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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 tubiculous 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

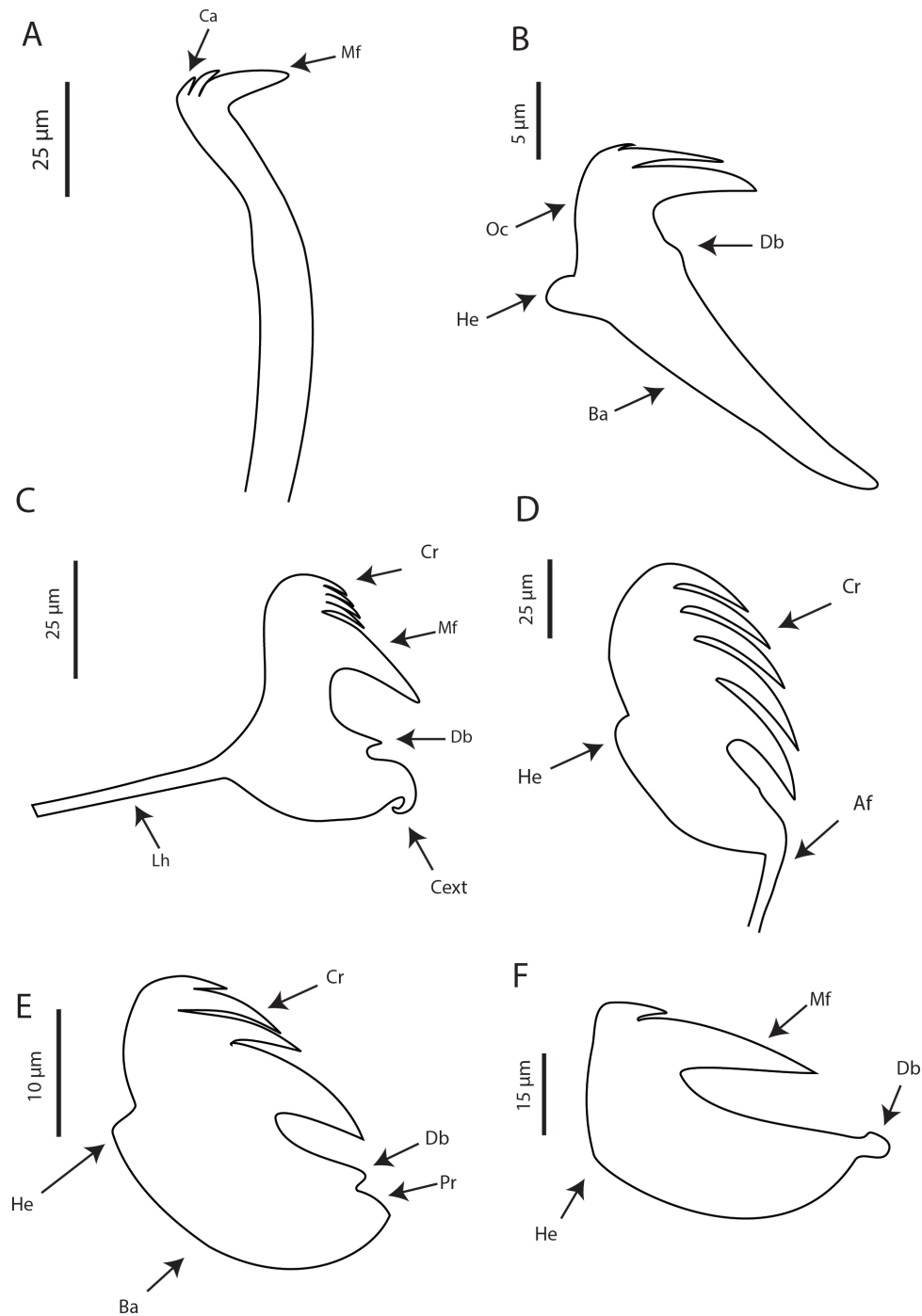


Fig. 1. Schematic illustrations of different uncini morphologies, in lateral view (following Nogueira *et al.* 2010). **A.** *Terebellides* sp., SG IX (SMA-BR-Terebellides-KER1). **B.** *Polycirrus catalanensis* Lavesque, Hutchings, Daffé & Londoño-Mesa, 2020, SG XX (holotype MNHN-IA-TYPE 2007). **C.** *Pista sauriaui* Lavesque, Daffé, 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, Daffé & 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 = capitulum; 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).

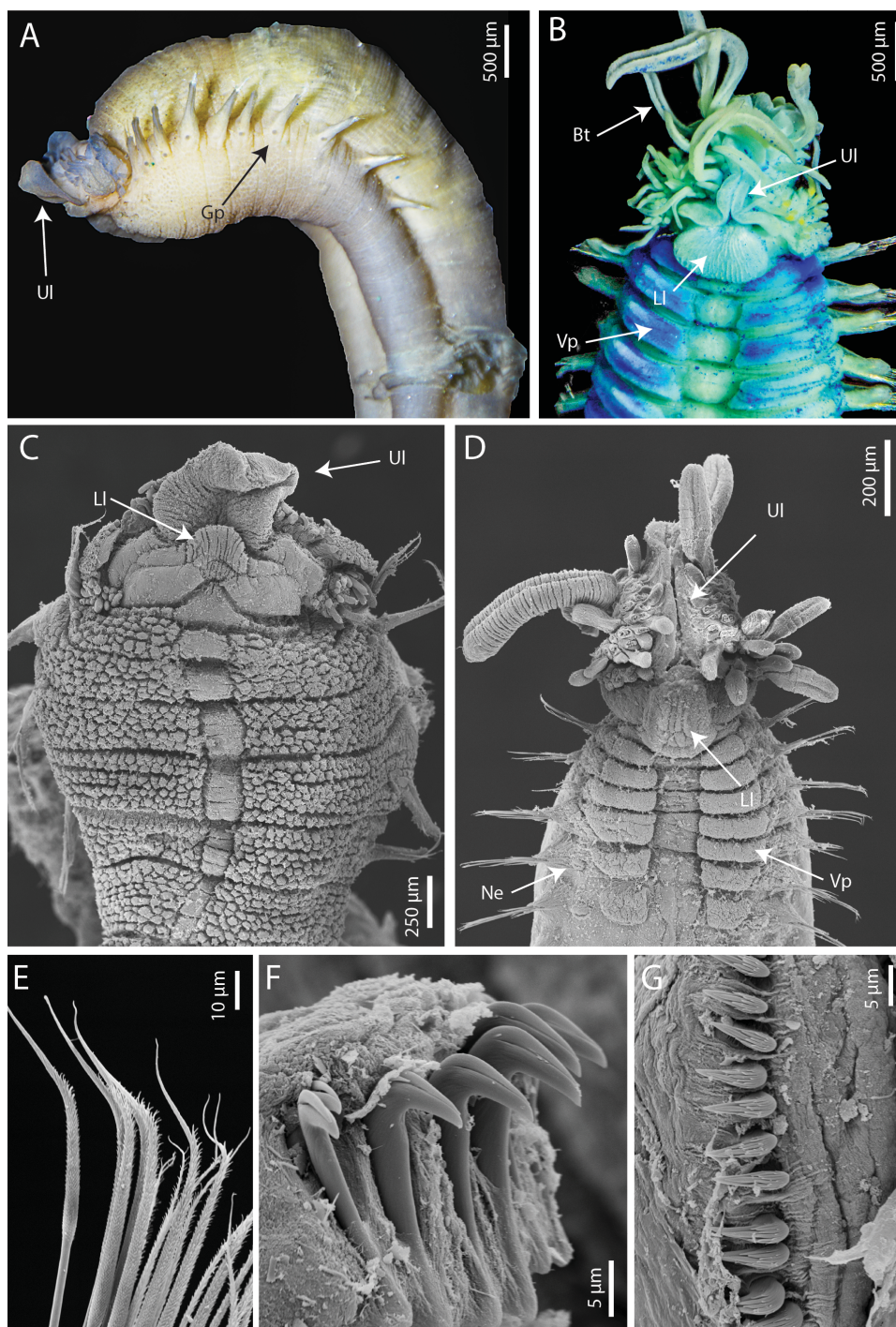


Fig. 2. Diversity of Polycirridae Malmgren, 1866. **A.** *Amaeana gremarei* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, anterior end, lateral view (MNHN-IA-TYPE 2006). **B.** *Polycirrus gujanensis* Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020, anterior end, ventral view (MNHN-IA-TYPE 2013). **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 gremare</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	NHMHK
	<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	NHMHK
	<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
Telothelepodidae	<i>Parathelepus 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 rzhavskyi</i>	Jirkov, 2020		Melilla, Morocco	MNCN
	<i>Amphitrite variabilis</i>	(Risso, 1826)		Mediterranean Sea, France	Cannot be traced
	<i>Amphitritides gracilis</i>	(Grube, 1860)	yes	Scilly Isles, UK	MNHB
	<i>Amphitritides kuehlmanni</i>	Arvanitidis & Koukouras, 1995		Eubolia Gulf, Greece	MZDAUT
	<i>Artacama proboscidea</i>	Malmgren, 1866	yes	Spitzbergen, Norway	Probably lost or never designated
	<i>Axionice maculata</i>	(Dalyell, 1853)		Scotland, UK	Cannot be traced
	<i>Axionice flexuosa</i>	(Grube, 1860)	yes	Greenland	MNHB
	<i>Baffinia hesslei</i>	(Annenkova, 1924)	yes	Barents Sea	ZIN
	<i>Eupolymnia gili</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Normandy, France	MNHN / AM
	<i>Eupolymnia lacazei</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Gulf of Lion, France	MNHN / AM
	<i>Eupolymnia meissnerae</i>	Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021		Bay of Brest, France	MNHN / AM
	<i>Eupolymnia nebulosa</i>	(Montagu, 1819)		Devon, England, UK	Cannot be traced
	<i>Eupolymnia nesidensis</i>	(Delle Chiaje, 1828)	yes	Gulf of Naples, Italy	Cannot be traced
	<i>Lanassa nordenskiöldi</i>	Malmgren, 1866	yes	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 bansei</i>	Saphronova, 1988		NW Pacific	ZIN
	<i>Pista colini</i>	Labrun, 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 labrunae</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 miosseci</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
Thelepodidae	<i>Pista wui</i>	Saphronova, 1988		Pacific Ocean	Cannot be traced
	<i>Pistella lornensis</i>	(Pearson, 1969)	yes	Scotland, UK	NHMOUK
	<i>Pistella rovigensis</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	NHMOUK
	<i>Sireblosoma bairdi</i>	(Malmgren, 1866)	yes	Sweden	Probably lost
	<i>Sireblosoma cabiochi</i>	Lavesque, Londoño-Mesa, Daffé & Hutchings, 2020		Northern Brittany, France	MNHN / AM
	<i>Sireblosoma hutchingsae</i>	Lezzi & Giangrande, 2019		Torre Insserraglio, Italy	MNCN
	<i>Sireblosoma intestinalis</i>	M. Sars in G.O. Sars, 1872		Oslo Fjord, Norway	UZMO
	<i>Sireblosoma lindsayae</i>	Lavesque, Londoño-Mesa, Daffé & Hutchings, 2020		Bay of Biscay, France	MNHN
	<i>Sireblosoma nogueirai</i>	Lezzi & Giangrande, 2019		Torre Guaceto, Italy	MNCN
	<i>Sireblosoma 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		Almería, Spain	KGB / MNCN
	<i>Thelepus setosus</i>	(Quatrefages, 1866)		Normandy, France	MNHN
	<i>Thelepus triserialis</i>	(Grube, 1855)		Mediterranean Sea	Cannot be traced

Table 1 (continued). European species of Terebellidae s.l.

Family	Species	Authority	Type species	Type locality	Type specimen collections
Trichobranchidae	<i>Octobrachius floriceps</i>	Kingston & Mackie, 1980		Northern North Sea	NHUK / NMSE
	<i>Octobrachius 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 bonifi</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 romingae</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. gremare* 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	<i>Polycirrus norvegicus</i> 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	<i>Polycirrus denticulatus</i> Saint-Joseph, 1894	
– With 16 segments with notopodia, lower lip wider than long	<i>Polycirrus elisabethae</i> McIntosh, 1915	
13. With 18 or more segments with notopodia, lower lip oval, ventro-lateral pads not separated by a large mid-ventral groove	<i>Polycirrus glasbyi</i> Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020	
– Fewer than 18 segments with notopodia, lower lip oblong, ventro-lateral pads separated by a large midventral groove	<i>Polycirrus readi</i> 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	<i>Polycirrus plumosus</i> (Wollebaek, 1912)	
16. Upper lip elongated, uncini with a main tooth above the main fang, ventro-lateral pads well developed	<i>Polycirrus nogueirai</i> Lavesque, Hutchings, Daffe & Londoño-Mesa, 2020	
– Upper lip semicircular, uncini without a main tooth above the main fang, ventro-lateral pads poorly defined	<i>Polycirrus arcticus</i> 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	<i>Polycirrus latidens</i> 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	<i>Polycirrus medusa</i> 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	<i>Polycirrus catalanensis</i> 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	<i>P. pennarbedae</i> 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*).

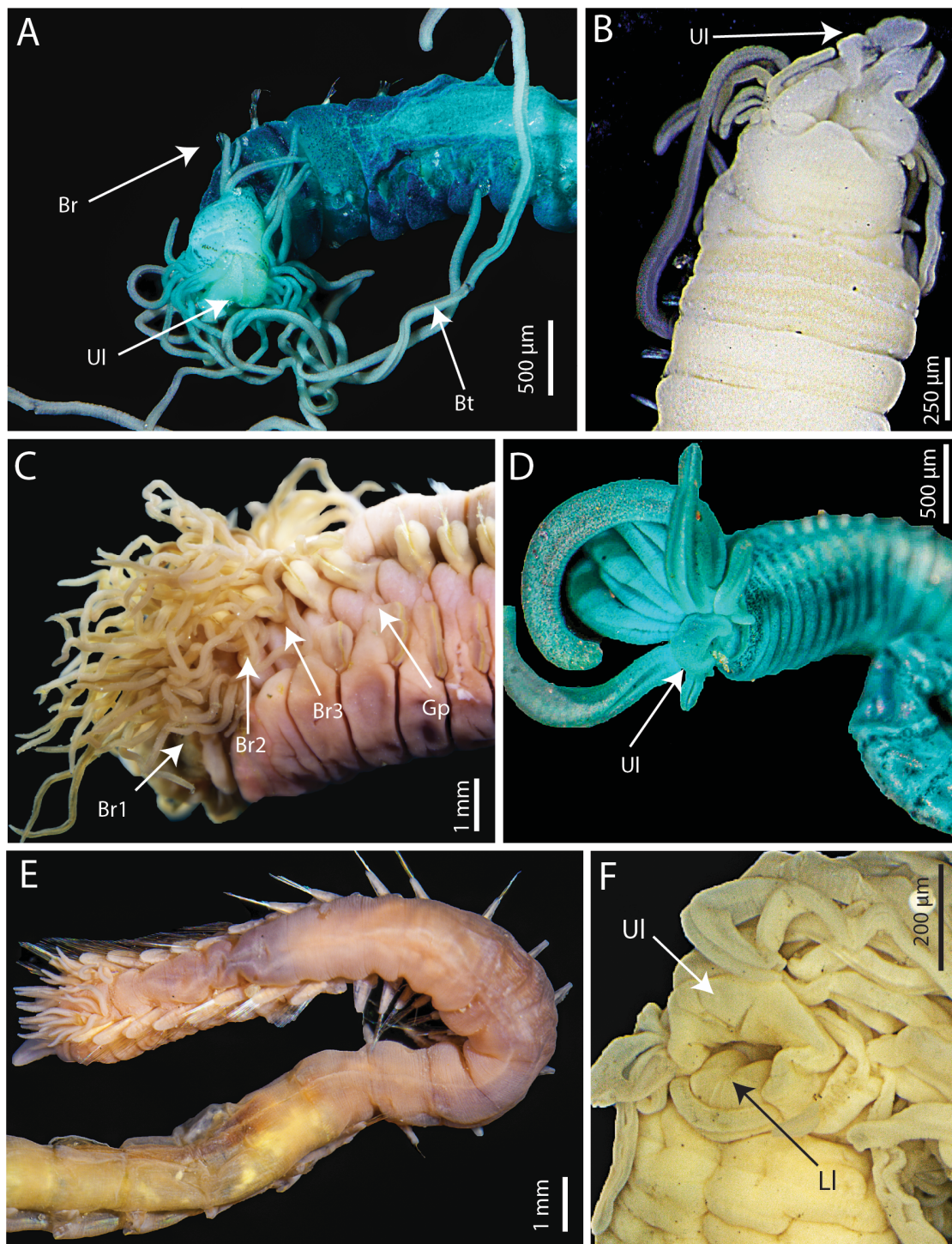


Fig. 3. Diversity of Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 and Thelepodidae Hesse, 1917. **A.** *Parathelepus collaris* (Southern, 1914), anterior end, frontal view (AM W.53063). **B.** *Parathelepus collaris*, anterior end, ventral view (NHMUK ANEA 1983.1696). **C.** *Thelepus japonicus* 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.

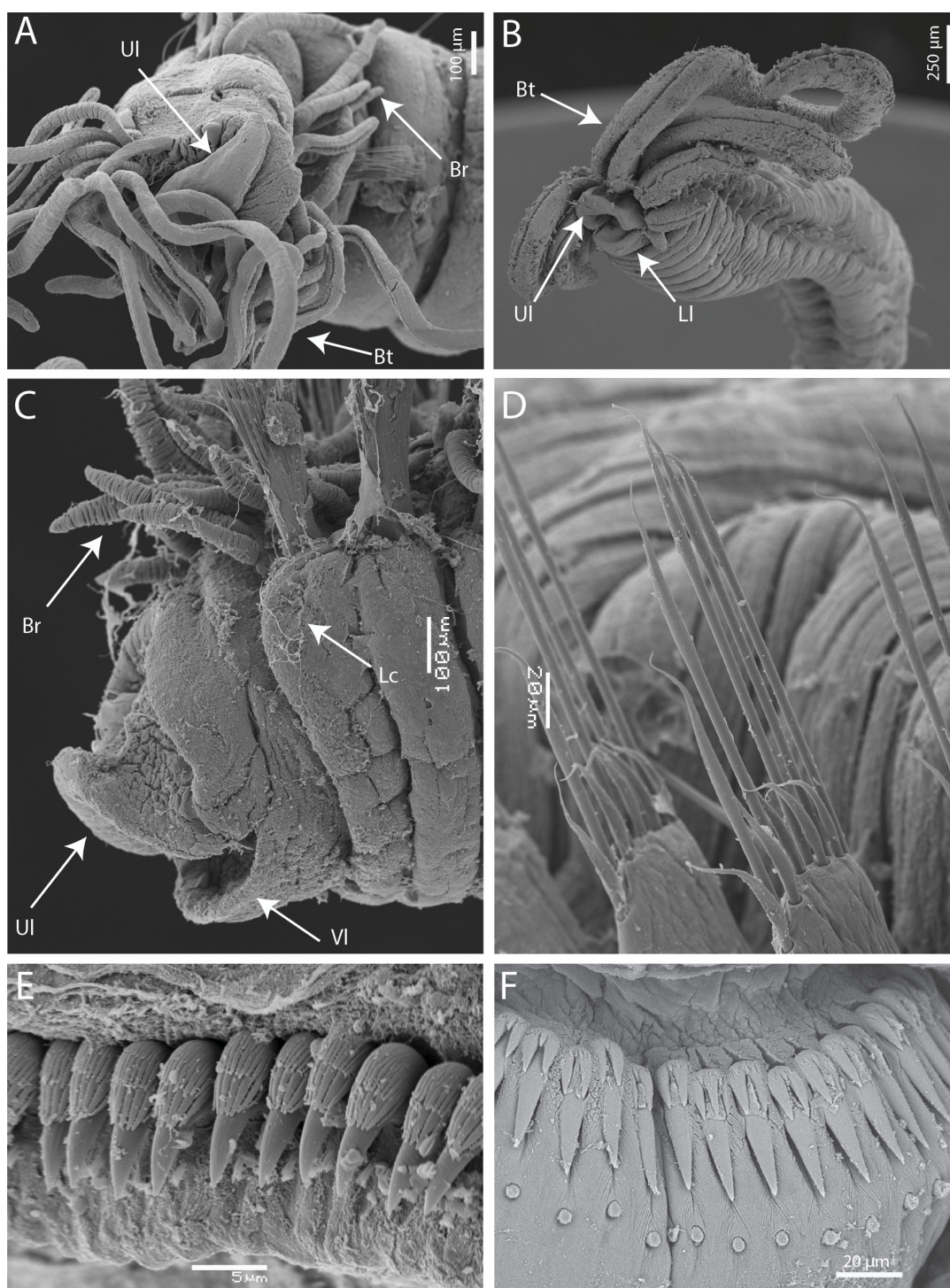


Fig. 4. Diversity of Telothelepodidae Nogueira, Fitzhugh & Hutchings, 2013 and Thelepodidae Hesse, 1917, SEM. **A.** *Parathelepus collaris* (Southern, 1914), anterior end, frontal view (AM W.53063). **B.** *Thelepus corsicanus* Lavesque, Londoño-Mesa, Daffe & Hutchings, 2020, anterior end, latero-frontal 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 abbranchiate; 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 types are 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

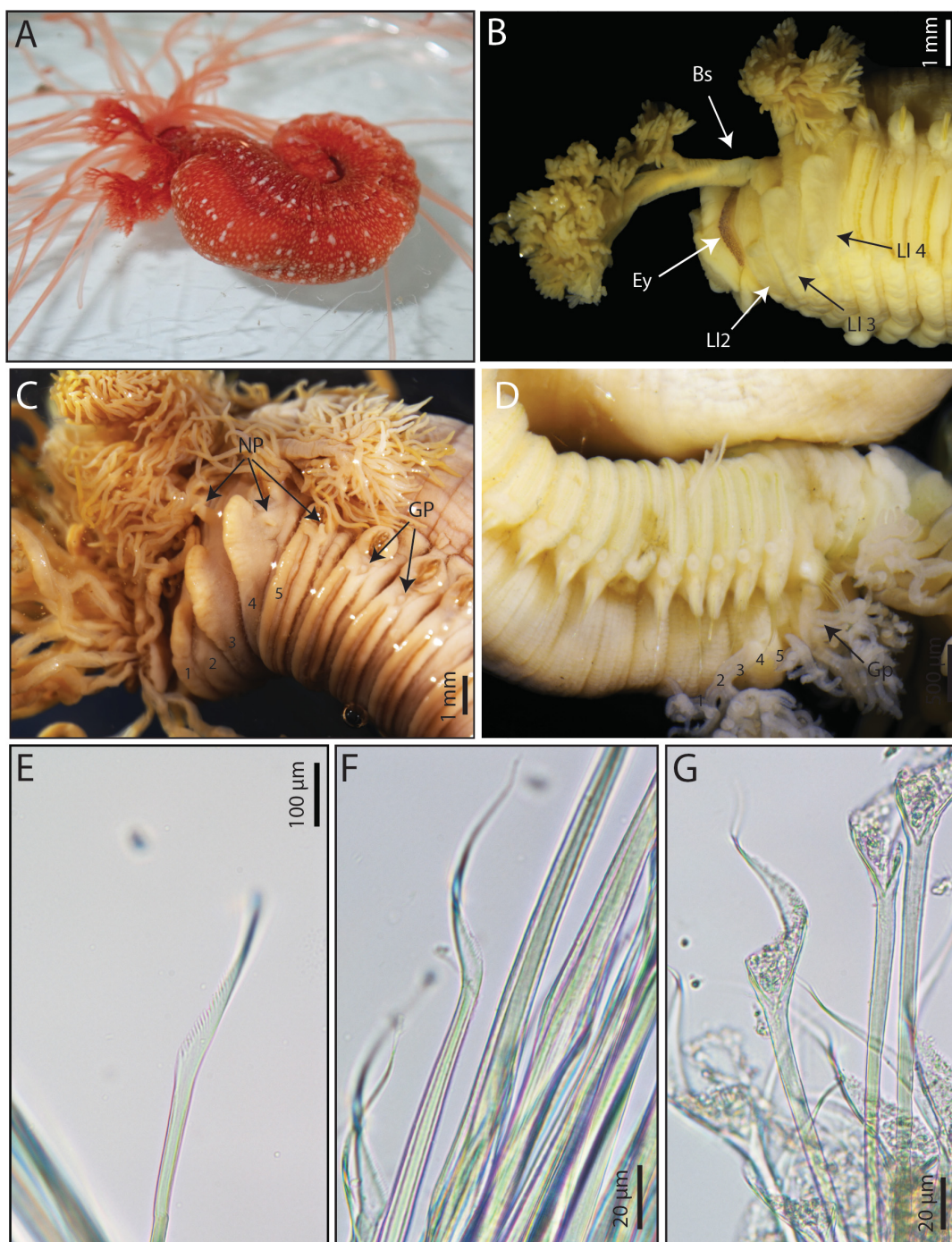


Fig. 5. Diversity of Terebellidae Johnston, 1846 (s.s.). **A.** *Eupolymnia lacazei* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, live specimen (paratype MNHN-IA-TYPE 2023). **B.** *Eupolymnia gili* Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (holotype MNHN-IA-TYPE 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.

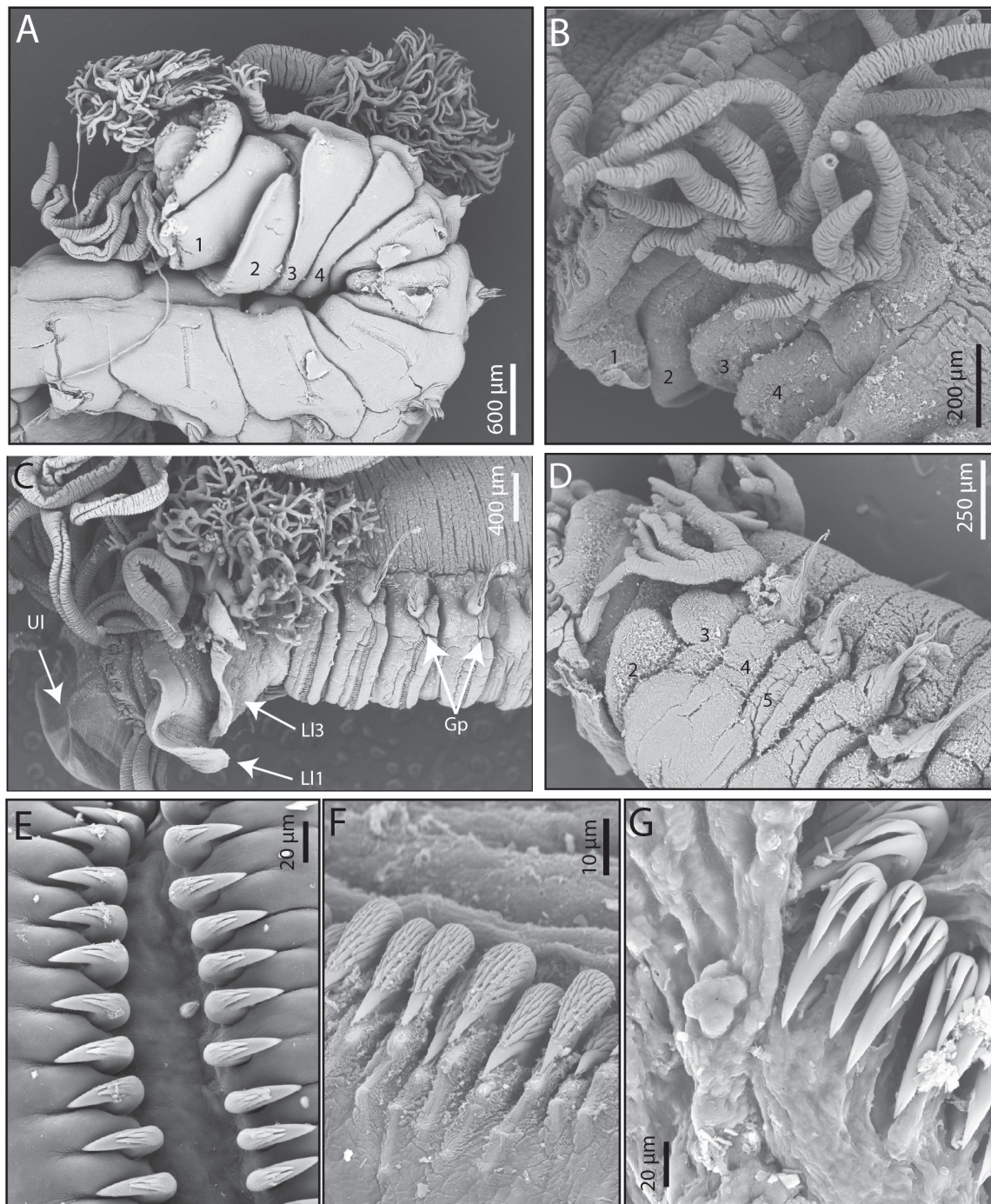


Fig. 6. Diversity of Terebellidae Johnston, 1846 (s.s.), SEM. **A.** *Pista sauriaui* Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (paratype MNHN-IA-TYPE 2036). **B.** *Paramphitrite dragovabeci* Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (paratype MNHN-IA-TYPE 2030). **C.** *Lanice kellyslateri* Lavesque, Daffé, Londoño-Mesa & Hutchings, 2021, anterior end, lateral view (paratype MNHN-IA-TYPE 2028). **D.** *Eupolymnia meissnerae* Lavesque, Daffé, 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 *Eupolyornia 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 rzhavskyi* 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	<i>Nicolea zostericola</i> (Ørsted, 1844)
– Notochaetae on 17–18 segments, branchiae with long stems	<i>Nicolea venustula</i> (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 (<i>Loimia</i>)
– Uncini avicular, with several transverse rows of secondary teeth	31 (<i>Lanice</i>)
30. Eyespots present, pygidium without distinct papillae, thoracic uncini with 4–5 rows of secondary teeth	<i>Loimia medusa</i> (Savigny, 1822)
– 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
31. Ventral shields fused on SGII–IV, notopodia short, neuropodia as low ridges, upper lip dorsally pigmented	<i>Lanice conchilega</i> (Pallas, 1766)
– Ventral shields well defined on SGIII–IV, notopodia well developed, neuropodia prominent, upper lip without pigmentation	<i>Lanice kellyslateri</i> Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
32. Notopodia on 15–16 segments, a single pair of short dichotomously branchiae	33 (<i>Axionice</i>)
– Notopodia on 17 segments	34
33. Notopodia on 15 segments	<i>Axionice flexuosa</i> (Grube, 1860)
– Notopodia on 16 segments	<i>Axionice maculata</i> (Dalyell, 1853)
34. Short-handled avicular uncini throughout	35
– Long-handled avicular uncini, at least on anterior neuropodia (i.e., SGV–VII)	40 (<i>Pista</i>)
35. A single pair of plumose branchiae	36 (<i>Pistella</i>)
– Three pairs of branching branchiae	37 (<i>Eupolymnia</i>)
36. Branchial filaments arranged in distinct tiers, ventral shields on SG II–XV, dorsal crest on SG III ..	<i>Pistella rovigensis</i> Mikac & Hutchings, 2017
– Branchial filaments arranged in spiral, ventral shields on SG VI–XX, dorsal crests on SG II–IV	<i>Pistella lornensis</i> (Pearson, 1969)
37. Branchiae with long stems	38
– Branchial stems short or absent	39
38. Abdominal neuropodia dorsally pointed, lateral lobes translucent	<i>Eupolymnia gili</i> Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
– Abdominal neuropodia rounded, lateral lobes not translucent	<i>Eupolymnia lacazei</i> 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 ...	<i>Eupolymnia nebulosa</i> (Montagu, 1819)
– First pair of branchiae with short stem, lateral lobes on SG III spherical, lateral lobes of SG II well-developed	<i>Eupolymnia meissnerae</i> Lavesque, Daffe, Londoño-Mesa & Hutchings, 2021
40. A single branchia inserted mid-dorsally on SG II	<i>Pista labrunae</i> 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
 - Lateral lobes present on SG II–III, well developed on SG III ***Pista bansei*** Saphronova, 1988* 45
45. Lateral lobes well developed on SG II, asymmetrical on SG III
 - Lateral lobes narrow on SG II, rectangular on SG III ***Pista colini*** Labruno, Lavesque, Bonifácio & Hutchings, 2019
 - ***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, Daffé, Londoño-Mesa & Hutchings, 2021
49. Lateral lobes on SG I small, on SG IV well developed, eyespots absent
 - Lateral lobes on SG I absent, on SG IV small, almost inconspicuous, eyespots present
 - ***Pista miosseci*** Lavesque, Daffé, 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 notochaetae 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 notochaetae 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 (capitulum), 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*

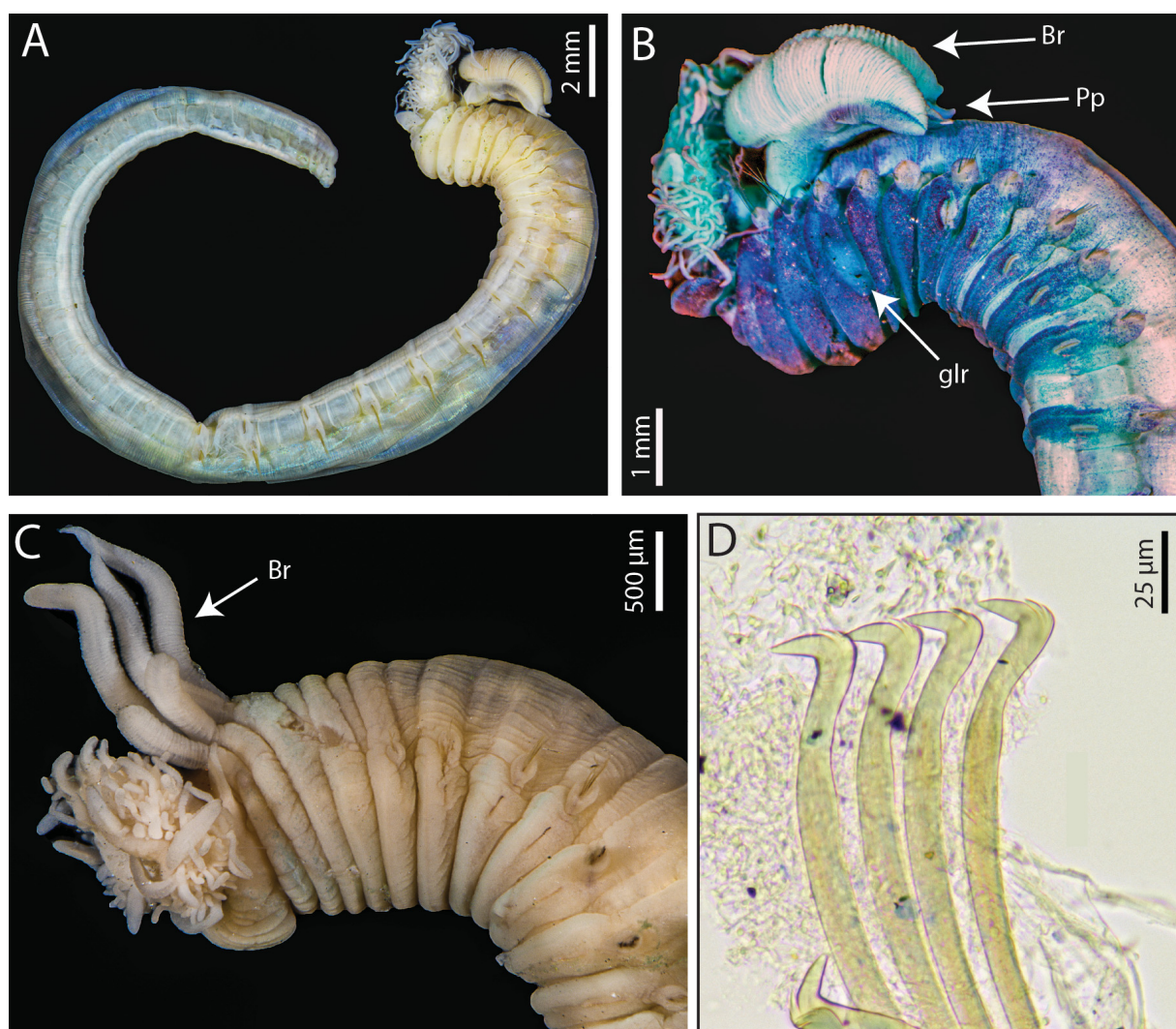


Fig. 7. Diversity of Trichobranchidae. **A.** *Terebellides lilasae* Lavesque, Hutchings, Daffe, Nygren & Londoño-Mesa, 2019, entire specimen, lateral view (MNHN-IA-TYPE 1879). **B.** *Terebellides lilasae*, anterior end, lateral view, methyl green staining (MNHN-IA-TYPE 1879). **C.** *Trichobranchus 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.

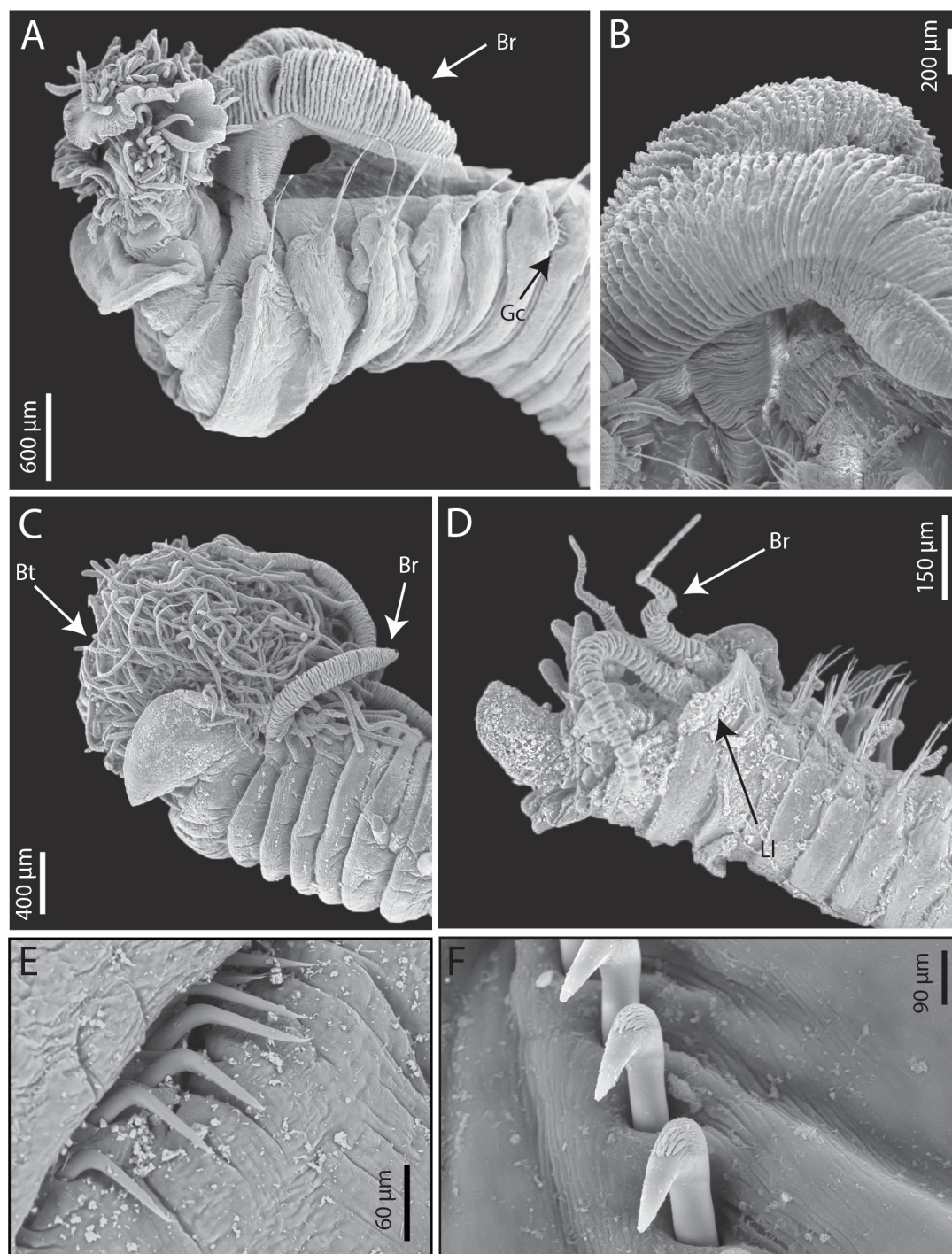


Fig. 8. Diversity of Trichobranchidae, SEM. **A.** *Terebellides gentili* Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019, anterior end, lateral view (MNHN-IA-TYPE 1873). **B.** *Terebellides lilasae* Lavesque, Hutchings, Daffé, Nygren & Londoño-Mesa, 2019, branchia, lateral view (MNHN-IA-TYPE 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. Geniculate acicular chaetae on CH5 (SG VII) and CH6 (SG VIII) *Terebellides bigeniculatus* Parapar, Moreira & Helgason, 2011
 - Geniculate 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 capitulum about 0.7 length of the main fang, capitulum 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 (capitulum of about same length as main fang, capitulum 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 capitulum length ratio 2(3)/1; capitulum with 2(3) large teeth, following ones much smaller)
 *Terebellides ronningae* Parapar, Capa, Nygren & Moreira, 2020
 – Thoracic uncini type 3 (main fang vs. capitulum length ratio 1/1; capitulum 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, Daffé, 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; Encarnação *et al.* 2019; Schäfer *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 (Encarnação *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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