *P. adriatica* Mikac & Hutchings, 2017 recently described from the Adriatic Sea.

The present study provides the description of a new species of *Pista* from the north-western Mediterranean Sea, based on morphological characters. Molecular data (COI gene) are provided for further investigations.

Materials and methods

Sampling and morphological analyses

The first specimens of the new *Pista* species were sampled in 2012 in the harbour of Banyuls-sur-Mer (French Mediterranean Sea; WGS84: 42°28.87'N, 3°08.15'E; 3 m depth; Fig. 1). Specimens examined in this study were collected in 2012 and 2017 using a van Veen grab. Live specimens (anaesthetised with menthol) were examined under a Zeiss stereomicroscope (V20 discovery-Plan S objective 1.0×) equipped with a camera (Axiocam 105) and preserved specimens with a Nikon SMZ25 stereomicroscope (Nikon DS-Ri 2) camera, a Nikon Eclipse E400 microscope, and a Zeiss Axio Lab.A1 microscope. Slides for uncini were prepared with lactic acid and observed under 100× oil immersion lens. A posterior parapodium of paratype MNHN-IA-TYPE 1853 was removed and fixed in 100% ethanol for molecular studies. All other material was fixed in 4% formaldehyde seawater solution, then transferred to 70% ethanol for morphological analyses. Several specimens were dehydrated in ethanol, critical point dried and covered with gold, and examined under a scanning electron microscope (SEM) at Macquarie University (JEOL JSM 6480LA) and at Arcachon Marine Station (Hitachi TM3030).

Holotype and most paratypes were deposited at the Museum national d'Histoire naturelle, Paris (MNHN), other paratypes were deposited in the Australian Museum, Sydney (AM). Non-type additional material was lodged in collections of Banyuls-sur-Mer and Arcachon Marine Stations in France.

DNA isolation, amplification, and sequencing

Samples for DNA analysis were removed from a live specimen (paratype MNHN-IA-TYPE 1853) placed in ethanol 96% and frozen at -20 °C. Extraction of DNA was done with QIAamp DNA Micro Kit (QIAGEN) following protocol supplied by the manufacturers. Approximately 650 bp of COI (cytochrome c oxidase subunit I) genes were amplified using primers polyLCO and polyHCO (Carr et al. 2011). The PCR (Polymerase Chain Reaction) was carried out with Gotaq G2 Flexi DNA Polymerase (PROMEGA), with 50 µL mixtures contained: 10µL of 5X Colorless GoTaq Reaction Buffer (final concentration of 1X), 1.5 µL of MgCl₂ solution (final concentration of 1.5mM), 1 µL of PCR nucleotide mix (final concentration of 0.2 mM each dNTP), 0.5 µl of each primer (final concentration of 1µM), 0.2 µl of GoTaq G2 Flexi DNA Polymerase (5U/µl), 1 µl template DNA and 33.8 µL of nuclease-free water. The tem-

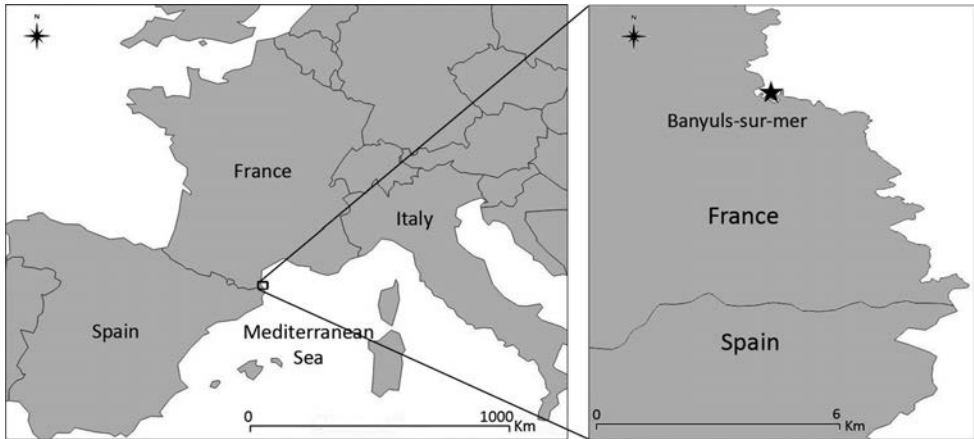


Figure 1. Location of Banyuls-sur-Mer harbour, France, where *P. colini* sp. n. was collected.

perature profile was as follows: 94 °C/600s – (94 °C/40s–44 °C/40s–72 °C/60s) *5 cycles –(94 °C/40s–51 °C/40s–72 °C/60s) *35 cycles –72 °C/300s –4 °C. Amplified PCR products were analysed by electrophoresis in a 1 % p/v agarose gel stained with ethidium bromide and were sent to GATC Biotech Company to complete double strain sequencing, using same set of primers as used for PCR. Overlapping sequence (forward and reverse) fragments were merged into consensus sequences and aligned using Clustal Omega. Sequences were translated into amino acid alignment and checked for stop codons to avoid pseudogenes. The minimum length coverage was around 660 bp. Sequence obtained in this study has been deposited in GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>). The accession number is given in the section Genetic data.

Taxonomic account

Family Terebellidae Johnston, 1846

Genus *Pista* Malmgren, 1866

Type species. *Amphitrite cristata* Müller, 1776, by original designation.

Diagnosis. Transverse prostomium attached to dorsal surface of upper lip; basal part as thick crest, eye spots sometimes present; distal part shelf-like. Buccal tentacles all uniformly cylindrical. Peristomium restricted to lips; relatively short upper lip, hood-like; swollen, cushion-like and mid-ventral lower lip. Segment I reduced dorsally, with pair of lobes of variable size and position; segments II–IV also with pairs of lobes of variable size and position, sometimes extending for a few more segments. Anterior segments highly glandular ventrally, with discrete, smooth to slightly corrugated, rectangular to trapezoidal mid-ventral shields. Paired arborescent, pectinate or plumose

branchiae present from segment II, typically two pairs, on segments II and III, rarely a single pair or three pairs. Conical to rectangular notopodia beginning on segment IV, all aligned, typically extending for 17 segments, until segment XX; notochaetae all distally winged, frequently broadly winged. Neuropodia beginning on segment V, as low ridges in conjunction with notopodia and short pinnules posteriorly; neurochaetae as long-handled avicular uncini, at least on anterior neuropodia, frequently until segment X or termination of notopodia, then short-handled; uncini in partial to completely intercalated double rows on segments XI–XX. Nephridial papillae present on segment III, genital papillae on variable number of segments, usually on segments VI–VII, posterior and dorsal to notopodia. Pygidium smooth to slightly crenulated (after Hutchings et al. 2017).

***Pista colini* sp. n.**

<http://zoobank.org/0532761D-4534-4C83-8D56-D7683468160B>

Figs 2–4

Material examined. Type material. Banyuls-sur-Mer harbour, Gulf of Lion, Mediterranean Sea, France (42°28.867'N, 3°08.154'E, 3 m depth), subtidal in gravely sands, all collected 16 July 2012 except MNHN-IA-TYPE 1853 collected 12 July 2017. Holotype: MNHN-IA-TYPE 1850, complete, 70 segments, total length 17.6 mm, thoracic length 4.8 mm, anterior width 0.6 mm, Paratypes: AM W.50625, 1 specimen, posteriorly incomplete, total length 11 mm, thoracic length 7 mm, anterior width 1.0 mm; AM W.50626, 3 specimens plus 1 posterior fragment 5 mm with pygidium, 1 complete, total length 11 mm, thoracic length 5 mm, anterior width 0.5 mm, 1 complete, total length 12 mm, thoracic length 5 mm, anterior width 0.5 mm, 1 posteriorly incomplete, length 16 mm, thoracic length 8 mm, anterior width 0.8 mm, 2 specimens mounted for SEM. MNHN-IA-TYPE 1851, 1 specimen, posteriorly incomplete, total length 14.3 mm, thoracic length 3.7 mm, anterior width 0.7 mm; MNHN-IA-TYPE 1852, complete specimen, total length 9.70 mm, thoracic length 4.6 mm, anterior width 0.9 mm; MNHN-IA-TYPE 1853, complete collected 12 July 2017, thoracic length 4.4 mm, anterior width 1.1 mm, posterior part cut for molecular analysis; MNHN-IA-TYPE 1854, complete length 18.2 mm, anterior width 0.7 mm, mounted for SEM; MNHN-IA-TYPE 1855, complete, 1 specimen, total length 9.0 mm, thoracic length 3.1 mm, anterior width 0.7 mm.

Additional material. Banyuls-sur-Mer harbour, Gulf of Lion, Mediterranean Sea, France (42°28.867'N, 3°08.154'E, 3 m depth), subtidal in gravely sands, all collected 16 July 2012. BAN.Pista.08, 1 specimen, complete, total length 10.0 mm, thoracic length 3.7 mm, anterior width 0.8 mm; BAN.Pista.09, 1 specimen gravid, posteriorly incomplete, thoracic length 5.1 mm, anterior width 0.7 mm; BAN.Pista.10, complete, 1 specimen, total length 22.7 mm, thoracic length 7.8 mm, anterior width 0.9 mm; BAN.Pista.12, complete, 1 specimen, total length 12.4 mm, thoracic length 4.6 mm, anterior width 0.6 mm.

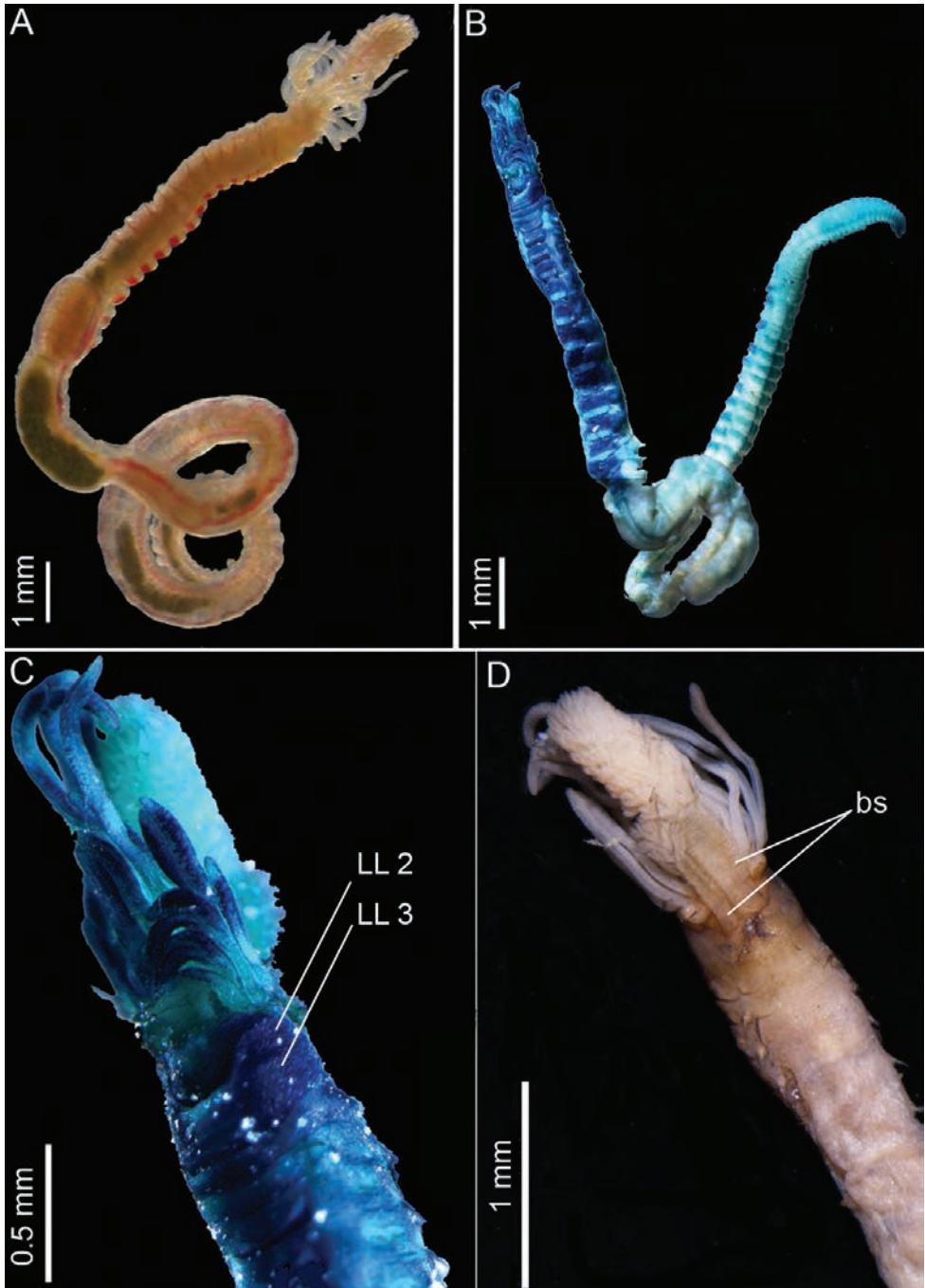


Figure 2. *Pista colini* sp. n.: **A** Live specimen, dorsal view **B** Entire specimen, ventral view, methyl green staining **C** Anterior part, ventral view **D** Anterior part, dorsal view. **B–D** from holotype MNHN-IA-TYPE 1850. Key: LL: lateral lobes, bs: branchial stalks.

Comparative material. *Pista bansei* Saphronova, 1988 Holotype reg. # 47667, 47°41'N, 139°34.1'E, Sea of Japan, Tartary Strait, off Nelma, 105 m; 4 paratypes reg. # 47668 according to Saphronova 1988 (but reg. # 32423 according to label in the museum vial) from same station, deposited in Zoological Museum of Russian Academy of Sciences in St Petersburg.

Additional material from R/V "Vityaz" stations 59, 119, 1587a, 3350, 3569, 1086. (For locality details see Saphronova (1988: table 1, no museum registration numbers allocated) deposited in the Zoological Museum of Moscow State University.

Description (based on holotype). Holotype is a complete specimen, 17.5 mm in length, 0.6 mm in width at segment X and with 70 segments (Fig. 2A, B).

Transverse prostomium attached to dorsal surface of upper lip. Buccal tentacles all of similar width inserted ventrally on prostomium, shorter than smallest branchia; long tentacles situated centrally in dorsal region, longer than largest branchia (Fig. 2C). Peristomium consisting of large rounded upper lip, forming a swollen cushion with one small fold on each side. Lower lip short, irregularly swollen (Fig. 3C). Segment I reduced, V-shaped, situated medio-ventrally (Fig. 3C), without lateral lobes. Segment II with well-developed lateral lobes, with anterior margins rounded merging with ventral pad to form a continuous minutely crenulated ventral collar. One pair of unequal-sized plumose branchiae inserted one just next to the other on segment II; all filaments strongly ciliated (Figs 2D, 3D), arranged in spiral around central axis with dichotomous filaments. Both stalks markedly wrinkled (Fig. 3A, B). Segment III with lateral lobes half width of segment, asymmetrical and slightly displaced dorsally, connected across ventrum (Fig. 3A–C). Segment IV lacking lateral lobes (Fig. 3A, B).

Notochaetae, broad-winged capillaries, with fine tips (Fig. 4A). Neuropodia from segment V (chaetiger 2), initially arranged in single rows, from segments XI to XX arranged in completely intercalated double rows face-to-face and then reverting to single rows on abdomen. Neurochaetae as long-handled avicular uncini on segments V and VI (Fig. 4B) then short-handled. Neuropodia with ca. 14 uncini (arranged in single row), thoracic uncini with dental formula MF: 3–4:5–6:α (Fig. 4D–E). Abdominal neuropodia becoming more erect posteriorly with ca. 12 uncini each, elongate extending from torus, dental formula MF: 6–7:6–7: α: α (Fig. 4C, F). Nephridial papillae on segments VI and VII (chaetigers 3 and 4), inserted posteriorly/laterally to notopodia, small spherical.

Pygidium with slightly crenulated margins (hardly visible even under stereomicroscope but clearly visible under SEM).

Methyl green staining pattern. Branchiae, lips and base of tentacles not stained. Extremity of tentacles staining and retained as blue/brown even after being washed in ethanol for some days (Fig. 2B, C). Thorax until segment XX, strongly staining ventrally, moderately laterally and poorly dorsally. Ventral stain on all shields, anterior half of each shield staining deeply, posterior part not staining (Fig. 2B, C). Anterior abdomen not coloured and posterior abdomen staining ventrally and dorsally with anterior half of each segment staining deeply, posterior part not staining; increasing colouration towards pygidium (Fig. 2B).

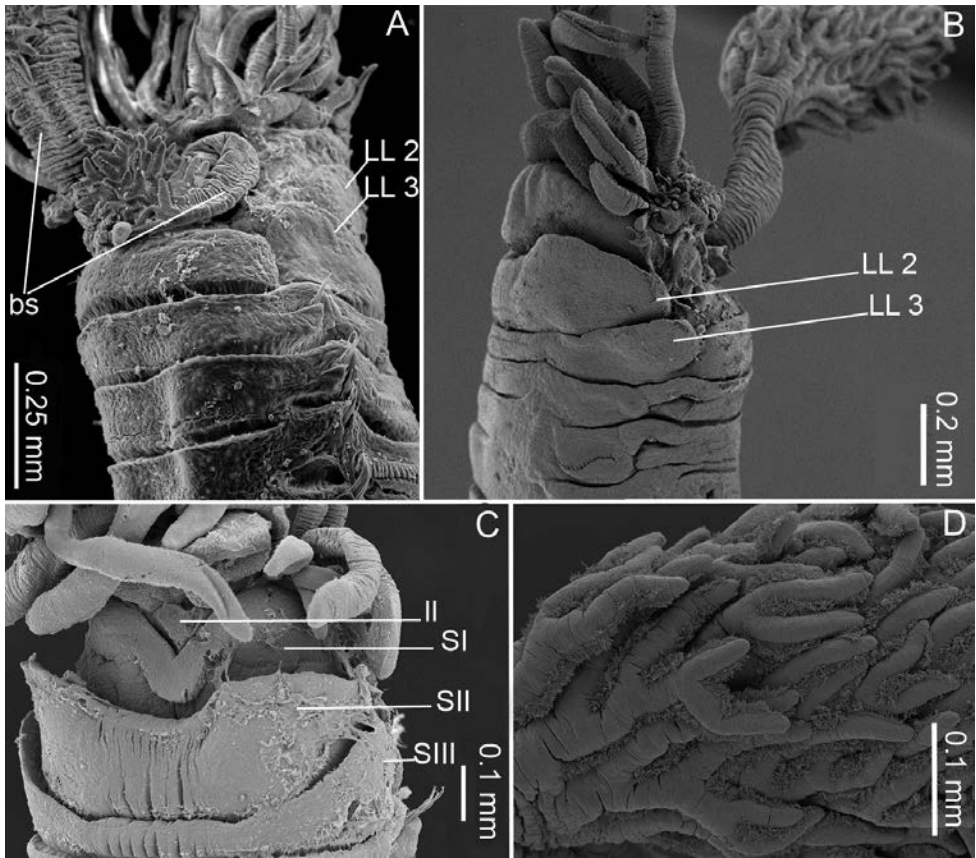


Figure 3. *Pista colini* sp. n., SEM images: **A** Anterior part, dorso-lateral view **B** Anterior part, lateral view **C** Anterior part, ventral view **D** Branchial filaments **A** from paratype MNHN-IA-TYPE 1854 **B–D** from paratype AM W.50626. Key: LL: lateral lobes, bs: branchial stalks, II: lower lip, SI, SII, and SIII: Segments I, II, and III.

Morphological variation. Complete individuals ranging from 9.0 to 22.7 mm in length, 0.5 to 1.1 mm in width at segment X and between 59 to 72 segments. Thoracic lengths vary between 3.1 and 7.8 mm. One gravid specimen was found (BAN. Pista.09). It was incomplete, but thoracic length was 5.1 mm and anterior width 0.7 mm. These measurements correspond to a small size species. Live specimens pinkish with translucent buccal tentacles; ventral shields divided in two parts, anterior part pinkish, posterior part blood red (Fig. 2A). Preserved specimens pinkish with ventral shields divided transversally in two parts. Crenulation of ventral collar of segment II is difficult to see under the binocular and not always visible under SEM. It probably depends on the contraction of the animal. All specimens, regardless of size, with a single pair of branchiae, one up to twice as long as the other (Fig. 2D). Eleven of the twenty observed specimens had the long branchiae on the right side. Number of anterior

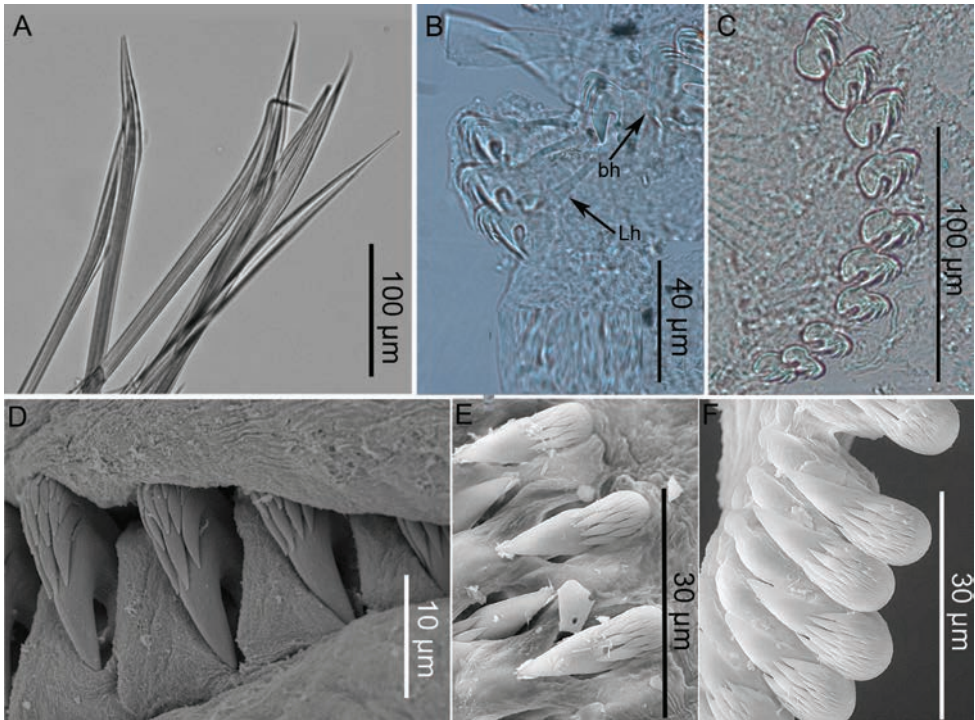


Figure 4. *Pista colini* sp. n.: **A** Thoracic notochaeta of segment VI **B** Thoracic uncini of segment V **C** Abdominal uncini **D** Thoracic uncini in single row **E** Thoracic uncini in double row **F** Abdominal uncini **A** from paratype MNHN-IA-TYPE 1853 **B, C** from additional material BAN.Pista.12 **D** from paratype AM W.50626 (SEM image) **E, F** from paratype MNHN-IA-TYPE 1854 (SEM images). Key: Lh: long-handled uncinus, bh: broken-handled uncinus.

thoracic uncinigers with long-handled uncini is variable (from 2 to 9). This difference seems to not be dependent upon size. Nephridial papillae not always visible.

Etymology. The name of species is dedicated to the nephew of the first author Colin Labrune who is already a little budding naturalist.

Type locality. Only known from Banyuls-sur-Mer harbour, France (Mediterranean Sea).

Ecological notes. *Pista colini* sp. n. was sampled at 3 m depth on gravelly sand recently deposited manually in Banyuls-sur-Mer harbour. It was found in very high densities (446 ind. m⁻² in April 2012 and 1176 ind. m⁻² in July 2012) a few weeks after the sediments had been deposited. We sampled again in November 2012 but there was no more gravel and *Pista colini* sp. n. was absent. The species is not found in the harbour if no gravel deposits are present. In the undisturbed part of the harbour, median granulometry was ca. 50 µm while the median granulometry of the gravelly sand in which this species is found was ca. 800 µm. In July 2017, we sampled a week after another fresh load of sediment with gravel had been deposited and we found high

densities of *Pista colini* sp. n. living in tubes made from heterogeneous sediment agglomerated with mucus.

Genetic data. The COI gene was successfully sequenced and published at NCBI GenBank for paratype MNHN-IA-TYPE 1853 with accession number MK584933.

Remarks and discussion. The presence of a single pair of branchiae is a stable character in *Pista colini* sp. n. More than 100 specimens were observed, of different sizes and all of them had a single pair of branchiae, some were also observed alive. Our observations support Hutchings et al. (2017) but are not in agreement with Saphronova and Jirkov (2001), who hypothesised that this character is size-related. A detailed morphological and molecular study needs to be performed in order to investigate this hypothesis across a range of species with varying number of pairs of branchiae.

Although Gil (2011) mentioned *Pista cristata* as having only one pair of branchiae, based on Saphronova (1988), we considered that this species has two pairs of branchiae. The absence of consensus on this species does not have any consequence for this new species which always had some long-handled thoracic uncini, whereas Gil (2011) records *P. cristata* as lacking such long-handled even on large specimens. Among the seven species with a single pair of branchiae, there is no possible confusion of *P. colini* sp. n. with *Pista mirabilis* and with *P. spinifera* as both lack plumose branchiae. *Pista colini* sp. n. is close to *P. adriatica* sharing the following characters: one pair of unequal sized plumose branchiae on segment II and presence of lateral lobes on segments II and III, lacking on segment IV. However, segment II of *P. adriatica* presents narrow lateral lobes while in *P. colini* sp. n. these lateral lobes are well developed. Lateral lobes of segment III are rectangular in *P. adriatica* rather than being asymmetrical and slightly displaced dorsally as in *P. colini* sp. n. Furthermore *P. colini* sp. n. can be differentiated by the absence of glandular ridges on segments II and III, which are present in *P. adriatica*. According to Mikac and Hutchings (2017), *P. godfroyi* and *P. dibranchis* which also have a single pair of branchiae, should be transferred to *Pistella* Hartmann-Schröder 1996 because they lack long-handled uncini. Therefore, they cannot be confused with *P. colini* sp. n. The lack of long-handled uncini is also the case for *Pista lornensis*. Furthermore, when first describing *Pista lornensis*, Pearson (1969) reported two obvious ligaments, one attached below the rostrum and the largest to the posterior basal corner of the uncini. These filaments are not present in *P. colini* sp. n.

According to Gil (2011), *Pista bansei* is the only *Pista* species in Europe to present one pair of “pom-pom like” branchiae and anterior long-handled uncini. The original description by Saphronova (1988) is based on an incomplete holotype with 16 segments, 3.2 mm wide collected at 105 m in Strait of Tartar, the Sea of Japan, north-western Pacific Ocean, and four damaged paratypes from the same locality. She also designated another eight paratypes (R/V “Vityaz” St 1576, 60°03'N, 168°46'E, 230 m, Olutorsky Bay, off Kamchatka Peninsula, Bering Sea, north-western Pacific Ocean) and 1 paratype (R/V “Sevastopol” St 1086, 495 m, 62°56'N, 9°19'W, between Iceland and Faroe Islands, North Atlantic Ocean), the material is deposited in Zoological Museum of Moscow State University. She also lists additional specimens not designated as type material from localities such as Davis Strait, Norwegian, Kara Sea (off Novaya Zemlya), White Sea in the North Atlantic, and Arctic Oceans, as well as Sea of Ja-

pan, Sea of Okhotsk, and Bering Sea in the north-western Pacific Ocean in depths of 120–606 m. Such a wide distribution is highly unlikely and we suggest that *P. bansei* sensu stricto is restricted to the north-western Pacific Ocean, while the rest of the material, including the one paratype from the North Atlantic Ocean represents another species, most likely part of the same species complex. Although, much of the material in Zoological Museum of Moscow State University is in poor condition, it most certainly belongs to multiple species. Therefore, Saphronova's (1988) hypothesis that only adults have anterior thoracic uncini with well-developed handles, while such handles are absent in juveniles, cannot be accepted. Furthermore, her diagrammatic illustrations indicate neither the sizes of individuals nor where the specimens were collected.

All the specimens of *P. colini* sp. n. examined here, even the smallest (59 chaetigers, thoracic width at segment X: 0.5 mm), which are comparable in size with the individuals that Saphronova (1988) identified as juveniles (width between 0.4 and 1.15 mm), had well-developed long-handled uncini, at least on chaetigers 1 and 2. Furthermore, in the original description, Saphronova (1988) described *P. bansei* with (1) an upper lip high and narrow while upper lip of *P. colini* sp. n. is large and rounded (2) large lateral lobes, positioned vertically and connected mid ventrally by a wide fold, although the connection between the two lateral lobes in *P. colini* sp. n. does not form a fold and does not look like the illustration in Saphronova (1988, fig. 8g–i). Moreover, Hilbig (2000) reports *P. bansei* with (1) moderate numbers of tentacles, usually broken off, although all specimens of *P. colini* sp. n. had some short and some long tentacles, rarely broken and (2) glandular ridges on segments II and III, which were not observed in *P. colini* sp. n. Furthermore, based on the holotype 1/47667, paratypes, and several additional specimens, Jirkov and Leontovich (2017) reported the presence of small lateral lobes on segment I in *P. bansei* which are not observed in *P. colini* sp. n. Therefore, *P. colini* sp. n., while similar to *P. bansei* in a number of characters, differs by the presence of long-handled uncini, even in the smallest specimens, and the fact that no glandular ridge was observed on segments II and III. Furthermore, the type locality of *P. bansei* is from the northern Pacific in cold deeper water (105 m).

Based on examination of the type material of Saphronova (1988) in Moscow and St Petersburg museums by Hutchings in 2018 (see Comparative material), *Pista bansei* is a North Pacific species currently only known with certainty from Tartar Strait and therefore, its range cannot overlap with that of any Mediterranean species. For these reasons, we describe *P. colini* as a new species from the Mediterranean Sea. Finally, this paper reinforces the need for a complete revision of the group of terebellids with long-handled uncini using both molecular and morphological data, especially those species with only a single pair of branchiae.

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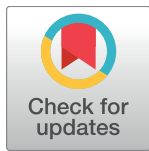
RESEARCH ARTICLE

A mega-cryptic species complex hidden among one of the most common annelids in the North East Atlantic

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Abstract

We investigate mitochondrial (*COI*, *16S rDNA*) and nuclear (*ITS2*, *28S rDNA*) genetic structure of North East Atlantic lineages of *Terebellides*, a genus of sedentary annelids mainly inhabiting continental shelf and slope sediments. We demonstrate the presence of more than 25 species of which only seven are formally described. Species boundaries are determined with molecular data using a broad range of analytical methods. Many of the new species are common and wide spread, and the majority of the species are found in sympatry with several other species in the complex. Being one of the most regularly encountered annelid taxa in the North East Atlantic, it is more likely to find an undescribed species of *Terebellides* than a described one.

Introduction

The revelation of cryptic species has increased exponentially since the use of molecular data in taxonomic studies became common practise, but our understanding of the magnitude and importance of this neglected biodiversity is still at an early stage [1±3]. To unravel, describe and explain this hidden and unexplored dimension of life on earth is one of the major challenges to practising taxonomists [1].

This paper is a case study on the genus *Terebellides* Sars, 1835 (Annelida) based on specimens collected from North East Atlantic waters, ranging from the British Isles in the south, to the Polar Basin in the north. The genus and its first member, *Terebellides stroemii* Sars, 1835, was described from the west coast of Norway near Bergen. Even though a few other species of

the Swedish Taxonomy Initiative [<https://www.artdatabanken.se/en/the-swedish-taxonomy-initiative/>] (Polychaete species complexes in Swedish waters, dnr 140/07 1.4 and 166/08 1.4), and Kungliga Fysiografiska sällskapet Nilsson-Ehle donationerna [<https://www.fysiografen.se/sv/>] to AN; and by the ForBio Research School funded by the Research Council of Norway [https://www.forskningsradet.no/en/Home_page/1177315753906] (project no. 248799) and the Norwegian Taxonomy Initiative (pnr 70184215) and the Ramon y Cajal program (RYC-2016-20799) funded by Spanish Ministerio de Economía, Industria y Competitividad, Agencia Estatal de Investigación, Comunidad Autónoma de las Islas Baleares and the European Social Fund to MC; and by Akvaplan Niva [<http://www.akvaplan.niva.no/en/>] to AS and JP. Publication fees were covered by NTNU's [<https://www.ntnu.no/>] Publishing Fund to MC. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

Terebellides were described during the 19th and 20th century, *T. stroemii* has, as many of the early described polychaetes, been considered to be a cosmopolitan species reported from all over the world and from a wide variety of habitats [4±5]. About 150 years after its description, Williams [6] revealed the existence of different morphotypes among members traditionally considered as *T. stroemii*, and described a few of them as new species, and since then, the number of descriptions of new species of *Terebellides* has increased [7±13]. Recently, Parapar and Hutchings [14] redescribed *T. stroemii*. The material used in the original description has been lost, but they designated a neotype from museum specimens collected by Michael Sars from a nearby locality [4, 14]. Today *T. stroemii* is considered to be restricted to the North East Atlantic where it coexists with other species of *Terebellides* [11, 15].

Terebellides is the most species-rich of three genera in Trichobranchidae, with 52 species considered valid [16]. Trichobranchidae is closely related to the more commonly known spaghetti worms (Terebellidae), ice-cone worms (Pectinariidae) and Pompeii worms (Alvinellidae) [17]. The genus *Terebellides* is morphologically a homogenous group characterized by its unique branchiae with a single mid-dorsal stalk on segment 3. Differences between species are mainly based on detailed branchial morphology, shape and size of anterior lobes, and on details of chaetae [14, 18, 19] (Figs 1 and 2).

Members of *Terebellides* are tube-dwelling surface deposit feeders, and they occur predominantly in soft bottoms on continental shelves and slopes. The information on reproductive biology of the species is referred to *T. stroemii* exclusively. *Terebellides stroemii* spawns annually from the age of one or two years for the rest of their life (until the age of three to five years). Breeding season is reported to be in October±November in Greenland waters [20], in May in the Kiel Bay [21], and in March±April in the Mediterranean [22]. Further, *Terebellides stroemii* has been described to deposit their eggs in a compact, slimy mass, attached to pieces of decaying seagrass, or at the entrance to their tube. Fertilization probably occurs before the eggs are deposited, larvae emerge as trochophores, and the free-swimming larval stage is thought to be very short and supposedly spent in near-bottom layers [21].

In the North East Atlantic, including the Arctic region but excluding the Mediterranean, seven species have been described or reported to date based on morphology alone, and these are *T. stroemii* with type locality in south-west Norway in 55±110 m, *T. gracilis* Malm, 1874 with type locality in Skagerrak in 65±230 m, *T. atlantis* Williams, 1984 with type locality on the New England slope in 400 m, *T. williamsae* Jirkov, 1989 with type locality in the Barents Sea between northern Norway and Svalbard in 385±390 m, *T. irinae* Gagaev, 2009 with type locality in the Canada Basin in Beaufort Sea off Alaska in 2570±2678 m, *T. bigeniculatus* Parapar, Moreira & Helgason, 2011 with type locality north-west of Iceland in 333 m, and *T. shetlandica* Parapar, Moreira & O'Reilly, 2016 with type locality between Shetland and the Norwegian coast in 160 m (Fig 3). Among these, *T. williamsae* is considered a junior synonym to *T. gracilis* [15].

In this paper, we report on a series of molecular genetic analyses of *Terebellides* from North East Atlantic waters using both mitochondrial (*COI*, *16S rDNA*) and nuclear genes (*ITS2*, *28S rDNA*). The main aim of the study is to answer how many species of *Terebellides* that are actually inhabiting the North East Atlantic. With species we mean separately evolving metapopulation lineages sensu de Quieroz 2007 [23], identifiable as such using a combination of mitochondrial and nuclear markers, see also [2] for a discussion on the species concept we use in this paper. Further, the study examines if the currently recognized species are to be considered valid, and if there are additional species not yet reported in the area. We also want to investigate the geographic and bathymetric distribution for the different *Terebellides* species, in order to answer whether the species are predominantly sympatric or allopatric, and whether there are any biogeographical and/or bathymetrical patterns. Finally, we also intend to explore the population structure within the different species.

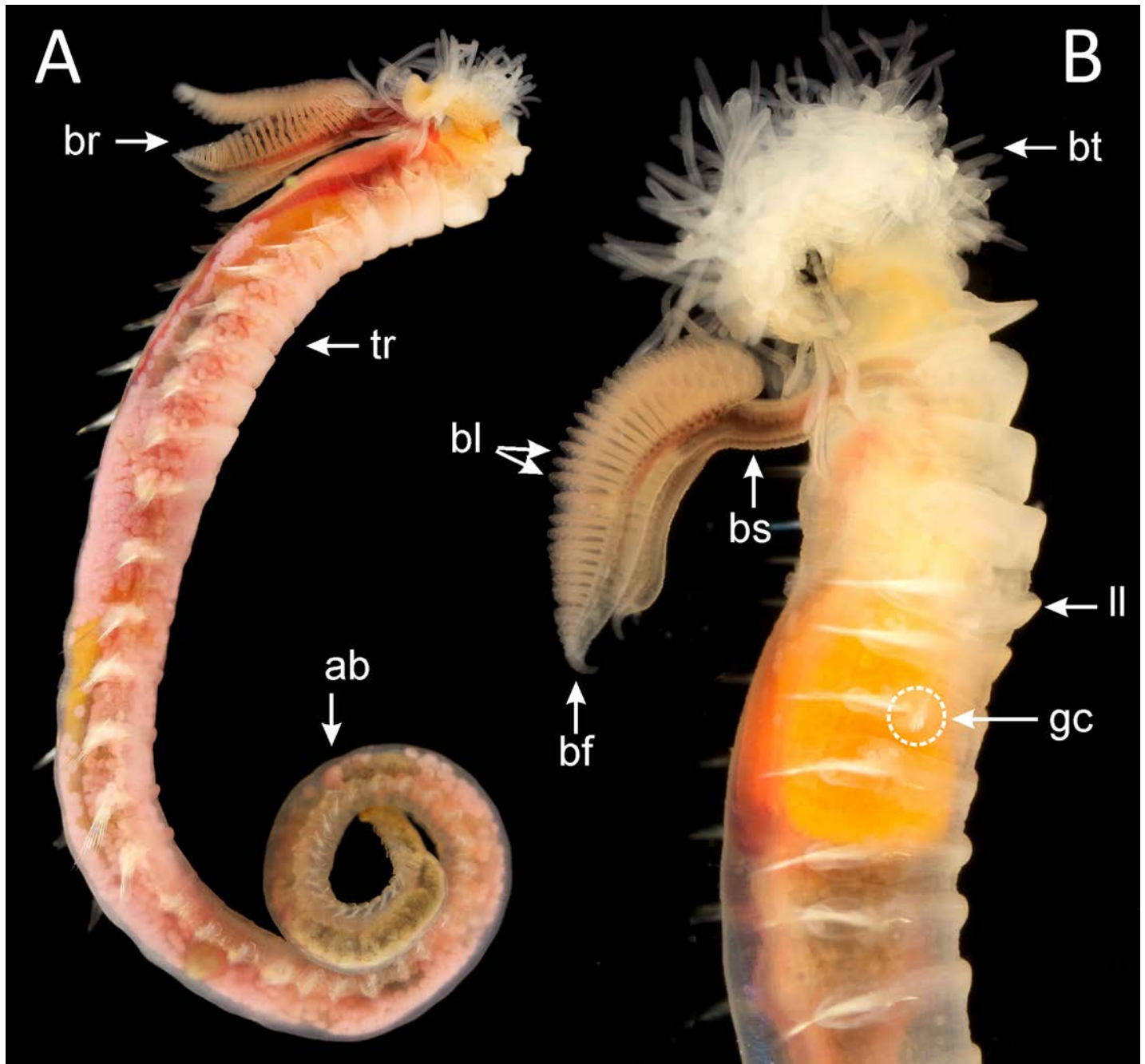


Fig 1. Live specimens of A) *Terebellides williamsae* (specimen 2181_2), in lateral view, with oocytes in the coelomic cavity and B) species 7 (specimen 2448_7), in lateral view. *Abbreviations:* ab (abdomen), bl (branchial lamellae), br (branchiae), bs (branchial stalk), bt (buccal tentacles), gc (geniculate chaetae), ll (lateral lappets), tr (thorax).

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Material and methods

Specimens, and study area

Specimens were collected between 2005 and 2014 on collecting trips, or by the following scientific expeditions, monitoring programs or institutes: Survey of Utsjöbankarna, SAMARIN (Marine surveys done by the Swedish Taxonomy Initiative), BIOICE (Benthic Invertebrates of

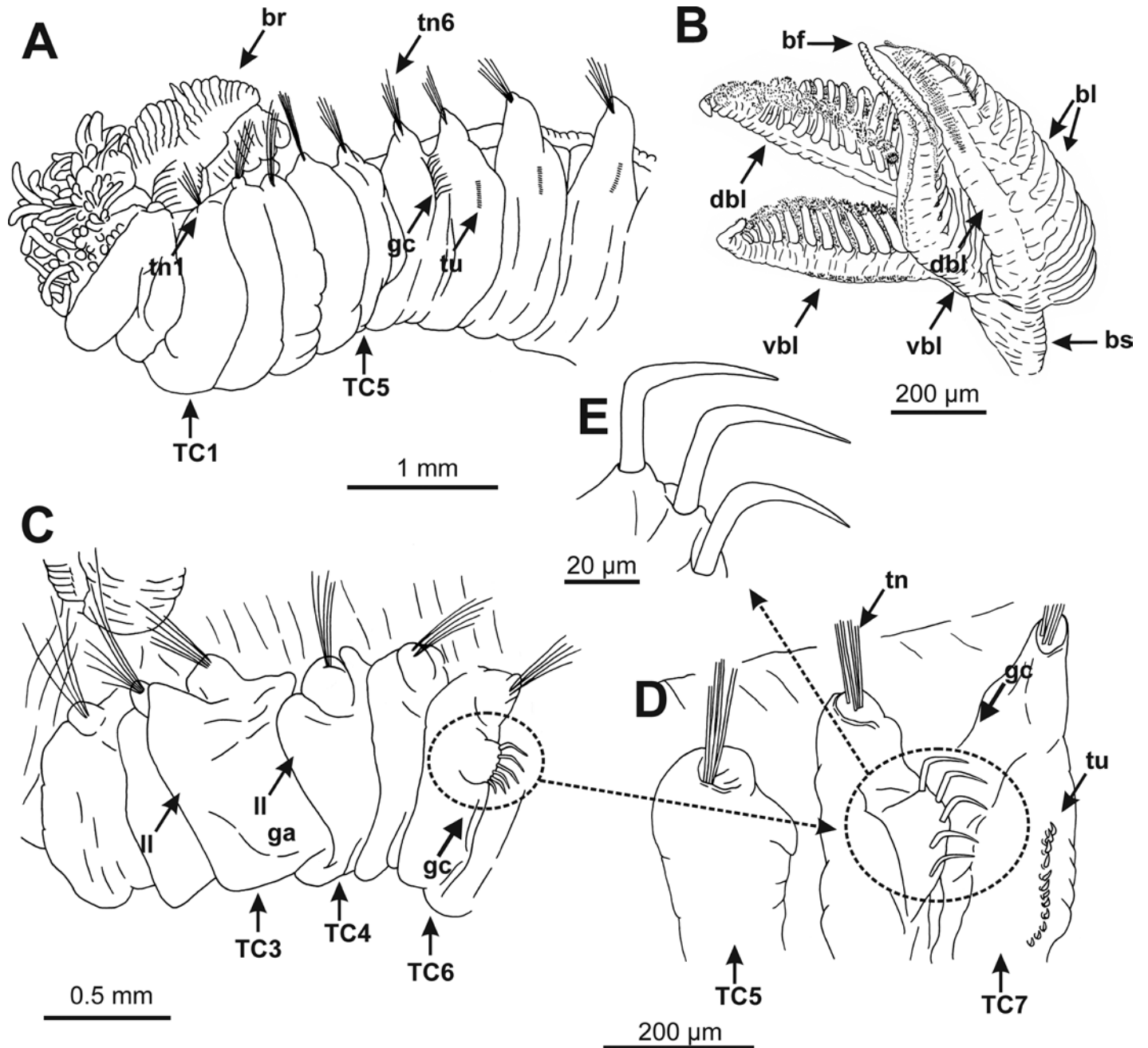


Fig 2. Line drawings made from different *Terebellides* species showing main macroscopic body characters with taxonomic relevance. A. Ventro-lateral view of *T. gracilis* or *T. williamsae* from Iceland showing most relevant taxonomic characters (e.g. position of anterior 1 ± 5 thoracic chaetigers with whitish ventral colouration). B. Ventral view of branchiae in *T. shetlandica* from the Shetland Islands showing branchial stalk, size and shape of dorsal and ventral lobes, branchial lamellae, and branchial filaments. C. Left lateral view of anterior thoracic region of *T. cf stroemii* from Iceland showing lateral lappets in TC3 and TC4, position of geniculate chaetae in TC6 and enlarged glandular area in TC3. D. Detail of thoracic chaetigers TC5 to TC7 of *T. atlantis* from Iceland showing position of geniculate chaetae in TC6 and normal thoracic uncini in TC7. E. Detail of three geniculate chaetae. A, C, D, E redrawn from [11], B redrawn from [18]. *Abbreviations:* bf (branchial filament), bl (branchial lamellae), br (branchiae), bs (branchial stalk), dbl (dorsal branchial lobe), ga (glandular area), gc (geniculate chaetae), ll (lateral lappets), TC (thoracic chaetiger), tn (thoracic notopodium), tr (thorax), tu (thoracic uncini), vbl (ventral branchial lobe).

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Icelandic waters), MAREANO (Marine Area database for Norwegian waters), POLYSKAG (Marine bristle worms (Polychaeta) in coastal waters of Skagerrak), BIOSKAG 2 (Deep

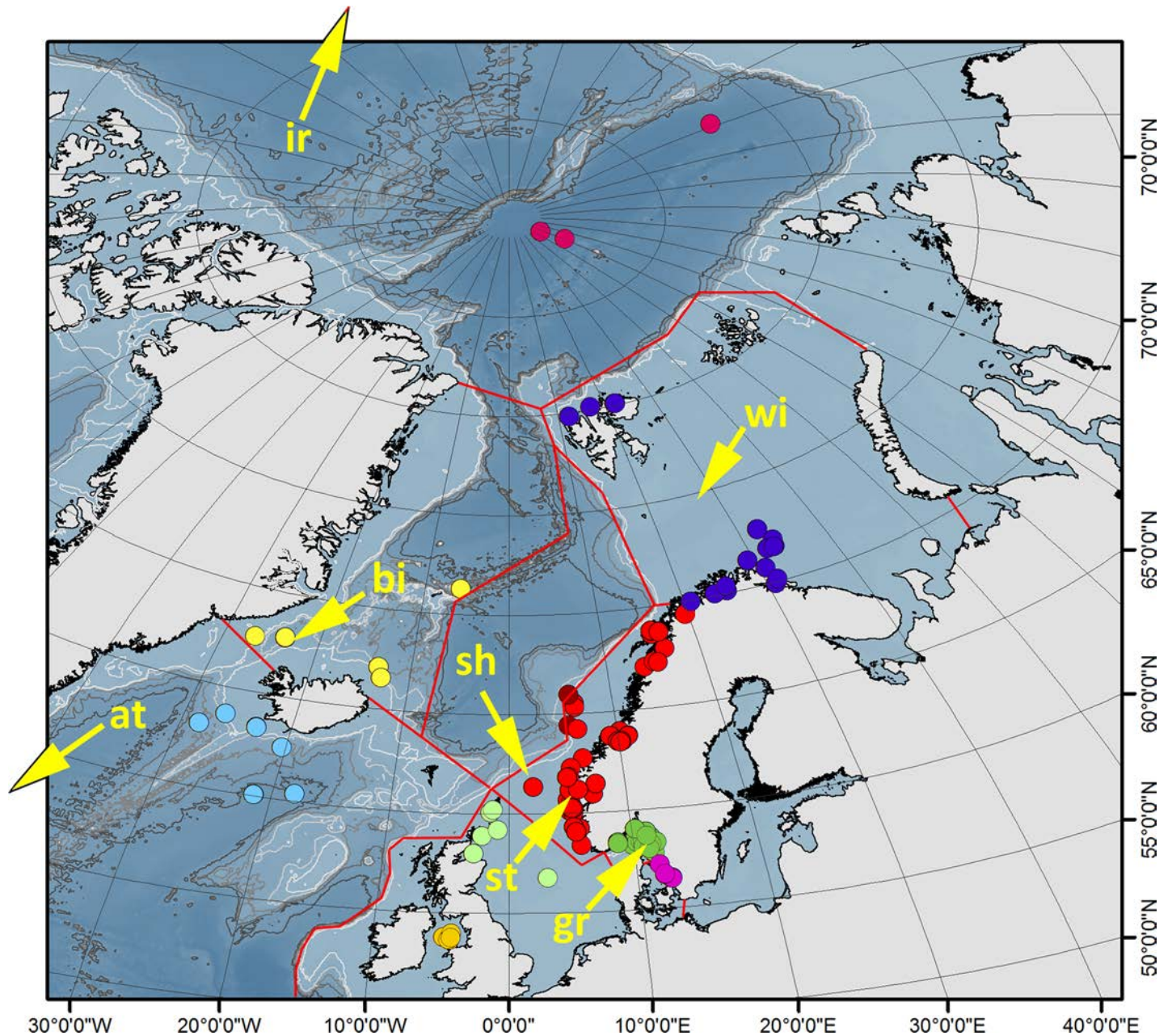


Fig 3. Collecting sites, biogeographic regions, and type localities for *Terebellides irinae* (ir), *T. atlantis* (at), *T. bigeniculatus* (bi), *T. shetlandica* (sh), *T. williamsae* (wi), *T. stroemii* (st), and *T. gracilis* (gr) indicated with an arrow. Type localities for *T. irinae* and *T. atlantis* are located outside the map's area. Biogeographic regions given by colours of samples (collecting sites) (see text for definitions): Kattegat (magenta); Skagerrak (dark green); North Sea (light green); Irish Sea, Celtic Sea (orange); Norwegian coast and shelf (red); Norwegian Sea (brown); Barents Sea (dark blue); Arctic Ocean (rose red); Greenland Sea (yellow); South of Iceland (light blue).

<https://doi.org/10.1371/journal.pone.0198356.g003>

Skagerrak), IceAGE (Icelandic marine Animals: Genetics and Ecology), UNIS 2009 (University Centre in Svalbard), ACCESS (Arctic Climate Change, Economy and Society) expedition Polarstern in 2012, UM/BIO (University Museum and Department of Biology, Bergen) surveys, and Marbank (Biobank of Arctic Marine Organisms), Institute of Marine Research, Tromsø. All samples were collected prior to that the Nagoya protocol entered into force, thus there was no need for specific permissions. Sampling did not include endangered or protected species.

We analyzed 513 specimens from 133 collecting sites, in the depth range 8±4380 m (Figs 3 and 4), with the majority of the samples and specimens coming from the continental shelf along the Swedish and Norwegian coasts.

The study area was divided into the following biogeographic regions according to topographic and oceanographic features [24±26] (Fig 3). *Kattegat* (magenta dots in Fig 3), is a rather shallow area dominated by water masses from the North Sea, and heavily influenced by the Baltic Stream; *Skagerrak* (dark green), also a shallow shelf area, technically a part of the eastern part of the North Sea; *North Sea* (light green), shallow shelf area dominated by warm North Atlantic water masses; *Irish Sea*, *Celtic Sea* (orange), shelf areas, western UK and Ireland; *Norwegian coast and shelf* (red), north of Egersund to Loppa, areas <600 m except in the fjords, dominated by North Atlantic water with a mix of the less saline Norwegian coastal current; *Norwegian Sea* (brown), off the shelf break at approximately 600 m and deeper waters. Deeper areas below 800 m with permanent sub zero temperatures with Norwegian Sea deep water; *Barents Sea* (dark blue), separated from the Norwegian Sea by the shelf break between Norway and Svalbard, shelf sea dominated by cold water areas, but with a strong influence of North Atlantic water in the western areas and along the Troms and Finnmark coast [27]; *Arctic Ocean* (rose red), proper Polar Basin with permanent sub zero temperatures; *Greenland Sea* (yellow), with cold water areas with inflow of water from the Arctic Ocean by the East Greenland current; *South of Iceland* (light blue), area south of the Scotland-Faroe-Greenland ridge. Collecting data for specimens, together with voucher and GenBank accession numbers can be found in S36 Appendix and Table 1. Specimens are deposited in one of the following museums: Department of Natural History, University Museum of Bergen (ZMBN 116171±116514, 344 specimens), The Gothenburg Museum of Natural History (GNM 14625±15137, 74 specimens), Norwegian University of Science and Technology, NTNU University Museum, Trondheim (NTNU-VM 59990±72567, 36 specimens), and Senckenberg Museum Frankfurt (SMF 24368±24693, 59 specimens). All specimens are publicly deposited and accessible in a permanent repository.

Data retrieval

We extracted DNA with QuickExtract DNA Extraction (Epicentre). A small piece, usually one or two parapodia, were put in 50±100 µl QuickExtract, and treated with 65°C for 45 min followed by 2 min in 95°C in a dry block thermostat. We used the primers 16SANNF (GCGGTATCCTGACCGTRCWAAGGTA) [28] or 16SARL (CGCCTGTTTATCAAAAA CAT), together with 16SBRH (CCGGTCTGAACTCAGATCACGT) [29] for 16S rDNA; LCO1490 (GGTCAACAAATCATAAAGATATTGG) and HCO2198 (TAAACTTCAGGGTGACCAAAAAATCA) [30], or COIE (TATACTTCTGGGTGTCC GAAGAATCA) [31] for COI; 28S1 (ACCCGCTGAATTTAAGCAT) and 28SD2 (TCCGTGTTTCAAGACGG) [32] for 28S rDNA (D1-D2 region); and ITS58SF (GAATTGCAGGACACATTGAAC) and ITS28SR (ATGCTTAAATTCAGC GGGT) [33] for ITS2.

PCR mixtures contained 0.33 µl of each primer (10µM), 1 µl of DNA template, and 10 µl of RedTaq 1.1x MasterMix 2.0 mM MgCl₂ (VWR). Temperature profile was as follows: a denaturation step at 96°C for 1 minute, 29 cycles (95°C for 30 seconds± 52°C (for COI and 16S rDNA) or 62°C (for ITS2 and 28S rDNA) for 30 seconds± 72°C for 60 seconds), and a final step at 72°C for 7 minutes. PCR products were run for c. 15 minutes on a 1% agarose gel electrophoresis, containing GelRed Nuclear Acid Stain (Bioticum), and then visualized under UV-light. PCR products were purified using ExoSAP-IT PCR Product Cleanup protocol (Thermo Scientific). Sanger sequencing was performed on both strands at Eurofins Genomics, DNA

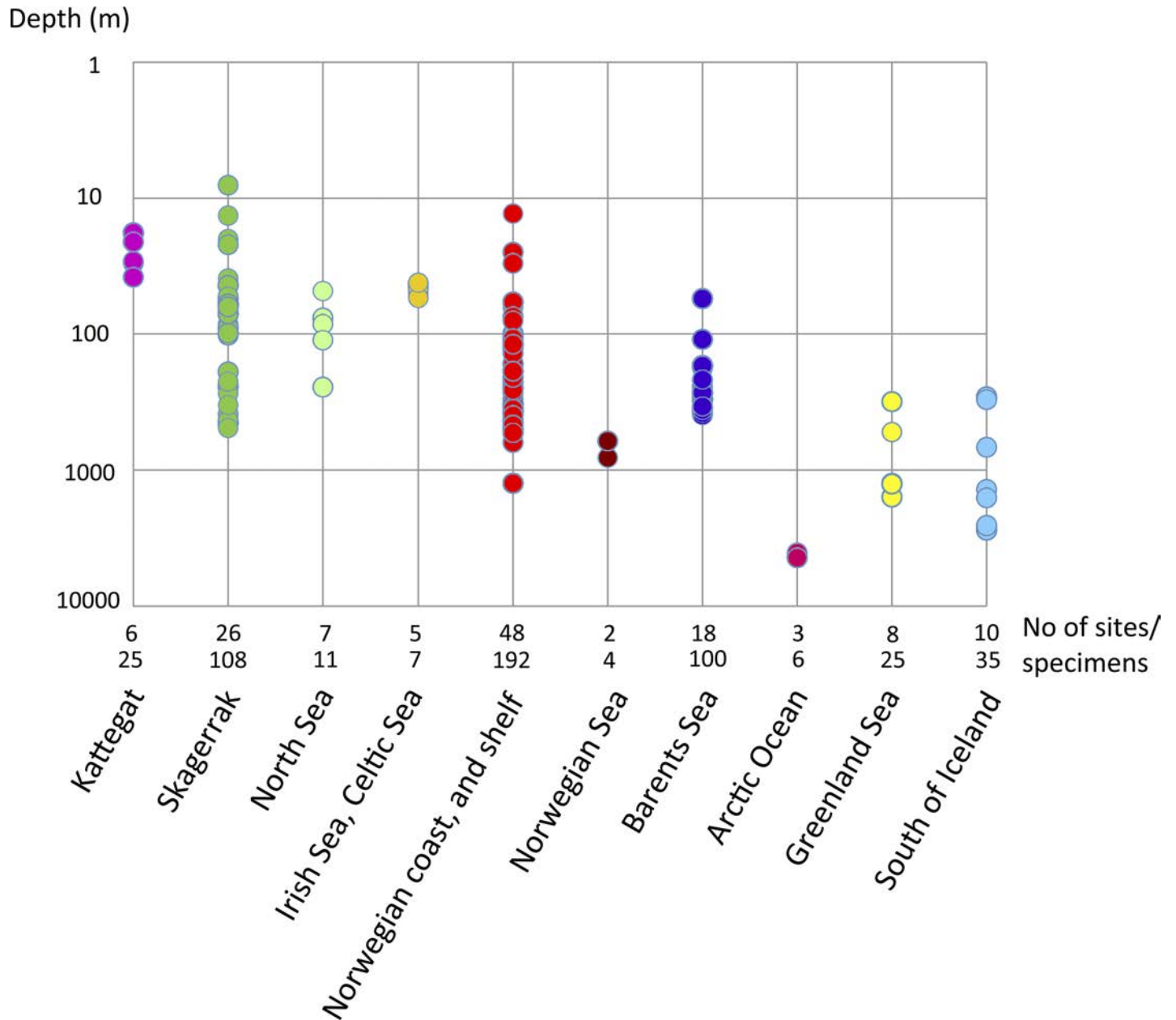


Fig 4. Depth distribution for collecting sites, including number of sites and specimens for each biogeographic region. Scale is logarithmic.

<https://doi.org/10.1371/journal.pone.0198356.g004>

Sequencing Department in Ebersberg, Germany. Overlapping complementary strands were merged into consensus sequences using Geneious version 7.0.6 [34].

Sequence data

In total, we amplified and sequenced the mitochondrial *COI* (up to 658bp) and *16S rDNA* (c. 440 bp), and the nuclear *ITS2* (290±419 bp) and *28S rDNA* (c. 760 bp) from 513 specimens of *Terebellides* spp from the North East Atlantic. Final data coverage was as follows: *COI*, 462 spms (90%) (GenBank accession numbers: MG024894±MG025355), *16S rDNA*, 75 spms (15%) (GenBank accession numbers: MG025443±MG025517), *ITS2*, 402 spms (90%)

Table 1. Locality and collecting data, including sample size, and species sampled.

SiteID	Geographic area	Locality	Sample size	Clades sampled	Latitud, longitud (DD)	Depth (m)	Collecting date	Habitat	Gear
KA1	Kattegat	NE Hallands Väderö	11	4	56.44998, 12.60042	18±20	2007-05-25	Sand, fine gravel	Warén sledge
KA2	Kattegat	NE Hallands Väderö	2	4	56.451, 12.59828	18±20	2007-05-25	Sand, fine gravel	Rectangular dredge
KA3	Kattegat	W Laholmsbukten	5	12	56.49483, 12.64515	21±22	2007-05-25	Fine mud, shells	Rectangular dredge
KA4	Kattegat	E Anholt	1	1	56.68285, 12.107	30±33	2007-05-23	Clay, sand	Rectangular dredge
KA5	Kattegat	E Anholt	2	1	56.68452, 12.1096	29±32	2007-05-23	Clay, sand	Rectangular dredge
KA6	Kattegat	Fladen	4	6	57.19717, 11.82517	38	2005-06-17	Silt, sand	Van Veen grab
SK1	Skagerrak	W Kungälv	1	6	57.80798, 11.56585	20±28	2008-06-09	Shell, gravel,	Rectangular dredge
SK2	Skagerrak	W Kungälv	1	6	57.81822, 11.40038	39±67	2008-06-09	Shell, gravel	Rectangular dredge
SK3	Skagerrak		1	1	58.0081, 11.20107	85±98	2006-08-23	Sand, mud, gravel	Warén sledge
SK4	Skagerrak		4	1, 2, 5	58.14457, 10.71923	245±297	2008-06-12	Mud	Warén sledge
SK5	Skagerrak		2	2, 3	58.19173, 10.6648	237±277	2008-06-12	Mud, silt	Warén sledge
SK6	Skagerrak	Bonden	2	6	58.21947, 11.38658	8±18	2006-04-26	Mud, shells	Circular dredge
SK7	Skagerrak		7	8, 13	58.2237, 9.9267	453±477	2009-05-13	Mud	Sneli sledge
SK8	Skagerrak	Gullmarsfjorden	1	12	58.29163, 11.51393	53±105	2006-04-27	Mixed bottom	Agassiz trawl
SK9	Skagerrak	Gullmarsfjorden	9	12	58.29293, 11.51555	44±101	2006-04-27	Mixed bottom	Warén sledge
SK10	Skagerrak	Byfjorden	1	4	58.3255, 11.86183	13,5	2012-09-18	Sandy silty clay	Grab
SK11	Skagerrak		2	3, 13	58.3532, 10.3300	390±406	2009-05-13	Fine mud	Agassiz trawl
SK12	Skagerrak		2	8, 13	58.36037, 10.24012	429±445	2006-05-29	Soft bottom	Agassiz trawl
SK13	Skagerrak	Aust-Agder, Ryvingdypet	4	1, 8	58.36978, 8.72617	190	2011-05-28	Mud	RP sledge
SK14	Skagerrak		1	13	58.40322, 10.51548	273±365	2006-08-21	Mixed bottom	Rectangular dredge
SK15	Skagerrak	Aust-Agder, ár oydydet	4	1	58.4066, 8.77758	90±100	2011-05-26	Mud	RP sledge
SK16	Skagerrak	Aust-Agder, Utnes	3	6	58.41023, 8.74602	22±32	2011-06-25	Algae, ascidians	Triangular dredge
SK17	Skagerrak		1	2	58.43017, 10.5800	248±335	2006-08-22	Soft clay	Agassiz trawl
SK18	Skagerrak		1	2	58.45702, 10.54635	224±286	2008-06-14	Hard bottom, mud	Rectangular dredge
SK19	Skagerrak		1	8	58.48285, 10.13443	491±531	2006-06-06	Soft bottom	Agassiz trawl
SK20	Skagerrak	E Väderöarna	4	6	58.58353, 11.08332	55±121	2008-06-15	Mixed bottom	Rectangular dredge
SK21	Skagerrak	W Grebbestad	1	1	58.68122, 11.11432	53±54	2008-06-16	Mixed bottom	Rectangular dredge
SK22	Skagerrak	W Tanum	2	6	58.73875, 10.73752	102±173	2008-06-15	Clay, mud	Rectangular dredge
SK23	Skagerrak	W Tanum	8	6, 12	58.7398, 10.73842	98±148	2008-06-15	Mixed bottom	Rectangular dredge

(Continued)

Table 1. (Continued)

SiteID	Geographic area	Locality	Sample size	Clades sampled	Latitude, longitude (DD)	Depth (m)	Collecting date	Habitat	Gear
SK24	Skagerrak	Koster Area	25	1, 6	58.86667, 11.1	60±80	2005±04	Mud	Warén sledge
SK25	Skagerrak	SW Yttre Vattenholmen	13	1, 7	58.87417, 11.09472	62±71	2008-04-08	Mud	Rectangular dredge
SK26	Skagerrak	Vestfold, Sandefjord	7	1	59.05485, 10.25047	63±75	2011-05-29	Mud	RP sledge
NS1	North Sea		1	1	56.75, 3	111	2008-02-07	Soft bottom	Van Veen grab
NS2	North Sea		3	1	57.98075, -2.83516	76	2008±07	Sand, fine gravel	Grab
NS3	North Sea	E Orkney Island	1	9	58.87267, -2.19	85	2008±07	Sandy clay, gravel	Grab
NS4	North Sea	E Orkney Island	1	6	59.18933, -1.91867	85	2008±07	Sand, shell gravel	Grab
NS5	North Sea	W Shetland Islands	1	9	60.0675, -1.54467	111	2008±07	Silty clay, gravel	Grab
NS6	North Sea	S Shetland Islands	1	9	60.17983, -1.38883	48	2008±07	Sandy clay, gravel	Grab
NS7	North Sea		3	1	61.34553, 2.06935	246	2014-05-31	-	Grab
ISCS1	Irish Sea, Celtic Sea	S Isle of Man	1	6	53.60867, -4.38783	50	2010±07	Sand, gravel	Grab
ISCS2	Irish Sea, Celtic Sea	S Isle of Man	2	6	53.626, -4.46967	43	2010±07	Sand, gravel	Grab
ISCS3	Irish Sea, Celtic Sea	S Isle of Man	2	6	53.72067, -4.28283	46	2010±07	Sand, gravel	Grab
ISCS4	Irish Sea, Celtic Sea	S Isle of Man	1	6	53.73567, -4.83767	54	2010±07	Sand, gravel	Grab
ISCS5	Irish Sea, Celtic Sea	S Isle of Man	1	6	53.952, -4.27867	42	2010±07	Gravel	Grab
NCS1	Norwegian coast, shelf	Rogaland, S Kvitøy	1	1	59.02712, 5.45419	64	2014-06-10	Sand, mud	Grab
NCS2	Norwegian coast, shelf	Rogaland, S Kvitøy	11	1	59.02985, 5.44881	58±60	2014-06-10	Stones, gravel, sand	Triangular dredge
NCS3	Norwegian coast, shelf	Rogaland	4	8, 13	59.20548, 5.78051	226±242	2014-06-11	-	-
NCS4	Norwegian coast, shelf	Rogaland, Karmøysundet	3	1	59.28789, 5.32506	74±79	2014-06-08	Mud	RP sledge
NCS5	Norwegian coast, shelf	Hordaland, Langenuen	7	3, 5, 8	59.99, 5.35	250	2007-06-26	-	Warén sledge
NCS6	Norwegian coast, shelf	Hordaland, St Kalsøy	8	5	60.12, 5.07	119	2005-04-15	-	-
NCS7	Norwegian coast, shelf	Hordaland, Lysefjord	5	1, 7	60.21465, 5.3472	25±47	2007-06-28	-	-
NCS8	Norwegian coast, shelf	Hordaland, Fanafjord	1	1	60.2333, 5.28042	103	2014-05-19	Clay	Grab
NCS9	Norwegian coast, shelf	Hordaland, Skogsvåg	3	1	60.2691, 5.1157	98	2006-05-02	-	-
NCS10	Norwegian coast, shelf	Hordaland, Skogsvåg	3	1	60.26915, 5.11583	102	2008-03-17	-	-
NCS11	Norwegian coast, shelf	Hordaland, Herdlafjord	2	5, 28	60.51018, 5.19228	375	2007-04-20	-	-
NCS12	Norwegian coast, shelf	Hordaland, Mangerfjord	1	11	60.62360, 4.94120	325	2006-02-07	-	-

(Continued)

Table 1. (Continued)

SiteID	Geographic area	Locality	Sample size	Clades sampled	Latitude, longitude (DD)	Depth (m)	Collecting date	Habitat	Gear
NCS13	Norwegian coast, shelf	Hordaland, Toskasundet	1	6	60.65862, 4.94718	13	2014-06-04	-	-
NCS14	Norwegian coast, shelf	Sogn & Fjordane, Aurlandsfjord	2	5, 11	60.90389, 7.16813	115	12-11-17	-	-
NCS15	Norwegian coast, shelf	Sogn & Fjordane, slope S Nesholmen	2	3, 13	61.08952, 5.21063	300±619	2012-11-15	-	Rectangular dredge
NCS16	Norwegian coast, shelf	Sogn & Fjordane DM øre & Romsdal	4	3	61.13339, 5.16632	631±644	2012-07-22	-	RP sledge
NCS17	Norwegian coast, shelf	Sogn & Fjordane, Sognefjorden	10	3, 8	61.14484, 5.91575	1259±1268	2012-11-16	-	RP sledge
NCS18	Norwegian coast, shelf	Sogn & Fjordane, Lustranattropefjorden	20	3, 28	61.43212, 7.47763	327±337	2012-11-18	-	RP sledge
NCS19	Norwegian coast, shelf	Sogn & Fjordane DM øre & Romsdal	12	1, 3, 5, 8	61.80178, 5.08135	370±375	2012-07-20	-	RP sledge
NCS20	Norwegian coast, shelf	Sogn & Fjordane DM øre & Romsdal	5	3, 8, 13	61.82371, 5.21031	446±453	2012-07-20	-	RP sledge
NCS21	Norwegian coast, shelf	Sogn & Fjordane DM øre & Romsdal	1	7	62.27842, 5.45413	169±188	2012-07-21	-	-
NCS22	Norwegian coast, shelf	Møre & Romsdal, Harøyfjord	1	13	62.71988, 6.58989	126	2012-05-20	-	-
NCS23	Norwegian coast, shelf	Sør-Trøndelag, Trondheimsfjord	2	1	63.44500, 10.17010	30±51	2013-01-17	Sand, clay	Triangular dredge
NCS24	Norwegian coast, shelf	Sør-Trøndelag, Trondheimsfjord	8	2, 3, 5, 8, 13	63.47672, 9.92872	534	2013-01-17	Mud	Snelli sledge
NCS25	Norwegian coast, shelf	Sør-Trøndelag, Trondheimsfjord	6	5, 8, 13	63.47903, 10.21283	502±505	2013-01-17	Mud	Snelli sledge
NCS26	Norwegian coast, shelf	Sør-Trøndelag, Trondheimsfjord	2	8, 11	63.48733, 10.37383	271±334	2002-01-15	Mud	Triangular dredge
NCS27	Norwegian coast, shelf	Sør-Trøndelag, Trondheimsfjord	1	8	63.71208, 10.89915	420	2012-05-27	-	-
NCS28	Norwegian coast, shelf	Sør-Trøndelag, Trondheimsfjord	2	8	63.73615, 10.97631	419	2012-05-27	-	-
NCS29	Norwegian coast, shelf	Sør-Trøndelag, Frohavet	7	8, 13	63.75767, 9.20882	350±357	2010-05-10	Mud	Agassiz trawl
NCS30	Norwegian coast, shelf	Sør-Trøndelag, Åfjord	2	10	63.99012, 10.04445	102±110	2007-07-11	-	-
NCS31	Norwegian coast, shelf	Storegga	2	11, 28	64.19888, 6.06965	387±388	2013-06-26	Muddy sand	RP sledge
NCS32	Norwegian coast, shelf	Skjoldryggen	1	2	65.28217, 6.28326	357±369	2013-06-24	Sandy mud	RP sledge
NCS33	Norwegian coast, shelf	Skjoldryggen	3	11, 20, 28	65.50056, 6.26848	397±420	2013-06-23	Sandy mud	RP sledge
NCS34	Norwegian coast, shelf	Nordland, Holmsund	1	13	67.039251, 13.85357	259	2012-05-13	-	-
NCS35	Norwegian coast, shelf	Nordland, Skjærstadfjord	2	8	67.21783, 15.27833	476	2010-10-14	-	-
NCS36	Norwegian coast, shelf	Nordland, Skjærstadfjord	1	8	67.26417, 14.86983	513	2010-10-13	-	-
NCS37	Norwegian coast, shelf	Nordland, Hellemofjord	1	8	67.86733, 16.37033	461	2008-03-04	-	-
NCS38	Norwegian coast, shelf	Nordland, Hellemofjord	1	8	67.87383, 16.353	466	2008-03-04	-	-

(Continued)

Table 1. (Continued)

SiteID	Geographic area	Locality	Sample size	Clades sampled	Latitude, longitude (DD)	Depth (m)	Collecting date	Habitat	Gear
NCS39	Norwegian coast, shelf	Sør-Trøndelag, Trondheimsfjord	1	13	68.47672, 9.92872	534	2013-01-17	Mud	Sneli sledge
NCS40	Norwegian coast, shelf	Nordland, Gullfjord	1	15	68.59100, 15.80474	131	2008-11-05	-	-
NCS41	Norwegian coast, shelf	Nordland, Sortlandssundet	1	10	68.62817, 15.34959	128	2008-11-07	-	-
NCS42	Norwegian coast, shelf	Nordland, Sortlandssundet	2	10, 15	68.62856, 15.35318	122	2008-11-07	-	-
NCS43	Norwegian coast, shelf	Nordland, Gullfjord	6	15	68.63708, 15.82157	165	2008-11-05	-	-
NCS44	Norwegian coast, shelf	Nordland, Gullfjord	3	15	68.64117, 15.83652	139	2008-11-05	-	-
NCS45	Norwegian coast, shelf	Nordland, Gullfjord	7	8, 15	68.71076, 16.01100	209	2008-11-06	-	-
NCS46	Norwegian coast, shelf	Nordland, Sortlandssundet	4	10, 13, 15	68.79015, 15.41222	108	2008-11-08	-	-
NCS47	Norwegian coast, shelf	Nordland, Sortlandssundet	4	10	68.79663, 15.41033	119	2008-11-08	-	-
NCS48	Norwegian coast, shelf	Troms, Balsfjord	14	14, 15	69.37333, 19.06167	187	2014-10-27	-	Sledge
NWS1	Norwegian Sea	Storegga	1	16	64.39374, 5.57426	814±819	2013-06-26	Sandy mud	RP sledge
NW2	Norwegian Sea	Skjoldryggen	3	2, 3	65.94317, 5.83320	610±612	2013-06-17	Sandy mud	RP sledge
BS1	Barents Sea	Finnmark, Varangerfjord	3	2	69.91217, 30.888	351	2014-04-15	Mud	RP sledge
BS2	Barents Sea	Troms, Ullsfjorden, S Karlsøya	3	8, 10	69.95333, 20.07183	243	2009-12-07	-	-
BS3	Barents Sea	Finnmark, Altafjord	2	8	70.1165, 23.07533	392	2009-12-09	-	-
BS4	Barents Sea	Finnmark	1	2	70.11767, 31.35033	303±304	2013-08-19	Mud	RP sledge
BS5	Barents Sea	Finnmark, Porsangerfjord	7	14, 15	70.12002, 25.18625	109	2011-10-08	Mud	Van Veen grab
BS6	Barents Sea	Finnmark, Porsangerfjord	2	2, 13	70.35324, 25.26369	178	2009-05-30	-	-
BS7	Barents Sea	Finnmark	2	2, 10	70.77383, 30.78117	377±378	2013-08-17	Mud	Beam traw
BS8	Barents Sea	Finnmark	1	13	71.056, 29.65567	337	2014-04-21	Muddy sand	Large Van Veen grab
BS9	Barents Sea	Finnmark	3	2, 13	71.321, 29.1965	362	2014-04-24	Mud	Beam traw
BS10	Barents Sea	Finnmark, TOO	6	2, 16, 21	71.61416, 33.0041	305	2013-08-09	Mud, clay	Beam traw
BS11	Barents Sea	Finnmark, TOO	8	2, 13, 16, 21	71.61527, 32.99719	305±306	2013-08-09	Mud, clay	RP sledge
BS12	Barents Sea	Finnmark, TOO	4	2, 16, 21	71.61817, 32.23133	297±298	2013-08-08	Sandy mud	RP sledge
BS13	Barents Sea	Finnmark, TOO	2	2, 16	71.9085, 33.44717	219±220	2013-08-06	Muddy sand, gravel	RP sledge
BS14	Barents Sea	Finnmark, TOO	26	2, 16, 28	72.57905, 32.38726	271±272	2013-08-03	Sandy mud	RP sledge
BS15	Barents Sea	Svalbard	10	12, 14, 25, 26, 27	79.8195, 12.0876	55	2009-09-01	-	RP sledge
BS16	Barents Sea	Svalbard	18	12, 21	80.1010, 22.2006	171	2009-09-01	-	RP sledge
BS17	Barents Sea	Svalbard	1	21	80.1086, 22.1414	216	2009-09-01	-	RP sledge
BS18	Barents Sea	Svalbard	1	21	80.1524, 16.9354	340	2009-09-01	-	RP sledge

(Continued)

Table 1. (Continued)

SiteID	Geographic area	Locality	Sample size	Clades sampled	Latitud, longitud (DD)	Depth (m)	Collecting date	Habitat	Gear
AO1	Arctic Ocean		2	24	81.927, 130.91666	4038	2012-09-04	-	Multi grab
AO2	Arctic Ocean		1	24	87.92683, 61.01217	4380	2012-09-19	-	Multi grab
AO3	Arctic Ocean		3	24	88.7865, 56.372	4373	2012-09-23	-	Multi grab
GS1	Greenland Sea	NE Iceland	2	16	66.53817, -12.86483	316±317	2011-09-22	Silty mud	RP sledge
GS2	Greenland Sea	NE Iceland	2	2	66.54383, -12.87467	315±317	2011-09-22	Silty mud	RP sledge
GS3	Greenland Sea	NE Iceland	1	13	66.55483, -12.86483	316±317	2011-09-22	Silty mud	RP sledge
GS4	Greenland Sea	NE Iceland	5	16	67.07867, -13.06383	1575±1581	2011-09-21	Silty mud	RP sledge
GS5	Greenland Sea	Denmark Strait	1	16	67.63583, -26.7665	315±316	2011-09-14	Silty mud	RP sledge
GS6	Greenland Sea	Denmark Strait	4	16	67.8465, -23.696	1249±1250	2011-09-15	Silty mud	RP sledge
GS7	Greenland Sea	Denmark Strait	9	10, 16	67.86783, -23.69633	1267±2181	2011-09-15	Silty mud	RP sledge
GS8	Greenland Sea	Jan Mayen	1	16	71.29733, -5.77350	528	2011-06-15	-	-
SI1	South of Iceland	Iceland Basin	1	16	60.0455, -21.46767	2747±2749	2011-08-28	Silty mud	RP sledge
SI2	South of Iceland	Iceland Basin	9	16	60.04617, -21.47567	2747±2750	2011-08-29	Silty mud	RP sledge
SI3	South of Iceland	Iceland Basin	2	16	60.35733, -18.13567	2568±2569	2011-08-30	Silty mud	RP sledge
SI4	South of Iceland	Iceland Basin	3	16	60.35733, -18.13567	2568±2572	2011-08-30	Silty mud	RP sledge
SI5	South of Iceland	Iceland Basin	3	18	62.55167, -20.39517	1385±1389	2011-09-02	Silty mud	RP sledge
SI6	South of Iceland	Irminger Basin	4	16, 19, 23	63.00767, -28.06817	1569±1594	2011-09-08	Silty mud	RP sledge
SI7	South of Iceland	Reykjanes Ridge	3	3, 17, 22	63.3085, -23.15767	285±289	2011-09-04	Silty mud	RP sledge
SI8	South of Iceland	Reykjanes Ridge	3	3	63.31467, -23.16017	288±294	2011-09-04	Silty mud	RP sledge
SI9	South of Iceland	Reykjanes Ridge	3	3	63.33333, -23.16667	305	2011-09-04	Silty mud	RP sledge
SI10	South of Iceland	Irminger Basin	4	3, 16, 20	63.70883, -26.38417	678±698	2011-09-09	Silty mud	RP sledge

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(GenBank accession numbers: MG024492±MG024893), and 28S rDNA, 86 spms (17%) (GenBank accession numbers: MG025356±MG025441) (S36 Appendix and Table 2).

Sequences from individual specimens can be identified by the extraction number and an appended clade-number (S36 Appendix), preliminary circumscribed from statistical parsimony haplotype networks [35], also known as TCS-analyses, of COI-data (see below). One other member of Trichobranchidae, *Trichobranchus roseus* (Malm, 1874), and two representatives of Terebellidae, *Polycirrus* Grube, 1850 and *Pista cristata* (Müller, 1776) were selected to root the tree [17]. Outgroups were used when assessing the general phylogeny of the *Terebellides* lineages, but not in the species delimitation analyses. Molecular data for outgroups were either retrieved as above (*Trichobranchus roseus*: COI (GenBank accession number MH1139

23), and *16S rDNA* (GenBank accession number MG025442), specimen voucher ZMBN 120609), or downloaded from GenBank (*Polycirrus*: *COI* = JX423769, *16S rDNA* = JX423681, *28S rDNA* = JN936481, and *Pista cristata*: *COI* = EU239688, *16S rDNA* = NC011011, *28S rDNA* = DQ790057).

Alignments

We used MAFFT version 7.017 [36] within Geneious version 7.0.6 with the following settings: algorithm = E-INS-i, scoring matrix = 200PAM / $k = 2$, gap open penalty = 1.53, to align *16S rDNA* and *28S rDNA*. Aligning was unproblematic since the sequences were of similar length and resulting alignments had a moderate number of indels. The *ITS2*-region was challenging to align due to a high number of indels, and we proceeded with aligning using two approaches. In the first approach, we removed identical haplotypes with the `uniqhaplo.pl` script (S35 Appendix) leaving a data set with 136 unique *ITS2*-sequences. As we experienced problems with two sequences that were shorter due to incomplete 3'-end, these sequences were first removed (1999_13 and 2865_24), and the remaining 134 complete, or nearly complete, sequences were aligned with the X-INS-i algorithm in MAFFT that takes into account the secondary structure of the sequence. Subsequently the short excluded sequences were reincluded with the `mafft-add` command. The resulting alignment is referred to as *ITS2x*-unique. In the second approach, the sequences in the *ITS2x*-unique alignment were realigned using the software RNAsalsa [37], using the secondary structure of *ITS2* modeled for *Eumida ockelmanni* Eibye-Jacobsen, 1987 (GenBank accession number HM358782) [38] as a constraint, and implementing default parameters. The resulting alignment is referred to as *ITS2s*-unique. Identical sequences removed in the first step with the `uniqhaplo.pl` script were then added back to the two alignments by hand in Geneious version 7.0.6 mimicking the gaps present in those identical sequences aligned. The two resulting alignments with all 402 *ITS2*-sequences are referred to as *ITS2x*-all, and *ITS2s*-all. Finally, we used the MUSCLE alignment option in Geneious version 7.0.6 to align all 462 *COI*-sequences (*COI*-all) which was trivial due to the absence of indels. Identical *COI*-sequences were removed using `uniqhaplo.pl` script creating an alignment with 271 unique *COI*-sequences (*COI*-unique). Where relevant, aligned gene partitions were concatenated using Mesquite v. 2.75 (Maddison and Maddison 2008) [39]. For the statistical parsimony haplotype analyses, we used *COI*-all, and the two *ITS2*-all alignments as a starting point. Sequences of each haplotype network were extracted separately, and subsequently these clade data sets were pruned to remove gaps in flanking positions that was caused by incomplete sequencing. The purpose of this was to obtain the same data coverage for all included specimens in each haplotype network, and allowing for an unambiguous assessment of haplotypes. In a few instances, one, or a few of the shortest sequences were removed prior to pruning the sequence ends (Tables 3 and 4). In the choice between removing short sequences or pruning we chose the method that kept the maximum number of haplotypes. As there were a few ambiguities assessing number of haplotypes between the two *ITS2*-alignments, although based on the same data, we decided to realign the *ITS2*-data from each network separately, using the E-INS-i algorithm in MAFFT, with scoring matrix = 200PAM / $k = 2$, and gap open penalty = 1.53. The rationale behind this is that aligning more similar sequences will result in a more accurate alignment. For the distance calculations we used *COI*-all, and *ITS2s*-all alignments. All different alignments, and data set combinations described above are available as S1±S9 Appendixes.

Data set combinations

For a robust assessment of the evolutionary relationships of the *Terebellides* lineages, specimens for which three or four of the genetic markers were present (i.e. *COI*, *16S rDNA*, *ITS2*,

Table 2. Overview of sequence coverage for each genetic marker (*COI*, *ITS2*, *16S rDNA*, *28S rDNA*) and respective clade, as well as the combination of *COI* and *ITS2* (used in the STACEY analysis), and the combination including specimens with at least three out of the four genetic markers (CONCAT).

Clade number	Number of specimens	COI	ITS2	COI and ITS2	16S rDNA	28S rDNA	CONCAT
1	82	63	63	44	3	5	5
2	36	32	28	24	3	4	4
3	57	50	55	48	4	5	5
4	14	14	13	13	4	4	4
5	19	19	18	18	4	4	4
6	36	33	25	22	2	4	4
7	12	12	6	6	4	5	5
8	41	40	29	28	3	3	3
9	3	2	2	1	2	2	2
10	12	12	7	7	3	3	3
11	5	5	3	3	3	3	3
12	23	23	17	17	3	6	6
13	27	26	25	24	3	5	5
14	20	18	19	17	3	4	4
15	18	15	16	13	3	4	4
16	62	55	50	43	6	6	8
17	1	1	1	1	1	1	1
18	3	3	2	2	2	2	2
19	1	1	1	1	1	1	1
20	2	2	2	2	2	2	2
21	18	18	2	2	1	1	1
22	1	1	1	1	1	1	1
23	1	1	1	1	1	1	1
24	6	5	4	3	4	3	4
25	4	4	3	3	2	2	2
26	3	1	3	1	2	2	2
27	1	1	1	1	1	1	1
28	5	5	5	5	4	2	4
	513	462	402	351	75	86	91

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28S rDNA), were combined into a data set comprising 91 *Terebellides* specimens (S36 Appendix and Table 2, last column) plus three outgroups. This was done by combining *COI*-all with either *ITS2x*-all or *ITS2s*-all, concatenating *16S rDNA* and *28S rDNA*, but excluding specimens that did not meet the criteria having three or four genetic markers. This resulted in two data set combinations, referred to as concatenated-xinsi-alignment (CONCATx) and concatenated-salsa-alignment (CONCATs).

For the three types of species delimitation analyses, we used the following data sets: *COI*-all, *ITS2x*-all, and *ITS2s*-all for TCS; *COI*-unique, *ITS2s*-unique, and *ITS2x*-unique for GMYC [40, 41]; the concatenated alignment of *COI*-all and *ITS2s*-all, keeping all specimens with both *COI* and *ITS2* data present, resulting in a data set with 351 *Terebellides* specimens (Table 2, 5th column) for STACEY [42].

Model selection

Best-fit models for phylogenetic analyses were selected using the Akaike information criterion in JModel [43]. The protein coding gene *COI* was divided into two partitions, one with the first and second codon positions, and one with the third codon positions. In the general

Table 3. Summary of haplotype and distance analyses for COI, with specification of excluded sequences, alignment length, number of haplotypes, and uncorrected intra- and interspecific distances. Species number to which the species is compared with, for the minimum and maximum interspecific distances, in parentheses.

Species number	Number of specimens	Removed sequences in haplotype analysis	Original alignment length	Pruned alignment length	Number of haplotypes	Uncorrected intraspecific distance	Minimum uncorrected interspecific distance (%)	Maximum uncorrected interspecific distance (%)
1	63		658	555	12	0±1.9	15.6±17.7 (7)	17.4±20.3 (8)
2	32		658	569	25	0±2.4	13.9±16.0 (3)	19.6±21.5 (21)
3	50		658	615	44	0±2.3	13.9±16.0 (2)	20.1±22.4 (21)
4	14		658	615	7	0±1.0	9.9±10.7 (26)	20.9±22.7 (10)
5	19		658	600	10	0±1.1	12.3±14.0 (16)	19.6±21.6 (15)
6	33	1314_6	658	609	10	0±0.8	8.8±10.8 (7)	19.2±20.4 (27)
7	12		658	627	8	0±0.6	8.8±10.8 (6)	19.2±20.9 (4)
8	40	1203_8	658	612	33	0±3.1	10.5±12.8 (7)	19.1±21.5 (15)
9	2		649	603	2	0.2	11.2±12.1 (7)	20.5±21.9 (4)
10	12		658	593	4	0±1.9	11.5±12.9 (11)	20.9±22.7 (4)
11	5		630	615	4	0±1.1	11.5±12.9 (10)	19.5±19.7 (26)
12	23		658	606	16	0±1.3	8.2±9.7 (13)	19.1±20.5 (2)
13	26	1959_13	658	597	14	0±1.9	8.2±9.7 (12)	19.5±21.3 (15)
14	18		658	615	5	0±0.3	16.0±17.4 (1)	20.1±21.1 (24)
15	15		658	567	4	0±0.5	17.2±18.6 (6)	19.5±21.8 (16)
16	55	2325_16	658	579	48	0±2.4	12.3±14.0 (5)	19.5±21.8 (15)
17	1		NA	NA	1	NA	14.6±15.6 (6)	20.6±21.4 (20)
18	3		627	624	3	0.5±0.6	13.0±14.3 (10)	20.7±21.4 (4)
19	1		NA	NA	1	NA	12.1±12.5 (10)	19.6±20.8 (3)
20/28	7		630	621	2	0±3.4	12.1±13.2 (21)	20.4±22.0 (22)
21	18		658	585	2	0±0.3	12.0±13.2 (20)	20.1±22.4 (3)
22	1		NA	NA	1	NA	13.1±13.6 (25)	20.4±22.0 (20)
23	1		NA	NA	1	NA	17.4±18.9 (16)	22.9 (24)
24	5		618	510	2	0±0.02	16.0±17.1 (25)	22.9 (23)
25	4		624	567	2	0±0.8	13.1±13.6 (22)	20.7±21.7 (23)
26	1		NA	NA	1	NA	9.9±10.7 (4)	22.1 (23)
27	1		NA	NA	1	NA	11.1±12.3 (4)	20.7±21.8 (10)

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phylogeny of *Terebellides*, *ITS2* and the neighboring *28S rDNA* were combined into a single partition.

Phylogenetic analyses

Mitochondrial (*COI* and *16S rDNA*) and nuclear data sets (*ITS2* and *28S rDNA*) were analyzed separately and combined using Bayesian inference (BI), and Maximum Likelihood (ML). This means five different analyses per method; 1) mitochondrial data alone, 2) nuclear data alone with *28S rDNA* combined with *xinsi-*, or 3) *salsa*-aligned *ITS2* sequences, and 4) mitochondrial data combined with nuclear data with *28S rDNA* combined with *xinsi-*, or 5) *salsa*-aligned *ITS2* sequences (S8 and S9 Appendixes). Bayesian analyses of separate and combined data sets were run in MrBayes version 3.2 [44]. Partitions were unlinked for the parameters *statefreq*, *revmat*, *shape* and *pinvar*. Rateprior for the partition rate multiplier was set to be variable. Two independent analyses were run for 10 million generations, with four parallel chains (three hot, one cold), that were sampled every 1000th generation. One fourth of the samples was discarded as burn-in. Maximum likelihood analyses were performed in raxmlGUI [45]. In

Table 4. Summary of haplotype and distance analyses for ITS2, with specification of excluded sequences, alignment length, number of haplotypes, and uncorrected intra- and interspecific distances. Species number to which the species is compared with, for the minimum and maximum interspecific distances, in parentheses.

Species number	Number of specimens	Removed sequences in haplotype analysis	Original alignment length	Pruned alignment length	Number of haplotypes	Uncorrected intraspecific distance (%)	Minimum uncorrected interspecific distance (%)	Maximum uncorrected interspecific distance (%)
1	63	856, 858, 1941, 1955, 2860, 2789, 2909	316	274	18	0±2.6	13.2±19.9 (26)	24.7±28.9 (15)
2	28		291	257	8	0±1.7	3.9±6.7 (3)	26.9±31.2 (25)
3	55		303		8	0±3.4	3.9±6.7 (2)	30.7±31.8 (23)
4	13		369		1	0	0.56±0.85 (26)	32.3±33.7 (15)
5	18		343		4	0±1.5	1.8±3.2 (16)	28.5±31.9 (21)
6	25		335	268	8	0±2.8	4.4±9.2 (10)	23.6±30.3 (14)
7	6		322		4	0±2.2	6.2±10.5 (8)	25.0±29.7 (14)
8	29	2896	327	292	5	0±1.2	6.2±10.5 (7)	29.6±33.0 (25)
9	2		317		1	0	6.7±10.7 (8)	26.3±30.4 (14)
10	7		326	295	1	0±0.33	4.9±6.6 (12)	26.2±28.5 (27)
11	3		350	323	2	0±0.31	9.8±12.4 (12)	30.2±32.9 (4)
12	17	2818	368	347	10	0±1.7	2.6±4.2 (13)	26.7±30.6 (14)
13	25		357	288	3	0±0.64	2.6±4.2 (12)	28.1±31.6 (14)
14	19	2477, 2479, 2852	361	332	6	0±1.5	9.4±13.9 (5)	30.6±35.3 (15)
15	16		305	273	1	0	16.9±18.4 (2)	30.6±35.3 (14)
16	50		348		4	0±0.87	1.8±3.2 (5)	28.9±32.2 (21)
17	1		315		1	NA	14.4±17.1 (1)	27.2±29.4 (21)
18	2		344		1	0	8.5±8.9 (10)	24.2±26.9 (14)
19	1		312		1	NA	6.4±11.9 (8)	23.5±27.5 (14)
20/28	7		410		1	0	3.0±3.3 (21)	30.2±31.9 (15)
21	2		419	391	1	0	3.0±3.3 (20)	32.1±33.4 (15)
22	1		303		1	NA	19.7±22.0 (24)	30.0±31.1 (21)
23	1		305		1	NA	8.8±9.7 (10)	24.3±28.0 (14)
24	4		324	223	1	0	9.9 (25)	30.2±33.4 (21)
25	3		309		1	0	9.9 (24)	32.6±34.4 (14)
26	3		365	184	1	0	0.56±0.85 (4)	22.3±33.9 (15)
27	1		375		1	NA	1.6 (4)	32.3±33.8 (15)

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RAxML, we used the same partitioning as in MrBayes, and node support was assessed with 1000 bootstrap replicates.

Species delimitation analyses

Minimum spanning haplotype networks were constructed with the software program TCS 1.2.1, using a 95% connection limit with gaps = missing. The General Mixed Yule Coalescent model (GMYC) uses a likelihood ratio test to compare a null model assuming a single coalescent branching rate across a clock-like tree (i.e. intraspecific population events) with a complex model including both coalescent and Yule (interspecific diversification events) branching rate models. The later also estimates the threshold time that maximizes the transition between coalescent and Yule branching models, and hence delimiting species boundaries. Species delimitation with the GMYC algorithm was performed with the R library splits v.1.0±19 [46] using a single threshold and the required R packages ape, paran, and MASS. Ultrametric trees for species delimitation using GMYC algorithm were built in BEAST v1.8.2 [47] setting a nucleotide

substitution rate for COI with a prior with log-normal distribution (log mean -4.466, standard deviation 0.075). This rate of 2.2% per my (95% interval $2.0 \pm 2.6\%$) is close the rate of 2.3% estimated by Brower [48] and widely implemented by many studies. Alternation of the GMYC algorithm permit to assess whether the branch leading to a node contains a threshold from coalescence to speciation under different coalescent models [41]. A node support value of 1 means that all coalescent models tested support the existence of a speciation event on that branch, and lower supports indicate that fewer coalescent models support such a speciation event. The number of species and so species limits would be influenced by the support cut-off selected. With lower cut-off value, the number of species will be more similar to the raw species delimitation estimated by GMYC algorithm without taking into account the support. On the other hand, higher cut-off values would reduce the number of species, generally merging closely related GMYC entities (species). We selected an arbitrary, but high, GMYC support value cut-off (0.9) to ensure that remaining species are discovered by GMYC algorithms (i.e. supported) under most of the different coalescent models tested (90%). The optimal cut-off value should be validated by simulation studies and with several empirical datasets but this is beyond the scope of our study. STACEY is a phylogenetic and a species delimitation method under a multispecies coalescent method (i.e. find the species tree and delimit species but allowing different coalescent gene trees and coalescent times). STACEY v. 1.2.0 analyses were run in BEAST2 v2.4.3 [49].

Haplotype analyses, genetic distances, maps and distribution analysis

Haplotype networks were constructed using the TCS network inference method with a 95% connection limit, and gaps treated as uninformative. Each individual network was plotted in PopART [50] including distribution information according to the geographic areas designated. Uncorrected p-distances, with gaps treated as uninformative, were calculated in PAUP* 4.0b10 [51], and Microsoft Excel v. 14.7.3. Distribution maps were compiled using ArcGIS 10.4.1 software package [52]. The geographic coordinate system GCS Sphere with Azimuthal Equidistant projection is used. Seafloor topography is accounted by the layer Etopo2. This is based on a global two minute gridded relief of ocean areas (ETOPO2v2, 2006) and provided by the National Oceanic and Atmospheric Administration (NOAA) of the U.S. Department of Commerce [53]. Bathymetric range, and clade composition for each biogeographic area, were analyzed and visualized using Microsoft Excel and Powerpoint for Mac 2011, version 14.7.3. Final design was completed in Adobe Photoshop Elements 12.0.

Morphological analysis

The aim of the morphological work in the present study was primarily to identify our species to available species names, and to allocate these available names to the correct clade circumscribed by the molecular analysis. The detailed morphological analyses of new species derived from this study will appear in forthcoming papers.

Results

Model selection

The selected best-fit models were a general time reversible model with a proportion of invariable sites and gamma distributed rate across sites (GTR+I+G) for the partitions *16S rDNA*, *ITS2*, and *ITS2* combined with *28S rDNA*, and *COI*-partition with third codon sites only, while a general time reversible model with a proportion of the sites invariable (GTR+I) was selected for the *COI*-partition including first and second codon positions. In RAxML, the analyses were

run with an independent GTRGAMMAI model for each partition, as the program do not allow the assignment of more than one model to different partitions.

Phylogenetic analyses

The combined data set of the two different combinations of *COI*, *16S rDNA*, *ITS2* and *28S rDNA* (CONCATx and CONCATs) consisted of 2574/2474 aligned positions, of which 993/1023 were parsimony-informative, and 172/171 were variable but not parsimony-informative. The results from the separate and combined analyses are summarized on the ML-tree from CONCATx (Fig 5). The phylogenetic tree is arbitrarily divided into four major groups, A±D, to make the presentation of the results more perspicuous. The results from each analysis (S10±S19 Appendixes), are presented in pie diagrams next to each node (Fig 5). The different analyses show high level of congruence between methods (ML or BI), alignment treatment (CONCATx or CONCATs), and data set combinations (mitochondrial, nuclear or combined). Out of the 49 nodes in Fig 5, 35 are identical among all five different analyses. There are few conflicting nodes between the topologies, most of them are related to the arrangement within group A, and most of them have low node support and therefore cannot be interpreted as incongruences. However, the analyses have recovered four well supported clades different to the topology illustrated in Fig 5: 1) clades 11 and 19 (group A) are sister taxa with BI-support of 0.97, in the separate nuclear data set with salsa-aligned *ITS2* sequences (S13 Appendix); 2) clade 18 (group A) is sister taxa to a clade with 11, 12, 13, 19, 20, and 21 with BI-support of 0.95 in the separate nuclear data set with salsa-aligned *ITS2* sequences (S13 Appendix); 3) clade 17 (group B) is sister taxa to a clade with 1, 4, 5, 14, 16, 26, and 27, with 0.98 in BI-support and 78 in ML-support, in the separate nuclear data set with xinsi-aligned *ITS2* sequences (S14 and S15 Appendixes); 4) clades 24 and 25 (group C) are sister taxa, with 0.93/1.0 in BI-support, and 70/95 in ML-support in both separate nuclear data sets (with xinsi- or salsa-aligned *ITS2* sequences) (S12±S15 Appendixes).

Species delimitation analyses: TCS, GMYC and STACEY

The statistical parsimony analysis of the *COI* data set, rendered 28 separate haplotype networks, while TCS analyses of *ITS2x* and *ITS2s* resulted in 24 and 23 networks respectively (S20±S22 Appendixes). GMYC analysis of the *COI* data set rendered 28 putative species, and GMYC of *ITS2x* and *ITS2s* resulted both in 24 putative species (S23±S31 Appendixes). In STACEY we treated the 28 haplotype networks from the *COI* data as the species to be tested, and in 98.8% of the resulting trees, all of these 28 clades were recovered and in 1.2% of the trees, clades 20 and 28 were lumped together (S32 Appendix) (see Fig 5). We used the most inclusive data sets for each species delimitation analyses, and in TCS all sequences of *COI* (n = 462) and *ITS2* (n = 402) were included, in GMYC all unique sequences of *COI* (n = 271) and *ITS2* (n = 136) were included, while all terminals with both *COI* and *ITS2*-data (n = 351) were included in STACEY.

The outcomes from the TCS, GMYC and STACEY analyses are identical for 17 of the 28 putative species, namely clades 1, 2, 3, 6, 7, 9, 10, 11, 14, 15, 17, 18, 19, 22, 23, 24, and 25. Looking at the instances where there is disagreement among methods, and starting with group A, clades 12 and 13 are separate in all analyses except for TCS on *ITSs*, where the haplotypes are connected into a single haplotype network, with the closest haplotypes for clades 12 and 13 separated by eight mutations (connection limit = nine). Clade 8 is further divided in the GMYC-analysis of *COI* where a group with six haplotypes (1197_8, 1198_8, 1999_5, 2013_8, 2014_8, 2214_8) is found as a separate putative species. The closest haplotype of this group is seven mutations from the closest haplotype in the main group of clade 8 in the minimum-

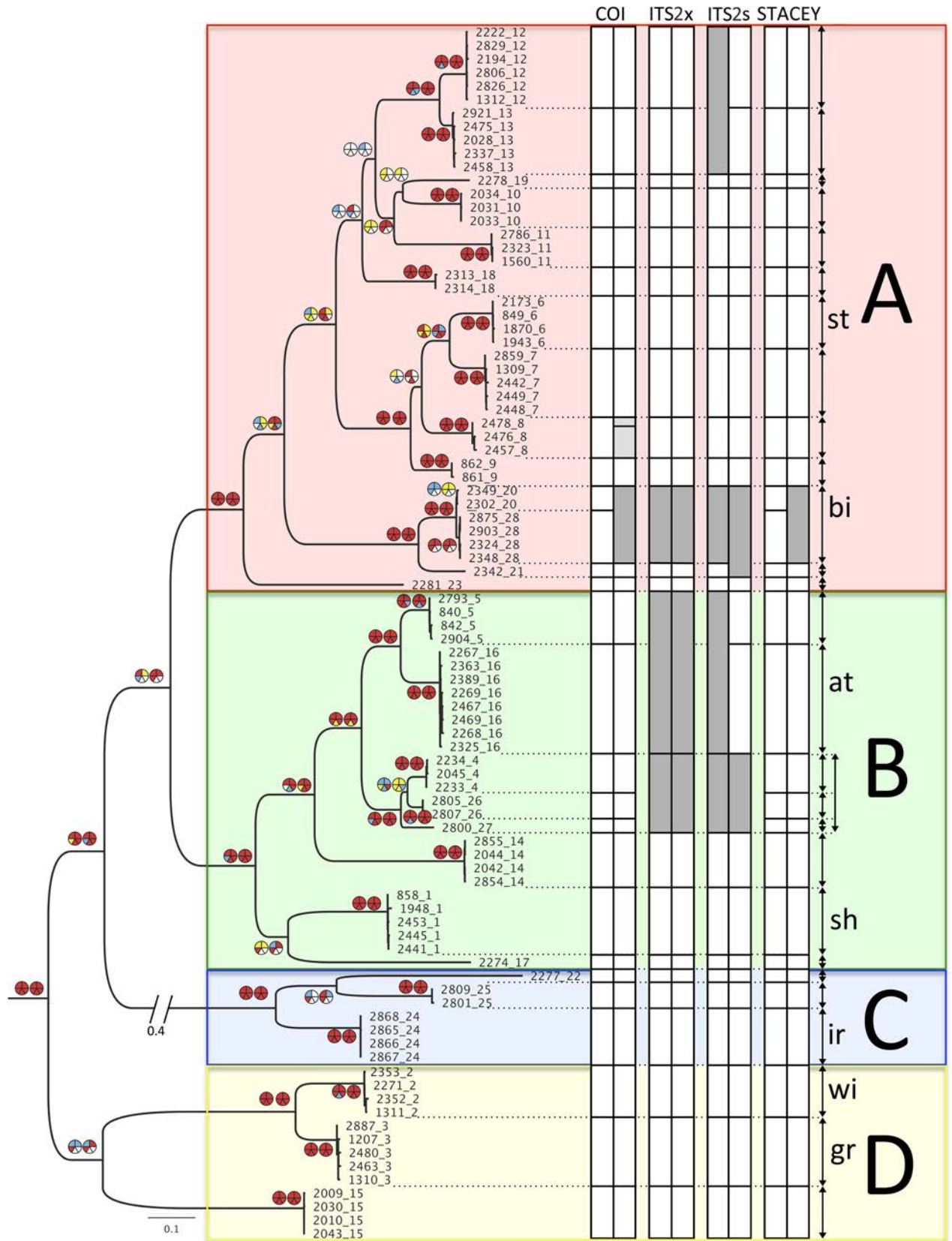


Fig 5. Results from the phylogenetic analyses, summarized on the ML estimate of the combined data set with xinsi-aligned ITS2-sequences including 91 terminals. Specimens are named according to the extraction-number and the appended clade-number. The phylogenetic tree is arbitrarily divided into four colour-coded groups, A±D. These colours are used as background colour in the distribution and haplotype network figures (Figs 6±8). Specimens with at least three of the genetic markers were included in the phylogenetic analyses, outgroups are not shown. Pie diagrams indicate support values for the node, left pie shows results from ML analyses, and right pie diagram results from Bayesian analyses. Upper two slices of a pie illustrate results from the combined data sets' two different alignments, with xinsi-aligned ITS2-sequences to the left, and salsa-aligned ITS2-sequences to the right. The three remaining slices illustrate results from the combined mitochondrial data (lower left slice), and the combined nuclear data sets' two different alignments, where lower median slice has xinsi-aligned ITS2-sequences, and lower right slice has salsa-aligned ITS2-sequences. Yellow, blue and red colour indicate low, moderate and strong support, which equals ML support in the intervals 50 ± 74 , 75 ± 89 , and 90 ± 100 , or BI posterior probabilities in the intervals 0.50 ± 0.84 , 0.85 ± 0.94 and 0.95 ± 1.0 respectively. White means support $< 50/0.50$ for the node. Columns show clustering of terminals according to different methodologies performed on more inclusive data sets where all specimens with COI or ITS2 data, or specimens with both COI and ITS2 data, were included. The first columns under the headings COI, ITSx and ITSs represent the results from TCS, and the second columns represent the results from GMYC. The columns under the heading STACEY show the two different outcomes from this analysis. White means that the network or species recovered is identical to the initial haplotype network found in COI including all COI-sequences, light grey means that less inclusive networks or putative species were recovered, and dark grey means that a more inclusive network or putative species was recovered. Double-headed arrows to the right of the columns show our final judgement of species delimitation. The two small letters to the right indicate our designation of described species, st = *T. stroemii*, bi = *T. bigeniculatus*, at = *T. atlantis*, sh = *T. shetlandica*, ir = *T. irinae*, wi = *T. williamsae*, and gr = *T. gracilis*.

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spanning haplotype network from the TCS-analysis on the same data. Clades 20 and 28 are connected in the GMYC-analysis of COI. The closest haplotypes for these clades are separated by 16 mutations in the minimum-spanning haplotype network from the TCS-analysis (using a fixed connection limit) on the same data. Clades 20 and 28 share the same haplotype in *ITS2*, and are thus connected in all analyses on *ITS2*; this haplotype is also connected to clade 21 in the GMYC-analysis of *ITS2*s. Haplotypes of clades 21 and 20/28 are separated by 11 mutations in the minimum-spanning haplotype network from the TCS-analysis (using a fixed connection limit) on the same data. Continuing with group B, clades 5 and 16 are connected in the TCS-analyses of *ITS2*x and *ITS2*s (where the closest haplotypes of clades 5 and 16 are separated by 6 and 5 mutations; connection limit = 9), as well as in the GMYC-analysis of *ITS*x. Clades 4, 26 and 27, all represented by single haplotypes in *ITS2*, are connected in all four analyses of the *ITS2*-data. The haplotypes are separated by between three and eight mutations in the minimum-spanning haplotype network in the two TCS-analyses.

In summary, we suggest that clades 12 and 13 represent different species even though they are connected in one of the *ITS2*-analyses. The two clades do not share any *ITS2*-haplotypes (Fig 6), and both lineages are fairly well sampled with 23 (clade 12) and 27 specimens (clade 13). There are also insertion/deletion events in the *ITS2*-sequence alignments that support the two clades, however, in the analyses presented here, we treated indels as missing data. We further conclude that the separate putative species in clade 8 found in the GMYC-analysis of *COI*-data could be ignored as intraspecific genetic variation (only seven mutations in the TCS-analysis), and there is neither any differences in the *ITS2*-data to support such a conclusion. We do think that there is evidence that clades 20 and 28 should be regarded as the same species even though they have separate haplotype networks in the TCS-analysis on the *COI*-data, both lineages are under-sampled with only two (clade 20) and five specimens (clade 28), and the difference between the lineages is within the variation that is found in better sampled clades (compare clades 20 and 28 in Fig 6 with clade 8 in Fig 7, and clade 16 in Fig 8), and there is a good chance that the haplotypes would be connected given a larger sample size. *ITS2*-data also support this conclusion as clades 20 and 28 share the same *ITS2*-haplotype (Fig 6). Results from STACEY also give some support to this deduction. In contrast, we believe that it is likely that clade 21 represents a separate species even though it is connected with clade 20/28 in the GMYC of the *ITS2*s, differences in *COI* between 20/28 and 21 is substantial ($12.1 \pm 13.2\%$) (Table 3), and there is also additional indel events in the *ITS2*-data alignment that suggests that they do represent different species. As was the case for clades 12 and 13, we also strongly argue

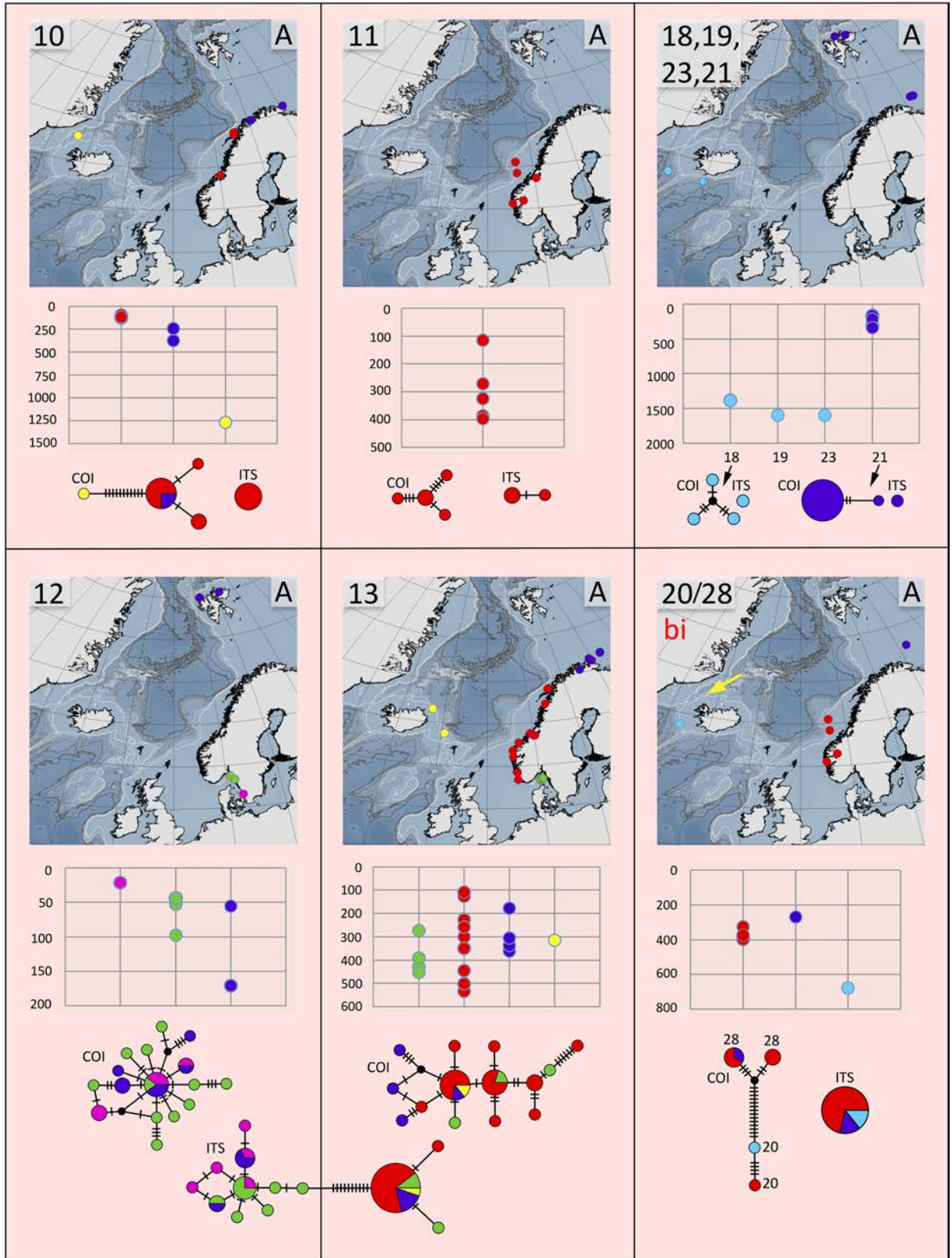


Fig 6. Distribution maps, depth distribution in meters, and haplotype networks for group A, species 10, 11, 18, 19, 23, 21, 12, 13, and 20/28. All species except for species 20/28 that we refer to *T. bigeniculatus* (bi) are undescribed. Sites are colour coded as in Fig 3. Type locality for *T. bigeniculatus* indicated with yellow arrow.

<https://doi.org/10.1371/journal.pone.0198356.g006>

that clades 5 and 16 represent different species, even though they are connected in three of the four ITS-analyses. The two clades do not share any *ITS*-haplotypes (Fig 8), and there are also indel events and morphological data (see below) supporting their separation. Finally, clades 4, 26, and 27 is suggested to represent different species, but the lineages are poorly sampled both in numbers and in geographic distribution, and more specimens are needed. However, *COI*-differences (13,3%) as well as *ITS2*-differences (Fig 7) in the two sympatric clades 26, 27 is comparable to the differences found between other closely related species pairs in the species complex, but as only 1 (clade 26) and 2 specimens (clade 27) were found of these clades, we are less certain in this case.

To conclude, we think we have strong evidence that we have between 25 and 27 different species of *Terebellides* among the sequenced specimens. In the analyses and discussion below we will proceed with the 27 species hypothesis, and the species will be referred to as species 1, 2 etc. following the original clade numbering, until the available names can be allocated to their proper clades. The clades 20 and 28 will be referred to as species 20/28.

Biogeographic and bathymetric analyses

The number of species varied rather much between the biogeographic regions (Figs 9+11). However, as the study was not designed to assess the differences in diversity for different areas, we cannot answer if certain areas are more diverse than others. Instead, the number of species strongly correlates with how many specimens that are sequenced (Fig 9), and this probably explain much of the differences found in diversity among areas. Some sort of saturation in discovering new species seems to be reached at about 100 sequenced specimens for a biogeographic area. We found more than one species in all biogeographic regions except for the two most poorly sampled regions, Arctic Ocean, and Irish and Celtic Seas (Fig 11), while the highest diversity was found in the best sampled regions with 13 species among 192 specimens in the Norwegian coast and shelf area, 13 species among 100 specimens in Barents Sea, and 10 species among 108 specimens in Skagerrak (Figs 9 and 10).

With regard to similarity in shared *Terebellides* species between the different biogeographic regions the following may be assumed (Fig 10), Kattegat is most similar to Skagerrak, with four out of its four species in common; Skagerrak is most similar to Norwegian coast and shelf, with eight out of its 10 species in common; North Sea is most similar to either Skagerrak, or Norwegian coast and shelf, with two out of its three species in common; the single species found in Irish and Celtic Sea is also present at the Norwegian coast and shelf, North Sea, Skagerrak and Kattegat; Norwegian coast and shelf is most similar to Skagerrak, with eight out of its 14 species in common; Norwegian Sea is most similar to either Skagerrak, Norwegian coast and shelf, Barents Sea, or Greenland Sea, with two out of its three species in common; the single species found in the Arctic Ocean is endemic for the area; Greenland Sea is most similar to Barents Sea, with four out of its four species in common; and the area South of Iceland is most similar to either Norwegian Sea, or Norwegian coast and shelf, with two out of its eight species in common. Endemic species are found in the Arctic Ocean (species 24), North Sea (species 9), Norwegian coast and shelf (species 11), Barents Sea (species 21, 25, 26, and 27), and in the area South of Iceland (species 17, 18, 19, 22 and 23).

Many of the species that that were found in the same biogeographic regions also overlapped in their bathymetric distribution (Fig 12). Yet, there is some sort of division between some of

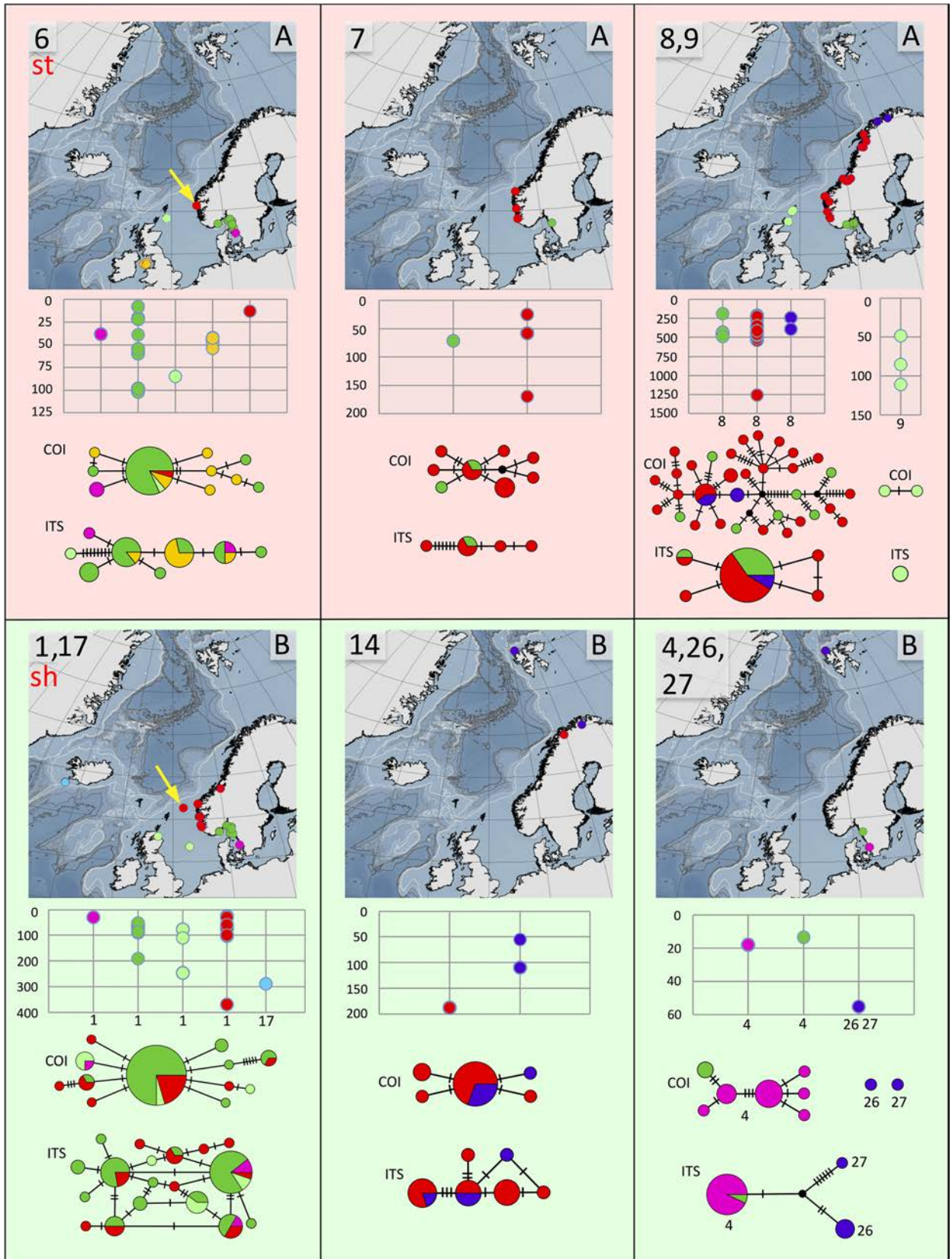


Fig 7. Distribution maps, depth distribution in meters, and haplotype networks for group A, species 6, 7, 8, and 9, and for group B, species 1, 17, 14, 4, 26, and 27. All species except for species 6 that we refer to as *T. stroemii* (st), and clade 1 that we refer to as *T. shetlandica* (sh) are undescribed. Sites are colour coded as in Fig 3. Type localities for *T. stroemii*, and *T. shetlandica* indicated with yellow arrows.

<https://doi.org/10.1371/journal.pone.0198356.g007>

the species, e.g. species 6 and 7 are found down to about 200 meters depth, while the closely related species 8 is found below 200 meters depth. Within the same biogeographic area, up to eight different species can be found in a depth span of 100 meters, and even in the same sample from a supposedly homogenous environment from a mud bottom from 534 meters depth, in the Trondheimsfjord in Norway, using a Sneli sledge, up to five different species were found (see Table 1, siteID NCS24). We can safely conclude that a majority of the species live in sympatry with several other species in the complex.

Haplotype and distance analyses

Distance calculations (S33±S34 Appendixes), uncorrected, are summarized in Tables 3 and 4, as are the results from the haplotype analyses. The latter are also visualized in Figs 6±8 for all different species. For most species, haplotypes, or group of closely related haplotypes, are generally not restricted to a certain area. A few species show a weak tendency towards geographic sorting, e.g. in species 16 (Fig 8), the haplotypes from the area South of Iceland (light blue) may to some extent be interpreted in this way. Haplotype diversity is generally high, and in a few of the well sampled species it is extreme. In species 2 there are 25 haplotypes among 32 specimens, in species 3 there are 44 haplotypes among 50 specimens, in species 8 there are 33 haplotypes among 40 specimens, and in species 16 there are 48 haplotypes among 55 specimens.

Morphological analyses

Group A comprises 13 species. For the time being we are not able to find any morphological character that unites the group, but two of the known species, *T. bigeniculatus* and *T. stroemii*, can be attributed to two of the clades found. *Terebellides bigeniculatus* is identified by the presence of geniculate chaetae (Figs 1B, 2A and 2C±2E) in both chaetigers 5 and 6, and this condition is found in species 21 and species 20/28, and as the latter of these two species is the only one found among our Icelandic specimens we suggest that the name *T. bigeniculatus*, that has its type locality north-west of Iceland, may be used for species 20/28. *Terebellides stroemii* on the other hand is characterized by a robust body, and relatively small branchiae, with partially fused lobes (Fig 1B) instead of unfused ones (Figs 1A and 2B). From the available diagnosis, any of the clades 6, 7, 8 and 9 are possible candidates for representing the true *T. stroemii*. *Terebellides stroemii* has a type locality from between 55±110 meters depth near Bergen in SW Norway, and species 8 is only found deeper than 200 meters and is thus excluded for being the nominal species, and with the same reasoning, we also exclude species 9 due to that it is only found in the North Sea region. However in the choice between species 6 and 7 we cannot say right now which one is more likely to be the correct *T. stroemii*, but our suggestion is that clade 6 could be used for the name, because in our samples it seems to be the most common and widely spread species of the two.

Group B comprises eight species. A possible morphological identifier for this group of species is that they all have small to medium sized, elongated bodies. In this group, two clades, 16 and 1, could be identified as already described taxa. Species 16 is characterized by having unfused branchial lobes, with a low number of lamellae. Due to this, and because of its distribution, found at great depths in Greenland Sea and in the area South of Iceland, congruent with the species original depth distribution, we suggest that the name *T. atlantis* might be

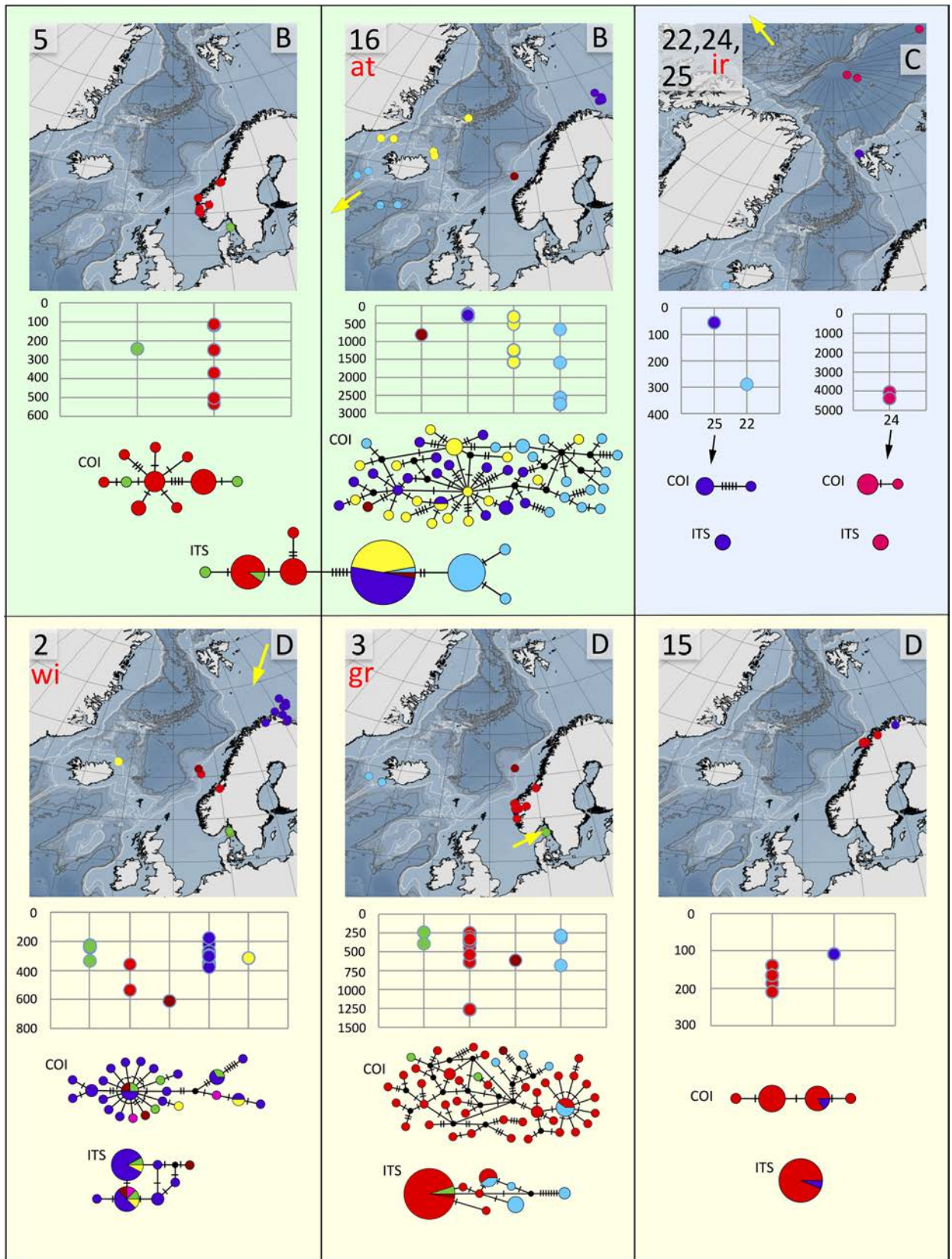


Fig 8. Distribution maps, depth distribution in meters, and haplotype networks for group B, species 5 and 16, group C, species 22, 24, and 25, and group D, species 2, 3, and 15. Species 5, 22, 25, and 15 are undescribed, while we refer species 16 to *T. atlantis* (at), species 24 to *T. irinae* (ir), species 2 to *T. williamsae* (wi), and species 3 to *T. gracilis* (gr). Sites are colour coded as in Fig 3. Type localities for *T. atlantis*, *T. irinae*, *T. williamsae*, and *T. gracilis* indicated with yellow arrows.

<https://doi.org/10.1371/journal.pone.0198356.g008>

applicable for this species. Species 1 should be referred to *T. shetlandica*, it is the only species we have found that have the characteristic gills with branchial lobes of different sizes, and provided with a long posterior filament (Fig 2B), diagnostic features for *T. shetlandica*. Moreover, in some specimens a parasitic copepod was found, as was also described for several specimens of *T. shetlandica* in the original description.

Group C comprises three species, with no apparent morphological identifier. We attribute the name *T. irinae* to the deep-water species 24 found only in the Arctic Ocean in our analysis. It fits the original description well, and even if our collecting sites are not near the type locality we think a distribution from Beaufort Sea to the Arctic Basin is likely.

Group D also comprises three species. The group is characterized by white ventral colouration in anterior thoracic chaetigers (1 to 4) (Fig 1A). Species 2 and 3 are further characterized by having branchiae with ventral and dorsal lobes of similar shape (Fig 2A). The combination of these characters fits the diagnosis of two already described species of *Terebellides*, *T. gracilis* and *T. williamsae*. *Terebellides williamsae* is considered to be a junior synonym to *T. gracilis* but we prefer to withdraw it from synonymy even though, at this moment, we do not have any morphological characters that separates them. Species 2 is suggested to represent *T. williamsae* as it is the only one of the two occurring in the Barents Sea (the type locality for *T. williamsae*), and thus species 3 is suggested to represent *T. gracilis* even though both species 2 and 3 are found in sympatry at the type locality for *T. gracilis*, the Swedish coast of Skagerrak.

No of species

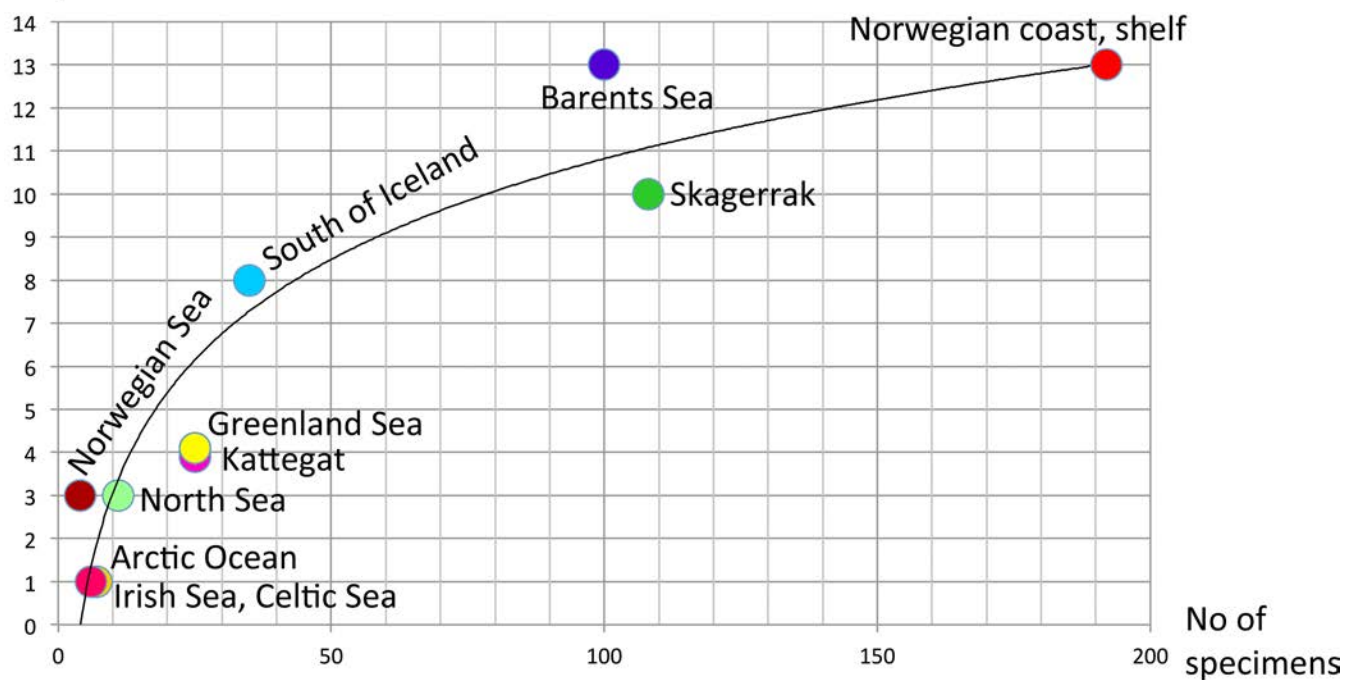


Fig 9. Accumulation curve showing the relationship between sampling size (number of specimens) and number of species found among the different biogeographic regions.

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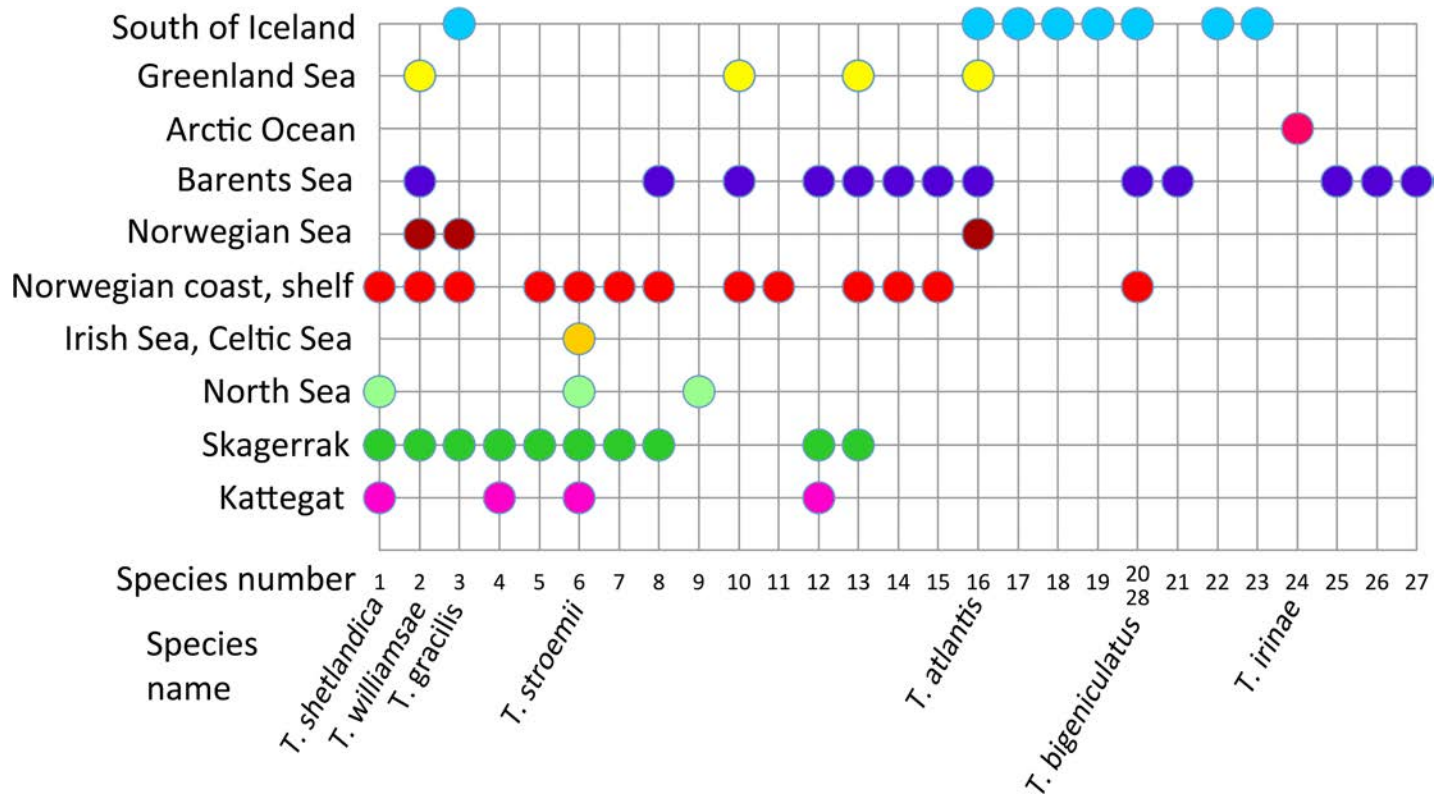


Fig 10. Diagram showing the distribution of different *Terebellides* species in the ten biogeographic regions.

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Discussion

Cryptic species are of paramount importance because of their commonality, and they are routinely found in genetic surveys, also in well-known taxa in well-studied areas [2, 54]. It is clear that the small fraction of morphological species that has been investigated so far still only represents the tip of the iceberg as Knowlton stated in her visionary paper on sibling species almost 25 years ago [55]. Considering that cryptic species literally are everywhere, in a taxonomic as well as in a geographic context, they can in no way be neglected if we want to correctly assess species diversity, understand biogeographic patterns or keep track of natural or man-made induced changes in the marine environment.

Terebellides is one of the most regularly encountered annelid taxa in environmental monitoring programs in the North East Atlantic [56], and it is normally reported under the species names *T. gracilis*, and *T. stroemii*, and in recent years *T. shetlandica* and *T. bigeniculatus* have been added to the list. Prior to this study, we suspected there might be cryptic species hiding among *Terebellides*, but it came as an overwhelming surprise to find so many of them, and that in cases some of them were so common.

Having a closer look at the best sampled areas (Fig 12), starting with Kattegat and Skagerrak, a very small part of the North East Atlantic. There are so far three different species reported from this area, and we have identified these in our sequenced specimens; *T. stroemii* (species 6), *T. gracilis* (species 3), and *T. shetlandica* (species 1). In addition we have a new record of *T. williamsae* (species 2), but the remainder, that is species 4, 5, 7, 8, 12 and 13 are unknown and undescribed. Out of the 133 specimens sampled and sequenced from the area, about roughly 1/3 (47 specimens) belong to this latter category of undescribed species.

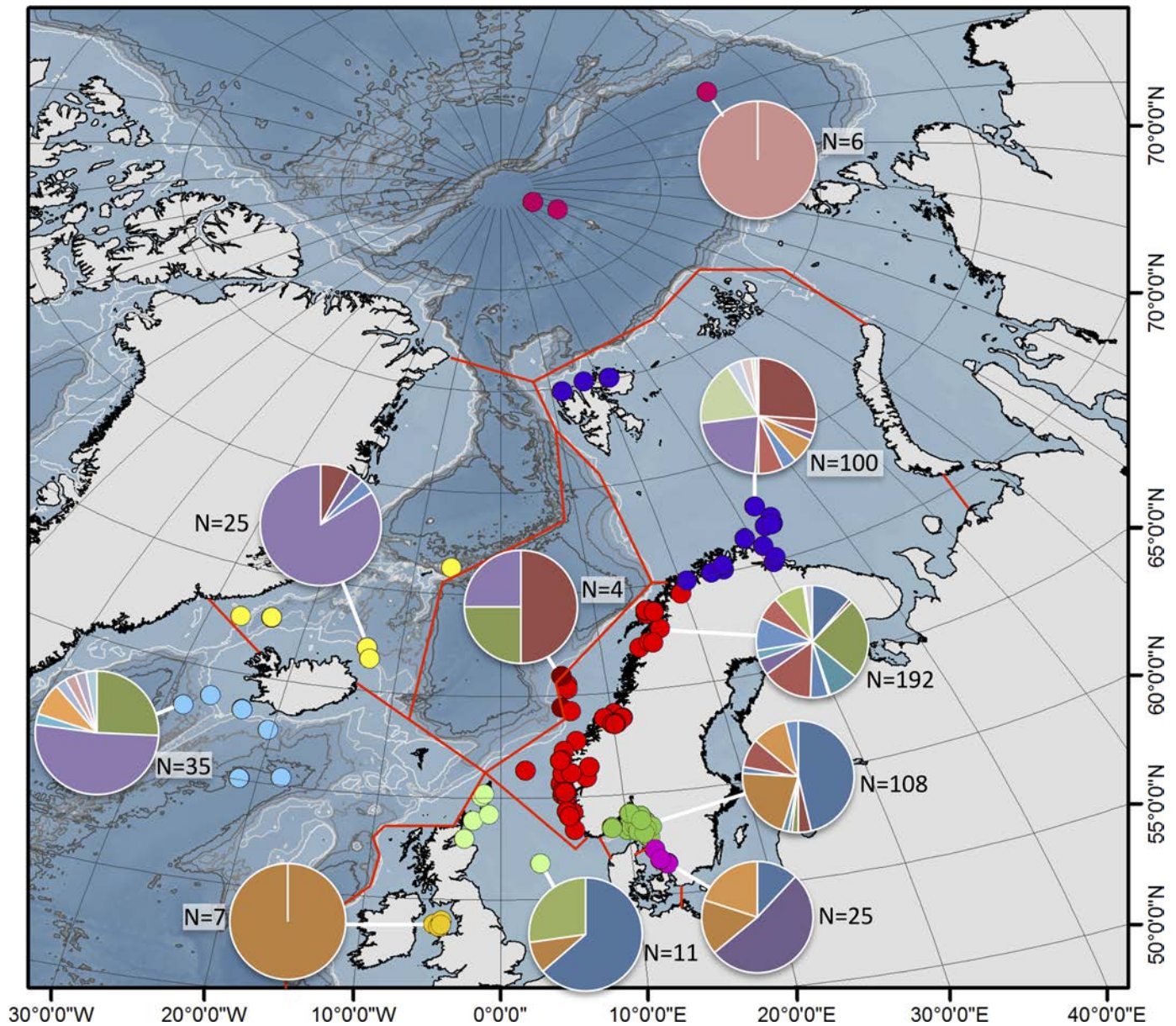


Fig 11. Overview of the diversity found in the ten biogeographic regions. Pie diagrams show the relative proportions of the different species found where all species have their own colour, sampling size (N) indicated next to the pie diagrams.

<https://doi.org/10.1371/journal.pone.0198356.g011>

Continuing with the Norwegian coast and shelf, we find the same four described species present in Kattegat/Skagerrak, and in addition *T. bigeniculatus* (species 20/28), but species 5, 7, 8, 10, 11, 13, 14, and 15 are all undescribed. These unnamed species gather more than half of the specimens sequenced (117 out of 192 = 61%), and that means in short, that the current probability of finding an undescribed species of *Terebellides* is larger than finding a described one! This is indeed astonishing given that we are dealing with one of the best investigated marine environments in the world, the relatively shallow waters just outside the coasts of Sweden and Norway, and one of the most frequently encountered annelid taxa in the area. The situation in the Barents Sea is similar, and we find *T. williamsae* (species 2), *T. atlantis* (species 16) and *T. bigeniculatus* (species 20/28), but neither *T. stroemii* (species 6) nor *T. gracilis* (species 3)

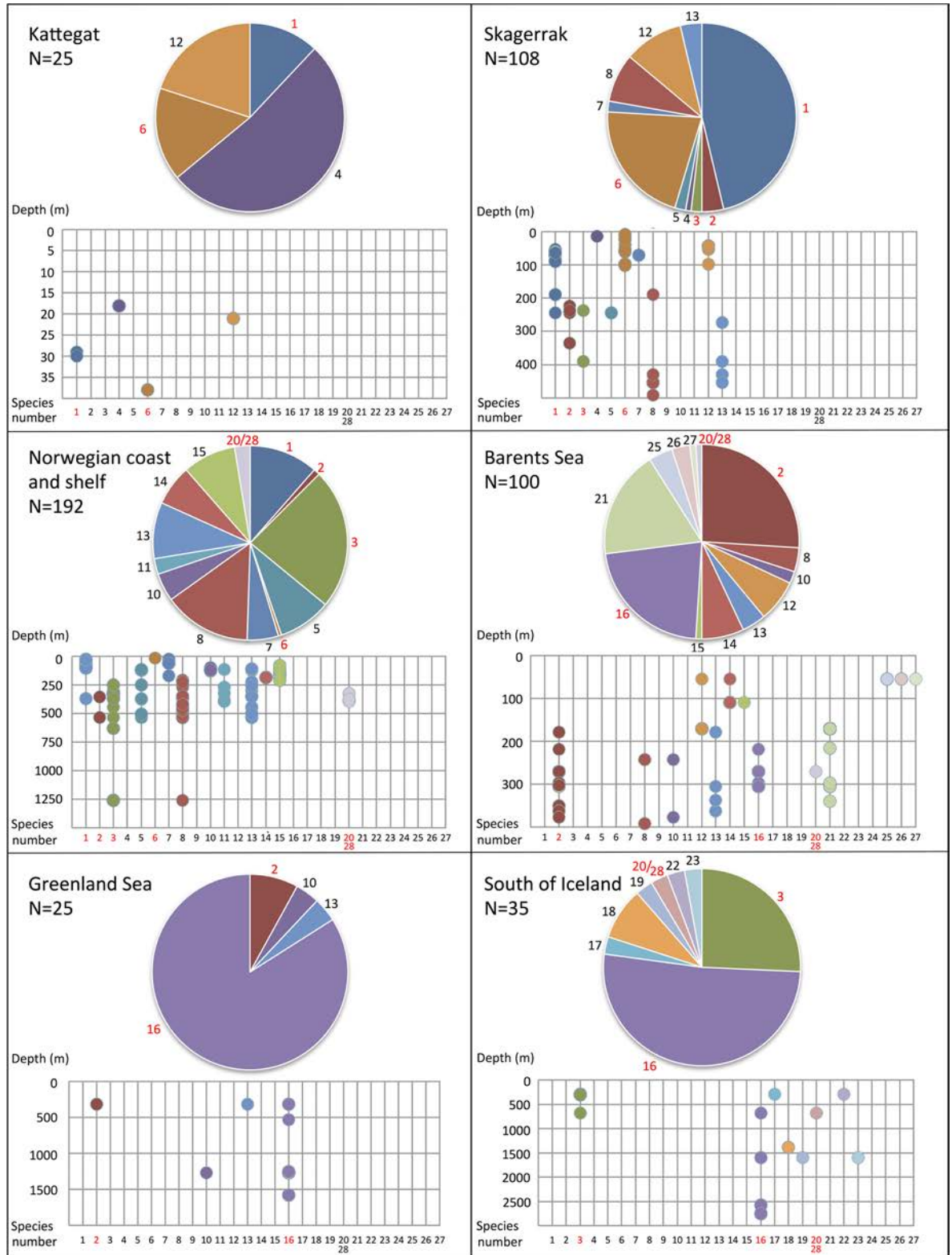


Fig 12. Pie diagrams from Fig 11 for the six best sampled biogeographic regions with bathymetric results in meters. Species number next to its slice in the pie diagrams, species number in red when the species is a described species, where species 1 = *T. shetlandica*, species 2 = *T. williamsae*, species 3 = *T. gracilis*, species 6 = *T. stroemii*, species 16 = *T. atlantis*, and species 20/28 = *T. bigeniculatus*.

<https://doi.org/10.1371/journal.pone.0198356.g012>

among our sequenced specimens; in addition we also find the undescribed species 8, 10, 12, 13, 14, 15, 21, 25, 26, and 27, and together these undescribed species represent c. 50% of the sequenced specimens. Greenland Sea and the area South of Iceland are dominated by specimens of *T. atlantis* (species 16), *T. gracilis* (species 3), and *T. williamsae* (species 2), but there are also quite a few undescribed species present here as well, but as the sample size is not as large as in Skagerrak, Norwegian coast and shelf, and Barents Sea the results are not really comparable.

Looking at the depth distribution for the different species in a given geographic area, we can see that most species overlap in depth, and there is, in most cases, no clear sorting of species at different depths (Fig 12). In the depth range 150±250 meters in the Norwegian coast and shelf region, we have nine species present, and they all more or less overlap and are present at most of the localities that we have been able to sample, e.g. in the area from Trondheim in the north to Bergen in the south, 11 species are found (Figs 6±8), indicating that they do not inhabit specific habitats like fjords or the open ocean. For most of our samples we have used a sledge, a dredge or a beam trawl, all these gears sample material from an unspecified area of the sea floor. But often, at least when a sledge is used, the area sampled is an apparently flat uniform habitat of mud. In 49 out of the 89 sites from where we have sequenced more than one specimen, we found more than one species (Table 1), and in the most species-rich samples, five different species of *Terebellides* were found, e.g. site NCS24, a sample from a flat mud bottom from 534 meters depth in the Trondheimsfjord. There are few samples taken with a grab, but in one of them (BS5) we found two species co-occurring. Anyway, as we did not sequence all specimens from all samples, it is difficult to assess how many species of *Terebellides* that do co-occur at the same site. For many of the sites only one or a few specimens were sequenced, thus it is likely that diversity for each separate site is underestimated, but when looking at a slightly larger scale this should not be the case.

Apart from the fact that so many species of *Terebellides* still go under the radar, and that these unknown and undescribed species are so common, and even constitute a major part of the diversity both in number of species and specimens, one other thing struck us: the extreme diversity of haplotypes found in COI among some species. The most note-worthy are *T. gracilis* (species 3), *T. williamsae* (species 2), *T. atlantis* (species 16), and species 8, where almost all specimens sampled and sequenced have their own unique haplotype (Figs 7 and 8, Table 3). This variation rarely has led to an amino-acid substitution within the species, and in *T. atlantis* (species 16) all 48 haplotypes found among the 55 specimens produce the same exact amino-acid sequence. As the sample size varies a lot between different species, it is difficult to make a direct comparison in haplotype diversity, but one thing to note is that all those four species mentioned above are found at greater depths than a couple of 100 meters (Figs 7 and 8), in contrast with two other species that also are well represented in the material, i.e. *T. shetlandica* (species 1), and *T. stroemii* (species 6), that are found at more shallow depths (Fig 7). The relatively low genetic diversity among these shallow water species may be explained by that they have been more affected by the recurrent ice ages that have occurred during the last 1.8 million years [57], than the species living at greater depths have been. Even so it is hard to understand and explain the extremely high diversity of haplotypes, and how it is maintained, in these deeper-living species, but see [58] that also reported high haplotype diversity in *Aonidella cf. dayi*, for possible explanations to this phenomenon.

Our angle on this study has been a molecular one, in order to find out how many species that occur in North East Atlantic waters, and the full morphological investigation has to await forthcoming studies. The main purpose of the morphological examination conducted in this paper has been to connect the described and known morphological species to the correct, or at least the best, molecularly recognized species. It is our hope that we in the future will be able to find

morphological characters that will help in standard morphological identification down to at least a group of possible species, and in the best of worlds also down to species level. Molecular data from this study will be vital to help us to sort out when this latter task is obtainable and when it is not.

Much water has passed under the bridge since Holthe [59] published his book on *Terebellomorpha* in the North East Atlantic, when he discussed the supposed cosmopolitan distribution of *T. stroemii*. He acknowledged that the worldwide reports were due to a confusion of closely related species, but nevertheless stated that 'I do not suspect that there are more than one species in the Norwegian material'. Still in these days, most *Terebellides* in the North East Atlantic are routinely identified as *T. stroemii*, and our comprehensive study make it clear that this is a severe underestimation of the true diversity among *Terebellides*. We do not think that *Terebellides* is an unusual example of cryptic species, on the contrary, when morphospecies are properly assessed molecularly, in terms of sampling strategy and number of specimens analyzed (e.g. [60]), it is commonplace to find more than one species, sometimes several, in the material. Already Grassle [61] asked the question 'How common are cryptic polychaetes' when she and her husband had discovered six cryptic species of *Capitella capitata* after an oil spill in West Falmouth, Massachusetts in September 1969 [62]; we think we now have taken a small step further towards the answer to this long-held question.

Supporting information

S1 Appendix. COI-unique.nex. Alignment, in nexus-format, with the unique 271 COI-sequences.

(NEX)

S2 Appendix. COI-all.nex. Alignment, in nexus-format, with all 462 COI-sequences.

(NEX)

S3 Appendix. ITS2x-unique.nex. Alignment, in nexus-format, with the unique 136 ITS2-sequences, aligned with X-INS-i in MAFFT.

(NEX)

S4 Appendix. ITS2x-all.nex. Alignment, in nexus-format, with all 402 ITS2-sequences, aligned with X-INS-i in MAFFT.

(NEX)

S5 Appendix. ITS2s-unique.nex. Alignment, in nexus-format, with the unique 136 ITS2-sequences, aligned with RNAsalsa.

(NEX)

S6 Appendix. ITS2s-all.nex. Alignment, in nexus-format, with all 402 ITS2-sequences, aligned with RNAsalsa.

(NEX)

S7 Appendix. COI_and ITS2s.nex. Alignment, in nexus-format, including specimens with both COI and ITS2-data, used in the STACEY analysis.

(NEX)

S8 Appendix. CONCATx.nex. Concatenated alignment, in nexus-format, of COI, 16S rDNA, ITS2s, and 28S rDNA, including specimens with data from three of the four genetic markers.

(NEX)

S9 Appendix. CONCATs.nex. Concatenated alignment, in nexus-format of COI, 16S rDNA, ITS2x, 28S rDNA, including specimens with data from three of the four genetic markers.

(NEX)

- S10 Appendix. CONCATmito_ML.tre.** Resulting tree with support values, using Maximum Likelihood on mitochondrial data only.
(TRE)
- S11 Appendix. CONCATmito_BI.tre.** Resulting tree with support values, using Bayesian inference on mitochondrial data only.
(TRE)
- S12 Appendix. CONCATnucls_ML.tre.** Resulting tree with support values, using Maximum Likelihood on nuclear data only, with salsa-aligned ITS2-sequences.
(TRE)
- S13 Appendix. CONCATnucls_BI.tre.** Resulting tree with support values, using Bayesian inference on nuclear data only, with salsa-aligned ITS2-sequences.
(TRE)
- S14 Appendix. CONCATnuclx_ML.tre.** Resulting tree with support values, using Maximum Likelihood on nuclear data only, with xinsi-aligned ITS2-sequences.
(TRE)
- S15 Appendix. CONCATnuclx_BI.tre.** Resulting tree with support values, using Bayesian inference on nuclear data only, with xinsi-aligned ITS2-sequences.
(TRE)
- S16 Appendix. CONCATs_ML.tre.** Resulting tree with support values, using Maximum Likelihood on the combined mitochondrial and nuclear data set, with salsa-aligned ITS2-sequences.
(TRE)
- S17 Appendix. CONCATs_BI.tre.** Resulting tree with support values, using Bayesian inference on the combined mitochondrial and nuclear data set, with salsa-aligned ITS2-sequences.
(TRE)
- S18 Appendix. CONCATx_ML.tre.** Resulting tree with support values, using Maximum Likelihood on the combined mitochondrial and nuclear data set, with xinsi-aligned ITS2-sequences.
(TRE)
- S19 Appendix. CONCATx_BI.tre.** Resulting tree with support values, using Bayesian inference on the combined mitochondrial and nuclear data set, with xinsi-aligned ITS2-sequences.
(TRE)
- S20 Appendix. COI_TCS_log.rtf.** Log-file from the TCS-analysis on COI-all.
(RTF)
- S21 Appendix. ITS2x_TCS_log.rtf.** Log-file from the TCS-analysis on ITS2x-all.
(RTF)
- S22 Appendix. ITS2s_TCS_log.rtf.** Log-file from the TCS-analysis on ITS2s-all.
(RTF)
- S23 Appendix. COI_GMYC_code_nodes.pdf.** Topology from the GMYC-analysis on COI-unique with node numbers.
(PDF)
- S24 Appendix. COI_GMYC_log.rtf.** Log-file from the GMYC-analysis on COI-unique.
(RTF)

S25 Appendix. COI_GMYC_support.xls. Support-values for nodes from the GMYC-analysis on COI-unique.

(XLS)

S26 Appendix. ITS2x_GMYC_code_nodes.pdf. Topology from the GMYC-analysis on ITS2s with node numbers.

(PDF)

S27 Appendix. ITS2x_GMYC_log.rtf. Log-file from the GMYC-analysis on ITS2s.

(RTF)

S28 Appendix. ITS2x_GMYC_support.xls. Support-values for nodes from the GMYC-analysis on COI.

(XLS)

S29 Appendix. ITS2s_GMYC_code_nodes.pdf. Topology from the GMYC-analysis on ITS2s with node numbers.

(PDF)

S30 Appendix. ITS2s_GMYC_log.rtf. Log-file from the GMYC-analysis on ITS2s.

(RTF)

S31 Appendix. ITS2s_GMYC_support.xls. Support-values for nodes from the GMYC-analysis on COI.

(XLS)

S32 Appendix. STACEY_log.txt. Log-file from STACEY analysis on the COI_and ITS2s data set.

(TXT)

S33 Appendix. Distances_COI.xlsx. Uncorrected distances from COI-all data set.

(XLSX)

S34 Appendix. Distances ITS2s.xlsx. Uncorrected distances from ITS2s data set.

(XLSX)

S35 Appendix. Uniqhaplo.pl. Pearl script originally downloaded from the web page of Dr. Naoki Takebayashi at University of Alaska Fairbanks (Department of Biology and Wildlife).

(PL)

S36 Appendix. Specimen list. List of sequenced specimens with voucher specification, site ID (see [Table 1](#)), sequence ID, and GenBank accession numbers.

(DOCX)

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