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Review of genera within the *Axionice/Pista* complex (Polychaeta, Terebellidae), with discussion of the taxonomic definition of other Terebellidae with large lateral lobes

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The definitions of terebellid genera have caused considerable confusion. Some genera, such as Pista *Malmgren, 1866, are clearly not monophyletic and the need to revise them is widely accepted. A phylogenetic analysis of genus level morphological characters within the* Axionice/Pista *complex and other Terebellidae with large lateral lobes revealed two well defined groups; these differed in the arrangement of different forms of lateral lobes on segments 1–3, the shape of the branchiae, structure of the ventral pads and, if present, the origin of the manubrium on the uncini. One of the groups includes the type species of* Pista*; the other includes the type species of* Axionice *and almost all the other genera whose taxonomic status is discussed in this paper (*Betapista, Eupistella, Lanice, Loimia, Paraxionice*) which we propose to treat as its junior synonyms. Three other genera –* Lanicides, Lanicola *and* Scionella *– did not fall within these two groups; they are accepted as distinct. A complete list of species of* Axionice *and* Pista *is provided; 39 species currently included in* Pista *should be moved to* Axionice*, thus* Axionice *includes at least 94 species. Many authors' descriptions of the type species of* Pista *(*Amphitrite cristata *Müller, 1776) conflict with the original description.* Amphitrite cristata *s. str. has been described as a new species:* Scionella lornensis *Pearson, 1969 and the type species of a new genus:* Pistella *Hartmann-Schröder, 1996.* Scionella lornensis *is here considered a junior synonym of* Amphitrite cristata*. Redescriptions of the type species of* Axionice *and* Pista *are provided.*

Keywords: *Amphitrite*, *Axionice*, *Betapista*, *Eupistella*, *Lanice*, *Lanicides*, *Lanicola*, *Loimia*, *Paraxionice*, *Pista*, *Pistella*, *Scionella*, Terebellidae

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INTRODUCTION

Terebellids are tubicolous polychaetes found worldwide from tidal to abyssal depths and from the North Pole to the Antarctic. However, as usually happens with polychaetes, when the number of genera becomes close to 100, definitions of genera have become confusing. Since publication of the 'pink book' (Fauchald, 1977), there has been no published key to all genera or discussion of the taxonomic value of different characters at the genus level. Holthe (1986b) published the most recent review of the family and proposed six taxa at the 'Tribus' level (a level not usually used in Polychaeta). Several authors (Garraffoni & Lana, 2008, 2010; Nogueira *et al.*, 2013) have carried out phylogenetic analyses but they came to different conclusions, even at the family group level. At genus level, their results are not satisfactory (see below), probably because generic revision was not their goal. We have tried to address this question: to clarify the taxonomic definitions of genera. As the first step, we chose genera with large lateral lobes. The largest genus of this group, *Pista*, is also the largest genus of Terebellidae *sensu lato*. According to Gil *et al.* (2016a, b, 2017) the genus *Pista* *sensu* Jirkov *et al.* (2001), including *Axionice* and *Pistella*, includes 95 valid species and subspecies, i.e. more than 10% of the family. The total number of valid species with large lateral lobes included in *Betapista* Banse, 1980, *Eupistella* Chamberlin, 1919, *Lanice* Malmgren, 1866, *Lanicides* Hessle, 1917, *Lanicola* Hartmann-Schröder, 1986, *Loimia* Malmgren, 1866, *Paraxionice* Fauchald, 1972, and *Scionella* Moore, 1903 is 130, or 20% of the family (Read, 2011a, b; Read & Bellan, 2011a, b; Gil & Read, 2016a, b, 2017; Read & Bellan, 2016). The group has a worldwide distribution and many varying diagnoses have been published. The taxonomic definitions and diagnoses of genera in this group also vary between authors, to different extents.

The goal of our review is to answer two questions:

(1) How is the type species of the genus *Pista* (*Amphitrite cristata* Müller, 1776) defined?
(2) How many genera have large lateral lobes and what are their definitions?

Abbreviations

Morphology: S, segment; C, chaetiger; TC, thoracic chaetiger; TU, thoracic unciniger (segment with uncini).

Combinations of abbreviations and numbers define the segment (e.g. TU1 is the first thoracic unciniger).

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Collections: APEM, APEM Ltd., UK; BCPM, British Columbia Provincial Museum, Canada; HZMI, University of Hamburg; Zoological Institute und Zoological Museum, Germany; IORAN, P.P. Shirshov Institute of Oceanology, Russia; KGB, Department of Hydrobiology Moscow State University, Russia; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; NHM, Natural History Museum, UK; NMC, National Museums of Canada; USNM, United States National Museum, USA; ZMMU, Zoological Museum of Moscow State University, Russia.

MATERIALS AND METHODS

Our focus is on Terebellidae with large lateral lobes (also called lappets). Although small and large are, in a biological sense, rather vague terms, there is general consensus in applying them (or similar terms) to terebellid genera. For example, Fauchald (1977) specified 'large lateral lappets' as characterizing *Lanice* (p. 130) and *Pista* (p. 132), in contrast to 'small lateral lappets', applied to *Eupolymnia* Verrill, 1900 (p. 130). Similarly, the terms 'largest', 'large' and 'small' in the diagnosis of *Pista* and its species have been used by Hessle (1917, p. 153): 'Die vorderen Segmente sind mit oft sehr kraftigen Seitenlappen versehen', Fauvel (1927, p. 262): ‚Souvent des lobes latéraux très développés aux premiers segments', Uschakov (1955, p. 385): 'well-developed lobes' and many others (Monro, 1936; Hartman, 1966, 1969; Day, 1967; Hilbig, 2000).

Malmgren (1866) described five genera with large lateral lobes: *Axionice*, *Lanice*, *Loimia*, *Pista* and *Scione*. According to his key (p. 373), these genera differ in the number of branchiae and thoracic segments. However, neither of these characters can be currently accepted as a valid criterion for the separation of genera.

Hessle (1917) included *Axionice* and *Scione* in *Pista* and added 'lateral lobes on anterior segments' to Malmgren's characters: 'Die vorderen Segmente sind mit oft sehr kräftigen Seitenlappen versehen'; this was accepted by all authorities. He also used the structure of the nephridial system as a characteristic but few authors, with the exception of Smith (1992), have since included nephridial structure in their species descriptions. Smith (1992) showed that the nephridial system is much more complicated than Hessle (1917) had supposed and probably not suitable for generic diagnoses. In any case, much more information is necessary to make final decisions about the taxonomic value of the nephridial system.

Although Hessle (1917) included the presence of a manubrium in his description of *Pista* ('Die Hakenborsten im Vorderkorper sind langschäftig'), it is clear that he did not consider it to be strictly diagnostic. This is shown by his inclusion of two genera (*Axionice* and *Scione*) in *Pista* whose type species have uncini without manubria and his description of *Pista macrolobata*, which has uncini without manubria. Fauvel (1927), Day (1967), Hartmann-Schröder (1971) and Hilbig (2000) also included in *Pista* species with uncini both with and without manubria.

Other contemporary authors, however, treated *Pista* as characterized by the presence of long-handled uncini in TU1. For species with large lateral lobes on anterior segments and uncini in TU1 without manubria, they used other genera: *Axionice* (Caullery, 1915; Chamberlin, 1919; Monro, 1936; Hartman, 1969, 1971; Fauchald, 1972, 1977; Hartmann-Schröder, 1996; Holthe, 1986a), *Scione* (Benham, 1916; Caullery, 1944), *Pistella* (Londoño-Mesa, 2009), combinations of these genera: *Axionice* and *Scionella* Holthe (1986a, b), *Axionice* and *Pistella* (Hartmann-Schröder, 1996), or various other genera (Nogueira *et al.*, 2015).

Several other genera have been described as having large lateral lobes (numbers in parentheses are numbers of species and they were included in our analysis: *Betapista* Banse, 1980 (1) (Read, 2011a, b); *Eupista* McIntosh, 1885, replaced by *Eupistella* Chamberlin, 1919 (4) (Read & Bellan, 2011a, b); *Lanicides* Hessle, 1917 (10) (Gil & Read, 2016a, b); *Lanicola* Hartmann-Schröder, 1986 (7) (Gil & Read, 2016a, b); *Paraxionice* Fauchald, 1972 (1) (Gil & Read, 2017); *Scione* Malmgren, 1866, replaced by *Euscione* Chamberlin, 1919; and *Scionella* Moore, 1903 (2) (Read, 2011a, b). The status of some of them is complex and the need for revision has been recognized by many authors (Londoño-Mesa, 2009; Nogueira *et al.*, 2015). We have also included *Amphitrite lobocephala* Hsieh, 1994 as it obviously belongs to this group. Some other genera seem to have large lobes but their descriptions are unsatisfactory, so we have excluded them from our analysis: *Colymmatops* Peters, 1854, *Opisthopista* Caullery, 1944 and *Parascione* Caullery, 1944.

We excluded from our analysis several genera sometimes reported as having large lateral lobes because most authors did not describe them with large lateral lobes. These include *Eupolymnia*, as its type species (*Amphitrite nesidensis* Delle Chiaje, 1828) has much smaller lobes than the genera included here, according to the re-description by Holthe (1986a) and our observations (Jirkov *et al.*, 2001); Fauchald (1977) also used the term 'small lateral lappets' to separate *Eupolymnia* from *Lanice* in his key (the latter having 'large lateral lappets'). The same is true for *Longicarpus* Hutchings & Murray, 1984 ('lateral lobes poorly developed' – Hutchings & Murray, 1984, p. 97), *Lizardia* Nogueira, Hutchings & Carrerette, 2015 ('low ventral lobes' – Nogueira *et al.*, 2015, p. 527) and *Reteterebella* Hartman, 1963 ('lobes on anterior segments… low' – Nogueira *et al.*, 2015, p. 502).

Thus, the genera included in our analysis (*Axionice*, *Betapista*, *Eupistella*, *Lanice*, *Lanicides*, *Loimia*, *Paraxionice*, *Pista*, *Pistella* and *Scionella*) are more or less equivalent to *Lanicini* Holthe, 1986b plus *Pistini* Holthe, 1986b. We have tried to include all of the species listed for these genera in WoRMS (Read, 2011a, b; Read & Bellan, 2011a, b, 2016; Costello *et al.*, 2013; Gil & Read, 2016a, b, 2017; Gil *et al.*, 2016a, b, 2017) but some have not been described in enough detail for inclusion. Also, several species have been included in the analysis that have not yet been formally described or are included in other genera but definitely belong to the group under study. We have tried to illustrate as many species as possible but, unfortunately, have not seen all of the species in the group and specimens of the investigated species were sometimes in a condition too poor for reasonable photographs.

We excluded *Pista indica* Fauvel, 1940; *Scione abyssorum* Caullery, 1944; *Pista pectinata* Hutchings, 1977 and *Pista trina* Hutchings, 1977 from our analysis for the following reasons.

Pista indica, according to Fauvel (1953: 423), has 'the first four uncinigerous tori short, with a transverse row of big, long, brown hooks with smooth tips. On the two following tori, a single row of small avicular uncini; next, the succeeding thoracic and abdominal segments bear two alternating

Table 1. Character coding.

#	Species	Character											Source
		1	2	3	4	5	6	7	8	9	10	11	
1	*Terebella lapidaria*	0	3	0	0	0	0	0	1	1	0	0	NHM 1928.4.26.330-32 det. Fauvel
2	*Axionice alata*	1	2	3	0	2	0	0	0	2	0	0	BMNH 1933.7.10.275/6; BMNH 1933.7.10.279/80; BMNH 1933.7.10.277/8; Hilbig (2000)
3	*Axionice alonsae*	1	3	3	1	2	0	0	0	2	0	0	Santos *et al.* (2010)
4	*Axionice atypica*	1	2	3	0	2	0	0	0	2	0	?	Hessle (1917)
5	*Axionice breviuncinata*	1	2	3	1	2	0	0	0	2	0	?	HZMI holotype P-15278; paratypes P-15279; Hartmann-Schröder (1965)
6	*Axionice cetrata*	1	2	3	1	2	0	0	0	2	?	0	Londoño-Mesa (2009)
7	*Axionice chloroplokamia*	1	2	3	1	2	0	0	0	1	0	0	Nogueira *et al.* (2015)
8	*Axionice corrientis*	1	2	3	1	2	0	0	0	2	0	0	NHM 1985.12.1.348 holotype
9	*Axionice cretacea*	1	3	3	0	2	0	0	0	2	0	0	Grube (1870)
10	*Axionice elongata*	1	3	3	1	2	0	0	0	2	0	0	Hilbig (2000); BCPM 974-305-2
11	*Axionice fasciata*	1	2	3	1	2	0	0	0	2	0	?	Day (1967); Fauvel (1932)
12	*Axionice flexuosa*	1	1	3	0	2	0	0	0	1	0	0	90 samples (307 specimens) non type material KGB
13	*Axionice foliigera*	1	2	3	1	2	0	0	0	2	0	1	BMNH 1941.2.15.67-70, Day (1967)
14	*Axionice foliigeraformis*	1	3	3	1	2	0	0	0	2	0	?	Syntypes ZIN 32508, 32509, 44338; Annenkova (1937)
15	*Axionice gibbauncinata*	1	2	3	0	2	0	0	0	2	0	?	Saphronova (1984)
16	*Pista godfroyi*	1	1	3	0	1	0	0	0	1	0	?	NHM 1928.2.29
17	*Axionice harrissoni*	1	1	3	0	2	0	0	0	1	0	?	Benham (1916)
18	*Axionice hataam*	1	2	3	1	2	0	0	0	2	0	0	Londoño-Mesa (2012)
19	*Axionice herpini*	1	2	3	0	2	0	0	0	2	0	1	NHM 1933.7.10.285; Fauvel (1953)
20	*Axionice incarrientis*	1	2	3	1	2	0	0	0	2	0	0	Holotype ZIN 32512
21	*Axionice kristiani*	1	2	3	1	2	0	0	0	2	0	0	Nogueira *et al.* (2015)
22	*Axionice lizae*	1	2	3	1	2	0	0	0	2	0	0	Londoño-Mesa (2012)
23	*Axionice maculata*	1	1	3	0	2	0	0	0	1	0	0	Non type material 113 samples (623 specimens)
24	*Axionice macrolobata*	1	2	3	0	2	0	0	0	1	0	0	Hessle (1917); Fauvel (1932; Day (1967)
25	*Axionice mirabilis*	1	1	3	0	2	0	0	0	2	0	1	Holotype NHM 2015.325
26	*Axionice moorei*	1	3	3	1	2	0	0	0	2	0	0	Hilbig (2000)
27	*Axionice pacifica*	1	3	3	1	2	0	0	0	2	0	?	Berkeley & Berkeley (1942)
28	*Axionice palmata*	1	2	3	1	2	1	0	0	2	0	0	Londoño-Mesa & Carrera-Parra (2005); Londoño-Mesa (2009); USNM 12319 det. Verrill (3 spec), USNM 496 det. Pettibone
29	*Axionice pachybranchiata*	1	2	3	0	2	0	0	0	1	0	?	Fauvel (1932)
30	*Axionice parapacifica*	1	3	3	1	2	0	0	0	2	0	?	Holotype HZMI P-15436; Hartmann-Schröder (1965)
31	*Axionice pegma*	1	2	3	1	2	0	0	0	2	0	0	Paratype NHM 1995:1656
32	*Axionice percyi*	1	2	3	1	2	0	0	0	2	0	0	Hiblig (2000); Leontovich & Jirkov (2011)
33	*Axionice qolora*	1	1	3	0	2	0	0	0	2	0	0	Holotype NHM 1961.16.85, paratype NHM 1961.16.86
34	*Axionice quadrilobata*	1	2	3	1	2	0	0	0	2	0	0	Day (1967); USNM 51249(1) Acc No 289362 det. JH Day
35	*Axionice robustiseta*	1	2	3	0	2	0	0	0	2	0	?	NHM 1937.9.2.513
36	*Axionice sinusa*	1	2	3	0	2	0	0	0	2	0	0	Paratype NHM 1986.9; Hutchings & Glasby (1988)
37	*Axionice spinifera*	1	1	3	1	2	0	0	0	1	0	?	Ehlers (1908); Hartman (1966)
38	*Axionice symbranchiata*	1	2	3	1	2	0	0	0	2	0	0	NHM 1928 2/29/463; APEM 55970, 55975; Ehlers (1913)
39	*Axionice trunca*	1	2	3	1	2	0	0	0	2	0	?	NHM 1986.256-259 det. Hutchings (non type material)
40	*Axionice turawa*	1	2	3	0	2	0	0	0	2	0	0	NHM 1986.93-95; Hutchings & Glasby (1988)
41	*Axionice* sp. A Kritzler, 1984	1	2	3	0	2	0	0	0	2	0	0	USNM 90526; Kritzler (1984)
42	*Axionice violacea*	1	2	3	1	2	0	0	0	2	0	?	Hartmann-Schröder (1984); Hutchings & Glasby (1988)
43	*Loimia tuberculata*	1	3	3	0	2	0	0	0	0	1	0	Nogueira *et al.* (2015)
44	*Loimia keablei*	1	3	3	0	2	0	0	0	0	1	0	Nogueira *et al.* (2015)
45	*Loimia juani*	1	3	3	0	2	0	0	0	0	1	0	Nogueira *et al.* (2015)
46	*Loimia pseudotriloba*	1	3	3	0	2	0	0	0	0	1	0	Nogueira *et al.* (2015)
47	*Loimia medusa*	1	3	2	0	3	0	0	0	0	1	0	APEM 8184; APEM 55109
48	*Lanice conchilega*	1	3	3	0	2	0	0	0	2	1	0	Numerous specimens from UK waters to Mediterranean (APEM, MNCN, KGB, ZMMU)
49	*Lanice abyssalis*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
50	*Lanice amphelisso*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
51	*Lanice auricola*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
52	*Lanice bidevo*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
53	*Lanice fauveli*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
54	*Lanice marionensis*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
55	*Lanice sinuta*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
56	*Lanice wallebneki*	1	3	3	0	2	0	0	0	1	1	?	Hutchings (2007)
57	*Lanice viridis*	1	3	3	0	2	0	0	0	1	1	0	Nogueira *et al.* (2015)

Continued

Table 1. Continued

		Character											
#	Species	1	2	3	4	5	6	7	8	9	10	11	Source
58	*Lanice lobocephala*	1	3	3	0	2	0	0	0	1	1	?	Hsieh (1994)
59	*Paxionice artifex*	1	1	2	0	2	0	0	0	1	?	?	Fauchald (1972)
60	*Betapista dekkerae*	1	2	3	0	2	0	0	0	2	?	?	Banse (1980)
61	*Eupistella dibranchiata*	1	1	3	0	2	0	0	0	2	0	2	Paratype NHM 1928.4.26.15; Fauvel (1909)
62	*Pista anneae*	2	2	1	1	3	0	0	0	2	0	2	Nogueira *et al.* (2015)
63	*Pista anthela*	2	1	2	3	1	0	0	0	1	0	?	Hutchings & Glasby (1990)
64	*Pista australis*	2	2	1	2	1	0	0	0	2	0	1	Paratypes NHM 1986.74-91
65	*Pista bansei*	2	1	1	2	1	0	0	0	2	0	2	Holotype 1/47667; all paratypes and numerous non type specimens
66	*Pista brevibranchia*	2	2	0	1	2	0	0	0	2	0	?	Caullery (1915); Day (1967)
67	*Pista cristata*	2	1	0	2	1	0	0	0	1	0	2	Topotypes Slettholmen (10 ex.); Ronsfjord (4 ex.), Kattegat Frederikshavn (1 ex.). Holotype of *Scionella lornensis* NHM 1968.15.
68	*Pista curtiuncata*	2	2	2	2	2	0	0	0	1	0	?	Holotype HZMI P-16500; Hartmann-Schröder (1981; Hutchings & Glasby (1988)
69	*Pista dibranchis*	2	1	1	3	2	0	0	0	1	0	2	NHM 1970:79
70	*Pista disjuncta*	2	2	0	1	2	0	0	0	2	0	2	USNM 16892; Moore (1923), Hartman (1969)
71	*Pista estevanica*	2	1	1	2	2	0	0	0	1	0	?	Saphronova (1991)
72	*Pista franciscana*	2	1	1	2	1	0	0	0	1	0	2	Nogueira *et al.* (2015)
73	*Pista* sp. A Saphronova	2	2	0	2	1	0	0	0	2	0	2	Saphronova's material. KGB
74	*Pista grubei*	2	1	1	1	2	0	0	0	2	0	1	Paratypes HZMI |V-1703; 1716; 1727; NHM 1953.3.1.506/504; Augener (1918)
75	*Pista gwoyarrma*	2	2	0	2	2	0	0	0	2	0	?	Hutchings (1997)
76	*Pista kimberliensis*	2	2	1	2	1	0	0	0	2	0	?	Hutchings & Glasby (1990)
77	*Pista mediterranea*	2	2	1	2	2	0	0	0	2	0	1	de Gaillande (1970)
78	*Pista microlobata*	2	2	0	1	2	0	0	0	2	?	?	Hessle, 1917; Imajima & Hartman,1964
79	*Pista paracristata*	2	2	0	1	2	0	0	0	2	0	2	Paratypes IORAN R/V Vitjaz 3577; NHM 186-165-167
80	*Pista papillosa*	2	1	1	1	1	0	0	0	1	0	2	Londoño-Mesa (2009)
81	*Pista patriciae*	2	2	1	2	2	0	0	0	2	0	?	Holotype HZMI P-18946, Hartmann-Schröder & Rosenfeld (1989)
82	*Pista typha*	2	2	0	2	2	0	0	0	2	0	1	Fauvel (1932); Hutchings & Glasby (1988), NHM 1986.154-157
83	*Pista typha aequibranchia*	2	2	0	2	2	0	0	0	2	0	?	Caullery (1944)
84	*Pista unibranchia*	2	1	1	2	2	0	0	0	2	0	2	Holotype NHM 1963:1:153; paratypes NHM 1963.1.154/7; MNCN 1782 1790
85	*Pista torquata*	2	2	0	1	2	0	0	0	2	0	?	Hutchings (2007)
86	*Pista wui*	2	2	1	2	2	0	0	0	2	0	2	Two paratypes NMCA 1986-0057
87	*Pista vossae*	2	2	1	1	2	0	0	0	2	0	1	Londoño-Mesa (2012
88	*Pista* sp. B Kritzler, 1984	2	1	0	2	2	0	0	0	2	0	?	Kritzler (1984); USNM 90532
89	*Pista ortodoxa*	2	2	0	1	3	0	0	0	2	0	?	Safronova (1984)
90	*Pista abyssicola*	2	1	0	2	0	0	0	0	2	0	?	McIntosh (1885), holotype NHM 1985.12.1.346
91	*Pista pencillibranchiata*	3	1	1	1	3	0	0	0	2	0	0	Safronova (1984); our data
92	*Lanicides rubra*	1	2	2	1	2	0	0	1	2	0	0	Nogueira *et al.* (2015)
93	*Scionella vinogradovi*	1	1	2	2	2	1	1	1	1	0	0	Saphronova (1991), our data
94	*Lanicola lobata*	1	2	3	0	2	0	0	0	1	0	0	Hartmann-Schröder (1986); holotype

?, absence of data.

rows'. All other species included in the analysis have abdominal neuropodia with a single row of uncini. Hutchings (1977) also suggested that this species should be removed from *Pista*.

In our opinion, *Scione abyssorum*, *Pista pectinata* and *Pista trina* have arrangements of lobes and branchiae that are very different from other species in the *Axionice*/*Pista* group and also from the wider group of species with large lateral lobes. Their position must be clarified by examination of type material. We have had the opportunity to study only the paratype of *P. pectinata* (NHM 1975.139) but it is, unfortunately, so poorly preserved that even identification to family level is difficult.

We consider the generic position of these four species to be unclear. Generic assignment would require a full revision of the Terebellini and the validity of some genera is questionable. The vagueness of generic diagnoses has become a threat to our understanding of relationships within the group.

Whenever possible, type material has been investigated; non-type specimens were examined where necessary. Material was reviewed from the collections of APEM, BCPM, HZMI, IORAN, KGB, MNCN, NHM, NMC, USNM and ZMMU. We also used original descriptions and later re-descriptions of type material. A total of 93 species was included (or 85% of the total number of species in the group – 108); the remaining species are either so poorly

Table 2. Illustrated worms.

Species	Collection	Cat. no., station etc.	Place	Remark
Axionice alata	NHM	1333.7.10.275	Galapagos Balboa Coiba	
Axionice corrientis	NHM	1930.10.8.2882	East Falkland Island	
		1744		
Axionice cretacea	MNCN	5799	Andalucía, Spain: 36°50′N 2°28′W, 2–4 m	
		5801		
Axionice elongata	BCPM	974-305-2	49°08′N 123°47′W	
Axionice flexuosa	KGB	R/V Maslov 10.33	69°29′N 60°00′E, 14 m	
Axionice foliigera	NHM	1961.19.1227/1232	South coast of Africa	
Axionice herpini	NHM	133.7.10.285		
		1928.4.26.31	India, Gulf of Manaar	Syntype
Axionice incarrientis	IORAN	R/V Vitjaz 1790	57°46′N 152°33′E, 221 m	
Axionice maculata	KGB	R/V Alaid 30.8	74°30′N 32°30′E, 190 m	
Axionice mirabilis	NHM	2015.325	74°77′33S 176°39′00, 351 m	
Axionice parapacifica	HZMI	P-15436		Holotype
Axionice palmata	USNM	496		
	USNM	12319		
Axionice agassizi	KGB		Vostok Bay: 42°53′N 132°45′E, few metres	
Axionice sinusa	NHM	1986.92	38°21.60′S 145°13.67′E, 13 m	Paratype
Axionice sp. A	USNM	90526		
Axionice symbranchiata	APEM	55970		
		55975		
Axionice trunca	NHM	1986.256-259	14°32.2′S 144°53.4′E, 11 m	Det. Hutchings (non types)
		1986.259-260		
Eupistella diabranchiata	NHM	1928.4.26.15		Paratype
Lanice conchilega	ZMMU		Naples	
Loimia medusa	APEM	8184		
		55109		
Lanicola lobata	HZMI	P-18630	Wallaroo, Australia, 1, 5 m	Holotype
Pista australis	NHM	1986.74-91	Channel, Merimbula, NSW, Australia	Paratype
Pista bansei	KGB	R/V Sevastopol 1086		Paratype
Pista cristata	KGB		Slettholmen, Ronsfjord: 58°06.30′N 8°06′E	Topotypes
				Topotypes
Pista curtiuncata	HZMI	P-16500		
Pista grubei	NHM	1953.3.1.506/504	Gold coast, West Africa	
Pista mediterranea	KGB	50/22		
	MNCN	5801	Andalucía, Spain: 36°50′N 2°28′W, 2–4 m	
Pista paracristata	IORAN	R/V Vitjaz 3577		Paratype
Pista penicillibranchiata	NHM	1986.186-188	R/V Vitjaz 618: 57°03.5′N, 168°30.5′E, 3875 m	
	IORAN			
Pista sp. B.	USNM	90532-3		
Pista typha	NHM	1986.154-157	16°23.2′S 145°34.0′E	
Pista unibranchia	MNCN	1790	Between Cabo de San Antonio and Puerto de Valencia	
		1782		
Pista wui	NMC	1986-0057		Paratypes
Scionella vinogradovi	IORAN	R/V Vitjaz 602		

described that, without examination of type material too few characters can be determined, or seem to belong to other genera (Table 1). Of the included species, we had no information about the arrangement of uncini in double rows for three species and we had information on ventral pads for 55 species only, so we needed three separate calculations. As an out-group, we selected the type species of the type genus of Terebellinae – *Terebella lapidaria* Linnaeus, 1767. Intraspecific variation was reviewed for several species, using the IORAN, KGB and MNCN collections (Table 3).

Specimens were studied using several different stereo- and compound microscopes (available in places of location of material). Photographs were taken under microscopes using different digital cameras. The specimens were held in position with entomological needles and photographed in a Petri dish. In order to increase contrast, specimens were stained with methylene blue (in water solution), which gives the best results, or sometimes methyl blue. Unless otherwise stated, neuropodia were removed from TU1, mounted on slides with 3C Polyvinylactophenol, examined and photographed, using compound microscopes. Images were produced and edited manually with CorelDRAW! software. For detailed information on the illustrated specimens, see Table 2.

Characters and character coding (Table 1)

1. **Branchial type**: 0. cirriform; 1. arborescent; 2. pompom-like (=bottle-brush, club-shaped, plumose, branching filaments in a spiral arrangement); 3. all branching filaments at the top.

Table 3. Material for investigation of individual variation.

Species	Number of specimens	Number of samples	Region	Collections
Axionice agassizi	41	8	See Leontovich & Jirkov (2011)	KGB, ZIN, NHM
A. cretacea	24	15	Iberian waters	MNCN
A. flexuosa	307	90	See Jirkov *et al.* (2001)	KGB
A. incarrientis	54	28	See Leontovich & Jirkov (2011)	KGB, ZIN, NHM
A. maculata	~500	>100	See Jirkov *et al.* (2001)	KGB
A. mirabilis	~100	10	See Jirkov *et al.* (2001)	KGB, IORAN
Lanice conchilega	>300	>150	See Jirkov *et al.* (2001) + Iberian and UK waters	KGB, ZMMU, APEM, NHM, MNCN
Pista cristata	39	16	European waters	KGB, MNCN, NHM
P. bansei	>500	~200	See Jirkov *et al.* (2001)	KGB, ZMMU, ZIN, IORAN
P. mediterranea	>250	>100	See Jirkov *et al.* (2001) + Iberian and UK waters	KGB, NHM, APEM, MNCN
P. unibranchia	15	9	Mediterranean	MNCN
Total	>2000	>700		

2. **Branchial number**: 1. one pair (including examples where only a single branchia is typically present); 2. two pairs; 3. three pairs.
3. **Lateral lobes of S1**: 0. absent; 1. small; 2. large, but not the largest; 3. the largest (Figures 2–5).
4. **Lateral lobes of S2**: 0. absent; 1. small; 2. large; 3. the largest.
5. **Lateral lobes of S3**: 0. absent; 1. small; 2. large; 3. the largest.
6. **Dorsal crest**: 0. absent; 1. present (Figure 5).
7. **Festoon-like arrangement of lobes of the first four segments** (Figure 5): 0. absent; 1. present.
8. **Notochaetae**: 0. smooth; 1. serrated.
9. **Shape of uncini** (Figures 6 & 7): 0. pectinate (=monopectinate sensu Holthe, 1986b), first type sensu Leontovich & Jirkov, 2011; 1. avicular (=breviavicular sensu Holthe, 1986b); second type sensu Leontovich & Jirkov, 2011; 2. with manubrium at least in S5 (=opisthavicular sensu Holthe, 1986b); this type is a derivative of avicular but, as shown below, in at least two different ways.
10. **Uncini in double rows**: 0. face-to face; 1. back-to-back (Figure 8). Although we demonstrate below that this subdivision is not absolute and that there are transitional states, current literature data do not allow us to propose another coding system.
11. **Ventral pads** (Figures 9 & 10): 0. colouration uniform; 1. posterior margin and lateral sides of pad whitish and granulated; 2. posterior part white. This character may be difficult to see in poorly preserved specimens.

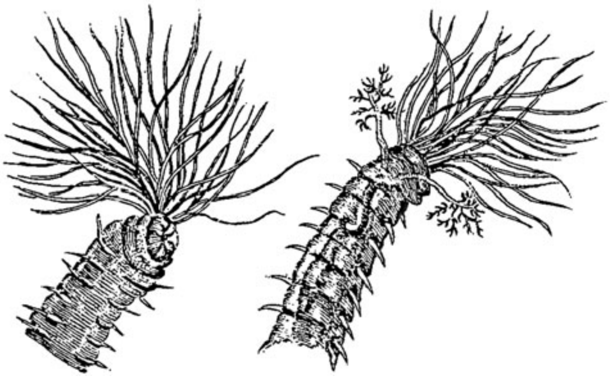

Fig. 1. Müller (1780) original drawings of *Amphitrite cristata*.

We compared the size of the lateral lobes (characters 3–5) between those segments with lateral lobes (S1–S3).

Observations of variation between individuals of over 2000 specimens of 12 species (*Axionice agassizi*, *A. cretacea*, *A. elongata*, *A. flexuosa*, *A. incarrientis*, *A. maculata*, *A. mirabilis*, *Lanice conchilega*, *Pista cristata*, *P. bansei*, *P. mediterranea*, *P. unibranchia*) (Table 3) showed that the relative size of the lobes does not correlate with the size of the worm.

The number of characters that we used is lower than used by others (Garraffoni & Lana, 2008; Nogueira *et al.*, 2013). We do not think that increasing the number of characters coded by itself increases the precision of the results unless all characters can be assumed to have equal value. For example, although Garraffoni & Lana (2008) used 81 characters, their results were either already known and long accepted (such as their separation of Terebellinae and Trichobranchinae), or confusing (Polycirrinae was included in Thelepinae). Nogueira *et al.* (2013) used 118 characters and got reasonable results at the subfamily level; in particular, we agree that Telothelepodidae is a quite separate taxon (not higher than subfamily in our opinion). However, use of over 100 characters did not prevent them from making some serious mistakes; for example: (1) *Pista cristata* (actually *P. mediterranea*) is shown far from *Pistella lornensis* (actually *P. cristata*) despite these species being members of the same genus and very close to *Scionella japonica*, although they are very different in appearance (compare Figures 4A & 5C–E, G); (2) a similar error was made in the case of *Amphitrite cirrata* and *A. affinis*, which were shown far away from each other, despite being members of the same genus. In our opinion, the reason for these anomalous results is in the different values of the characters used. Some characters provide taxonomic information, while others instead produce noise, which prevents meaningful results from being obtained. The only way to avoid noise in an analysis is to use only characters for which the taxonomic information content has been shown by practice to be diagnostic.

Also, we have avoided taxonomic characters that are used only for the separation of species, not genera. These include the number of TC, presence/absence of eyespots, lateral

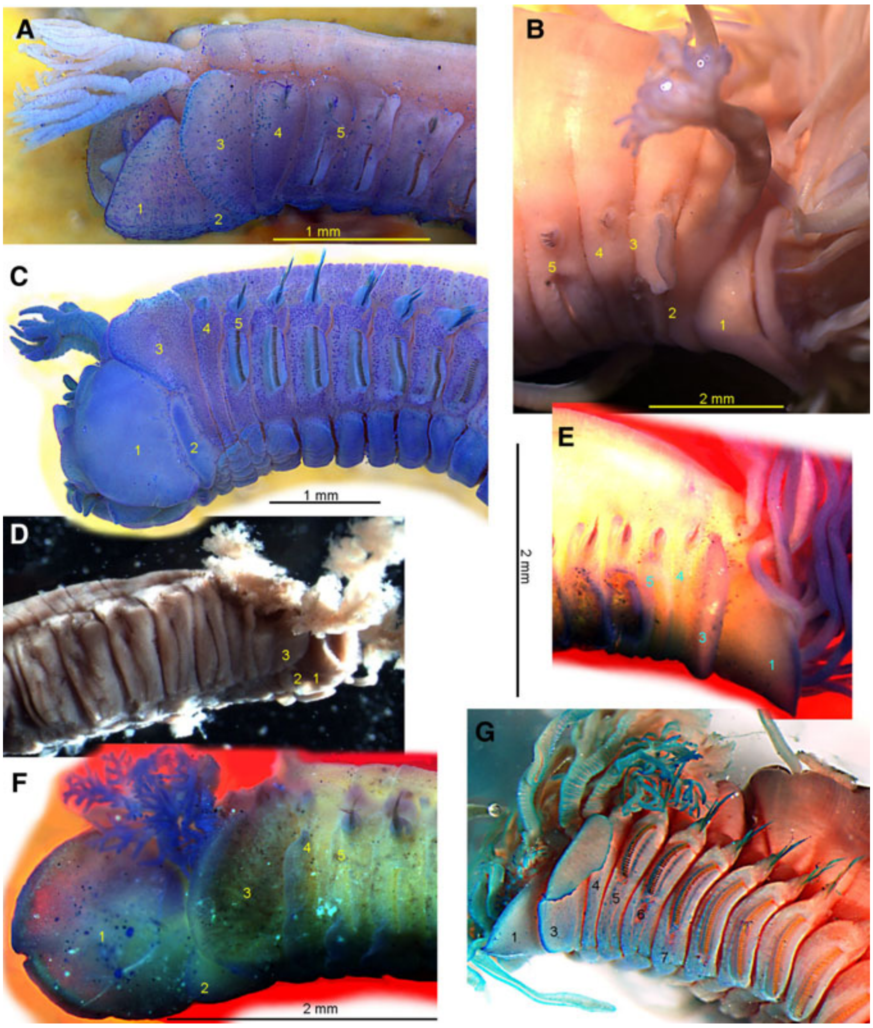

Fig. 2. Lateral lobes of some species of *Axionice* group. (A) *A. flexuosa* KGB R/V Maslov 10.33; (B) *A. mirabilis* NHM 2015.325; (C) *A. maculata* KGB R/V Alaid 30.8; (D) *A. parapacifica* HZMI holotype; (E) *A. herpini* NHM 133.7.10.285; (F) *A. trunca* NHM 1986_259-260; (G) *A. cretacea* MNCN 5799. Here and below numbers refer to segments. Detailed information on pictured specimens see Table 2.

lobes on S4 and later segments, number of segments with long-handled uncini and species-specific structures, such as dorsal lobes and crests. Ventral lobes are also excluded from our analysis, as they are very different in closely related species, such that the character is suitable for the separation of species, but not genera.

We used Neighbour-Joining multivariate cluster analysis (Saitou & Nei, 1987), with Euclidean distance as a measure. Calculations were carried out using Past3 (Hammer, 2015). As details of the structure of ventral pads are usually absent from descriptions, we needed separate calculations for characters 1–9 (Figure 11), characters 1–10 (Figure 12) and all characters (Figure 13).

HOW IS THE TYPE SPECIES OF THE GENUS *PISTA* DEFINED?

The type species of *Pista* by monotypy is *Amphitrite cristata* Müller, 1776. The type material is 'probably lost or never designated' (Holthe, 1986a: 112). The first stage in the definition of *Amphitrite cristata* Müller, 1776 (p. 216) is to review the original description; however, it is too short to adequately define the species: 'corniculis ramosis binis' (two arborescent horns). On the same page, Müller described three other Terebellidae: *Amphitrite cirrata* ('cincinnis utrinque tribus', three curls on both sides – an obvious reference to the branchiae), *A. cornuta* ('corniculis simplicibus horizontalibus', horns simple horizontal) and *A. pennacea* ('penicillis frontis quatuor; intermediis majoribus', four anterior brushes, intermediate origins). It becomes clear through comparison of these four 'descriptions', that 'horns' are branchiae and thus *Amphitrite cristata* has only one pair of branchiae. In 1779 (p. 87), Müller gave a much more complete description but did not describe the uncini and gave no figures, despite directly stating that he had. Although the figures eventually published in 1780 (Müller, 1780) are not very informative, it is clear that only one pair of branchiae is depicted (Figure 1). The figured branchiae appear to be arborescent but, considering that late 18th century figures were often inadequate, we do not consider this to be important. Also: (1) other species with a single pair of arborescent branchiae found in Norway have either 16 TC (*Axionice maculata*) or 15 TC (*Axionice flexuosa*), whilst the original description clearly states 'Segmenta

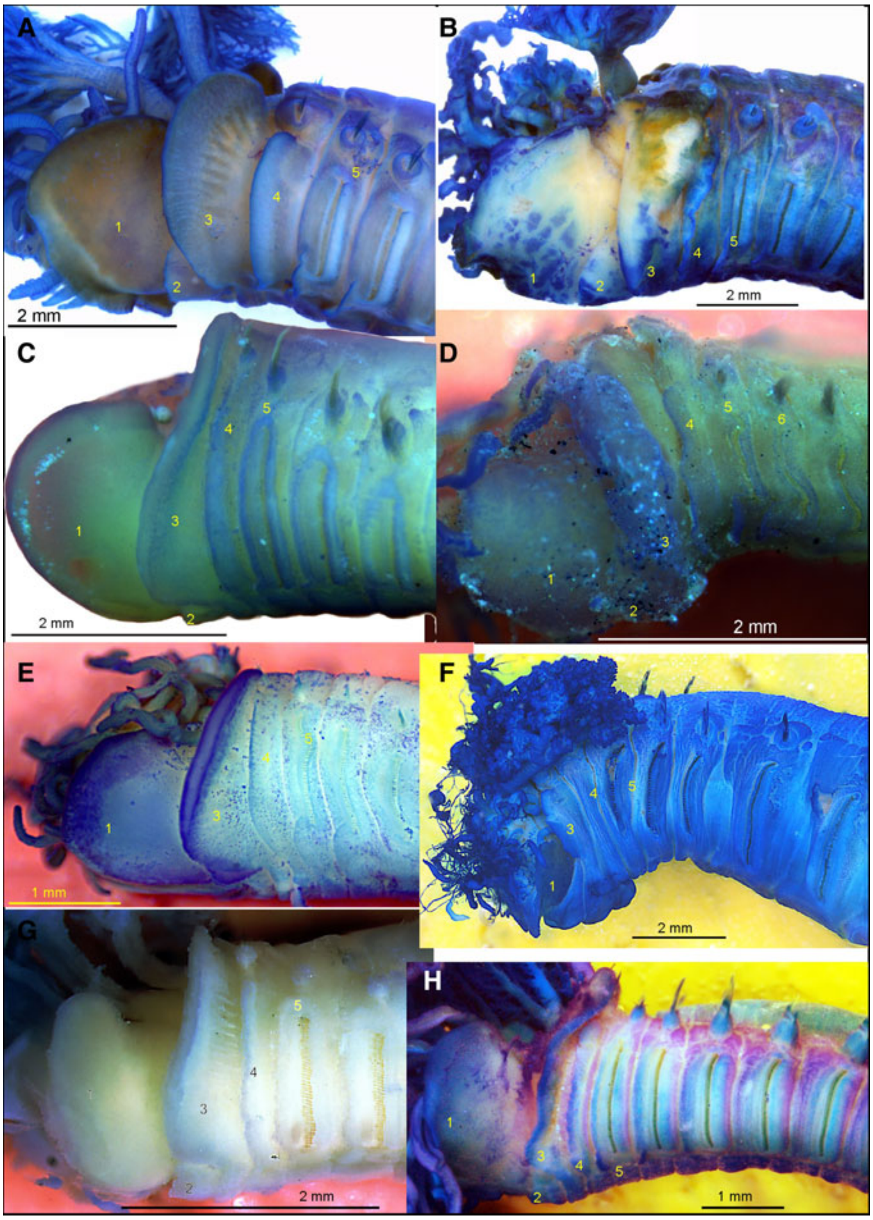

Fig. 3. Lateral lobes of some species of *Axionice*. (A) *A. agassizi* KGB; (B) *A. incarrientis* IO RAN R/V Vitjaz 1790; (C) *A. alata* NHM 1333.7.10.275; (D) *A. sinusa* NHM paratype; (E) *A. symbranchiata* APEM 55975; (F) *A. elongata* BCPM 974-305-2; (G) *A. corrientis* NHM 1930.10.8.2882; (H) *A. palmata* USNM 12319.

septendecim anteriora' (17 anterior thoracic segments); (2) clear lobes are shown on the branchiferous segment and no lobes on S1, whilst both other species with a single pair of branchiae have large lobes on S1 and small to absent lobes in S2. The first details of the uncini come from Malmgren's re-description: 'uncini in sex segmentis anticis uncinigeris processu inferiori elongato'. However, almost half of a century ago, Banse (1980) showed that Malmgren had two species in his hands: one with two pairs of branchiae and TU1 with long-handled uncini and another with a single pair of branchiae and TU1 without a manubrium on the uncini. According to Müller (1779), *A. cristata* was collected in Christianfjord (58°06′N 8°00′E). Since then, studies of European Terebellidae have described five morphologically different species with pompom-like branchiae from the region between the Barents and Mediterranean Seas (Hartmann-Schröder, 1971, 1996; Holthe, 1986a; Jirkov *et al*., 2001; Jirkov & Leontovich, 2013; Londoño-Mesa *et al*., 2016): *Pista bansei* Saphronova, 1988; *Pista mediterranea* de Gaillande, 1970; *Pista unibranchia* Day, 1963; *Pista wui* Saphronova, 1988; and *Pistella lornensis* (Pearson, 1969). As no other species have been discovered in the area for two and a half centuries, one of them is almost certainly a junior synonym of *A. cristata*; but which one?

Pista unibranchia has only a single branchia (not a pair!). Its range does not include the North Sea (much more southern), so it cannot be Müller's species.

Pista bansei has one pair of branchiae, but it inhabits greater depths than the source of Müller's material, so we consider it unlikely to be his species.

Pista mediterranea has a range that includes southern Norway but it has two pairs of branchiae. As it has long-handled uncini in TU1, we consider this to be the species described as *Pista cristata* by Malmgren and currently accepted

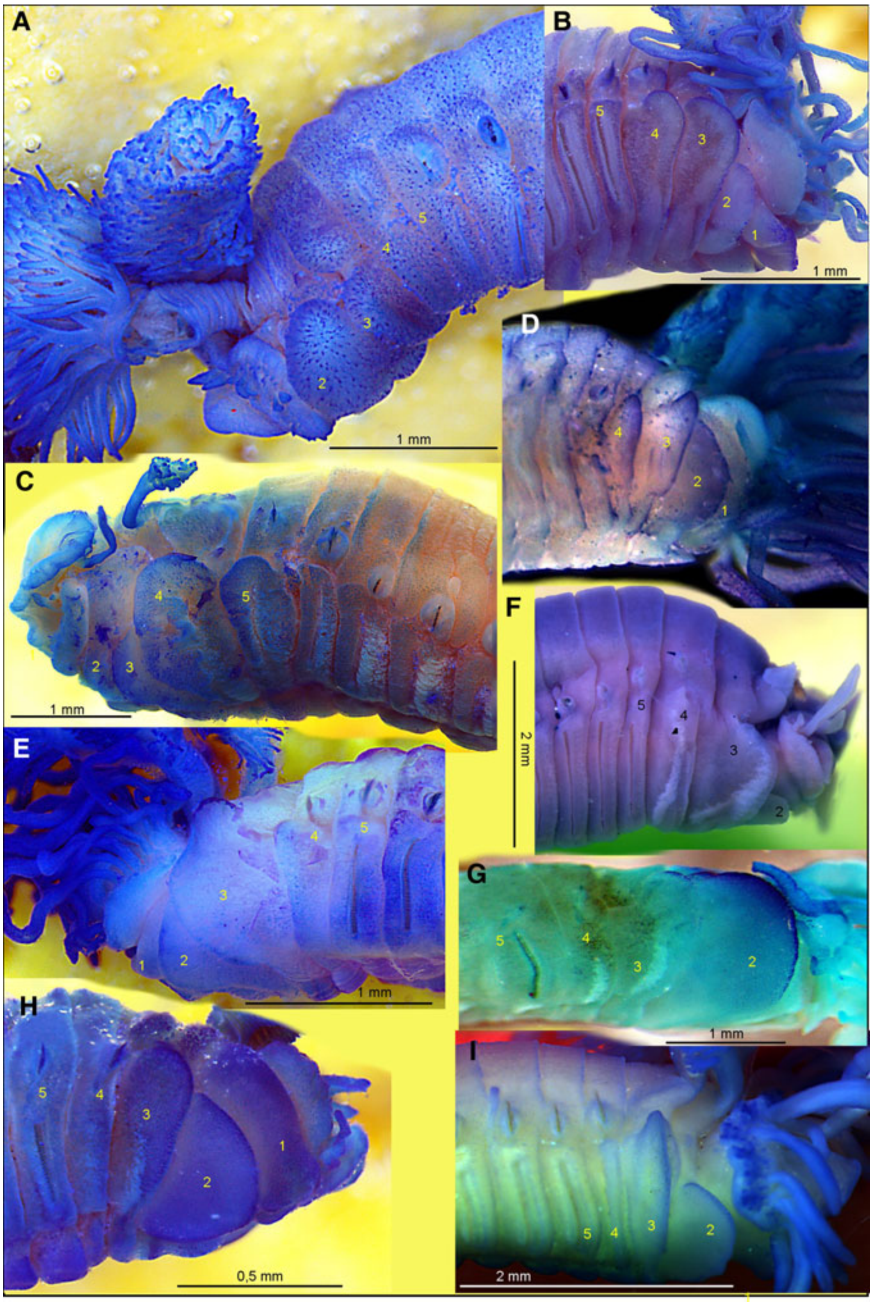

Fig. 4. Lateral lobes of some *Pista* species. (A) *P. cristata* KGB Slettholmen; (B) *P. wui* NMC 1986-0057; (C) *P. paracristata* IORAN R/V Vitjaz 3577; (D) *P. curtiuncata* HZMI; (E) *P. mediterranea* KGB 50/22; (F) *P. grubei* NHM 1953.3.1.506/504; (G) *P.unibranchia* MNCN 1790; (H) *P. bansei* KGB R/V Sevastopol 1086; (I) *P. typha* NHM 1986.154-157.

as such by most authors despite its obvious differences from the original description. It is interesting that *Pista cristata* sensu Malmgren has probably also been described by Müller, as *A. pennacea*. Hartman (1959) incorrectly gave the author of *A. pennacea* as Bosc (1802) and treated it as a *nomen nudum*; Holthe (1986b) made the same mistake. According to the glossary of the International Code of Zoological Nomenclature, *nomen nudum* refers to 'a name that, if published before 1931, fails to conform to Article 12'; Article 12.1 says: 'To be available, every new name published before 1931 must satisfy the provisions of Article 11 and must be accompanied by a description or a definition of the taxon that it denotes'. Müller's (1776) description of *A. pennacea* meets both conditions but, as it was not described satisfactorily and is in reality indeterminable, it is better to accept *A. pennacea* as a *nomen dubium* (glossary of Code: 'a name of unknown or doubtful application') and to disregard it. *Pista mediterranea* has also been described by us (Jirkov *et al*., 2001) as *Pista malmgreni* but comparison of our type material with topotypes of *P. mediterranea* shows that it is the same species.

Pista wui has been reported from Norway only once (Londoño-Mesa *et al*., 2016) without any morphological data. We doubt that this species, previously known only from Pacific coasts of the USA, really inhabits Norwegian waters. It has two pairs of branchiae and uncini of TU1 with a manubrium.

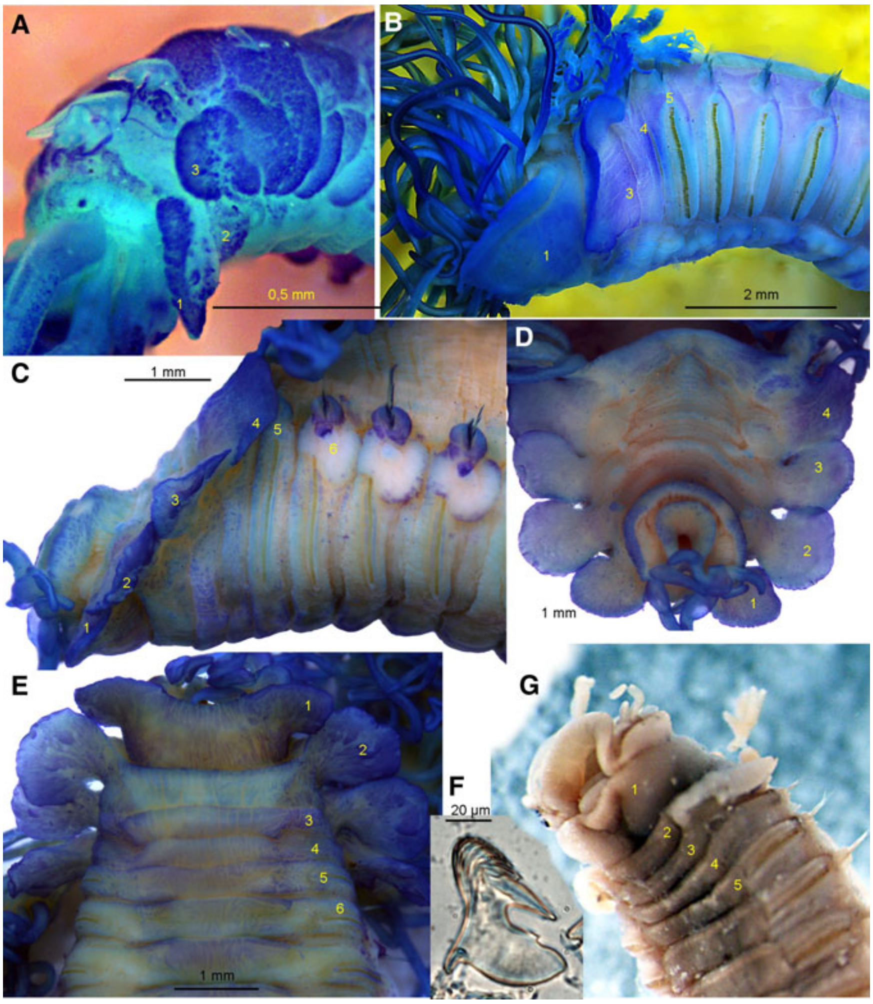

Fig. 5. Morphology of some genera with large lateral lobes (valid on 1 April 2017). (A) *Loimia medusa* APEM 8184; (B) *Lanice conchilega* ZMMU Neaples; (C–F) *Scionella vinogradovi*; (G) *Laonicola lobata* HZMI. (A) antero-frontal view, (B, C) lateral view, (D) antero-dorsal view, (E) ventral view; (F) uncinus TU1; (G) ventro-lateral view.

Pistella lornensis has a range that includes southern Norway and it has one pair of branchiae. It is the only species listed above that fits the description and thus should be synonymized with *P. cristata* s.str. Remarkably, it lacks long-handled uncini in TU1. It was originally described as *Scionella lornensis* Pearson, 1969 and was later transferred to its own genus: *Pistella* Hartmann-Schröder, 1996. As the type species of *Pistella* (*S. lornensis*) is a junior synonym of the type species of *Pista* (*Amphitrite cristata*), *Pistella* should be considered a junior synonym of *Pista*. According to Londoño-Mesa *et al.* (2016), *Pista cristata* (named *P. lornensis* in their publication) is genetically homogenous in Norwegian waters (type locality of *P. cristata* and close to Scotland, the type locality of *P. lornensis*).

We published these findings 15 years ago (Jirkov *et al.*, 2001) in Russian. Probably due to the linguistic barrier, Nogueira *et al.* (2015) did not accept our conclusions and wrote 'that synonymy, however, requires that all species currently assigned to *Pista* should be transferred to a new, still undescribed genus, due to the presence of long-handled uncini on anterior segments, which are absent in *P. cristata*'. However, restoration of the original taxonomic meaning of *Amphitrite cristata* Müller, 1776 does not require the description of a new genus. At the generic level, re-description can be limited to amendment of the diagnosis of *Pista* (i.e. removal of the requirement for the presence of long-handled uncini). This diagnosis of *Pista* was and is accepted by many authors (see above).

RESULTS AND DISCUSSION

The first calculation (Figure 11A) shows that the type species of *Lanicola* – *L. lobata* is outside the investigated group, so it is excluded from further discussion.

All calculations give almost the same results, showing two well-defined groups (bootstrap = 100). The positions of *Scionella* and *Lanicides* vary; they are sometimes included in one group, sometimes in the other, but in all cases they are somewhat apart. We think that these two genera should be accepted as distinct. As for the large groups, one includes the type species of *Pista* (*Amphitrite cristata*), the other includes the type species of *Axionice* (*Terebella flexuosa*); *Betapista* Banse, 1980 (*Betapista dekkerae* Banse, 1980); *Eupistella* Chamberlin, 1919 (*Eupista darwini* McIntosh, 1885); *Lanice* Malmgren, 1866 (*Nereis conchilega* Pallas, 1766); *Loimia* Malmgren, 1866 (*Terebella medusa* Savigny in

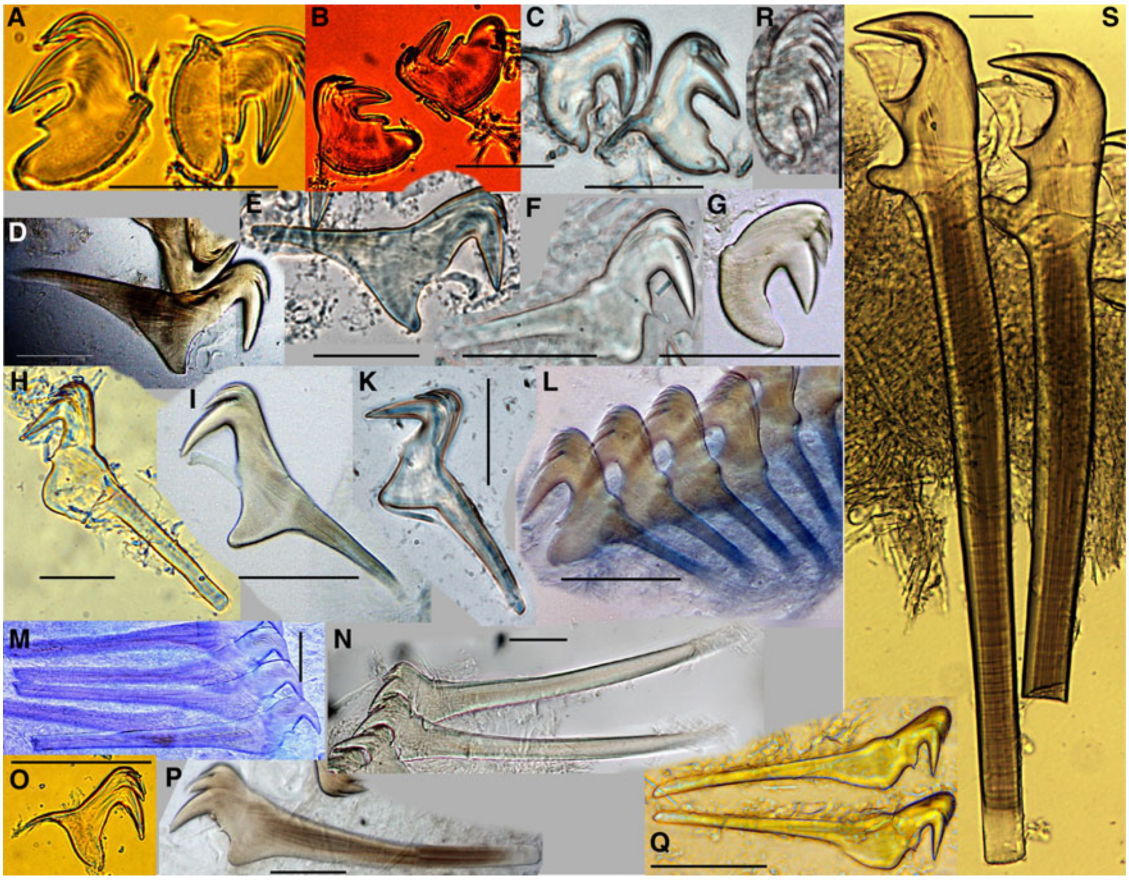

Fig. 6. Uncini of different *Axionice* species. (A) *A. flexuosa* KGB R/V Maslov 10.33; (B) *A. maculata* KGB R/V Alaid 30.8; (C) *A.* sp A USNM 90526; (D) *A. alata* NHM 1333.7.10.275; (E) *A. corrientis* NHM 1930 TU1; (F) *A. symbranchiata* APEM 55970; (G) *A. trunca* NHM 1986.256-259; (H) *A. agassizi* KGB Vostok; (I) *A. herpini* NHM 133.7.10.285; (K) *A. palmata* USNM 496; (L) *A. sinusa* NHM paratype; (M) *A. mirabilis* NHM 2015.325; (N) *A. cretacea* MNCN 1744; (O) *A. conchilega* (formerly *Lanice conchilega*) ZMMU Naples; (P) *A. foliigera* NHM 1961.19.1227/1232; (Q) *A. incarrientis* IORAN Vitjaz 1790; (R) *A. medusa* (formerly *Loimia medusa*) APEM 8184; (S) *A. elongata* BCPM 974-305-2. All uncini from TU1. All scale bars 50 μm.

de Lamarck, 1818); and *Paraxionice* Fauchald, 1972 (*P. artifex* Fauchald, 1972). We consider this group to be a single genus and the other names as its junior synonyms. The oldest genera are *Axionice*, *Lanice* and *Loimia*; they were erected in one paper, so they have equal taxonomic status. We prefer to use *Axionice* because in the usual sense in which the genus is used is clearer and we will avoid confusion with previously used binomens. Some comments on genera synonymized with

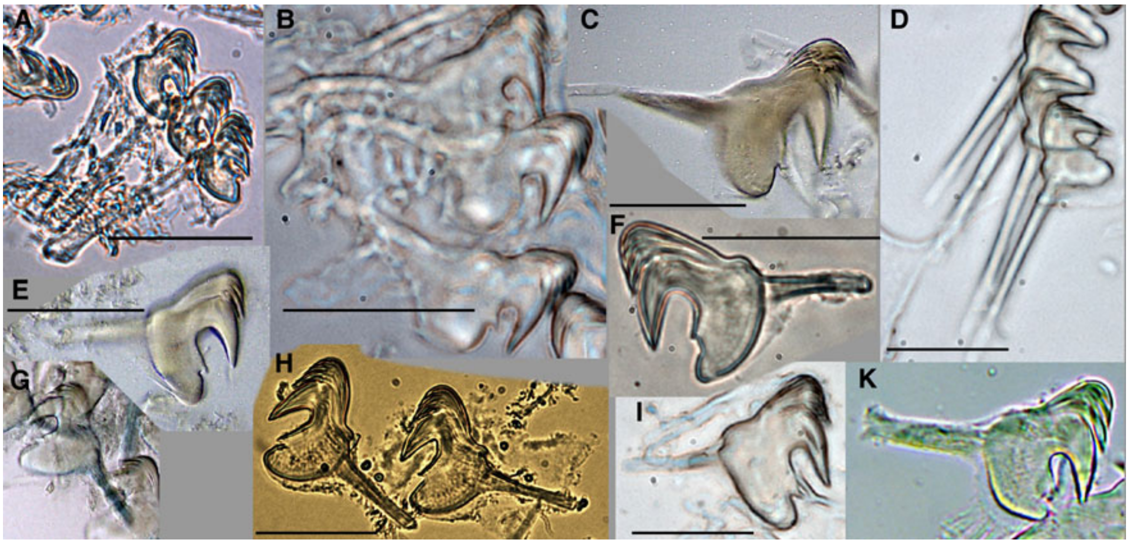

Fig. 7. Uncini of different *Pista* species. (A) *P. cristata* KGB Slettholmen; (B) *P. bansei* KGB R/V Sevastopol 1086; (C) *P. grubei* NHM 1953.3.1.506/504; (D) *P. paracristata* IORAN R/V Vitjaz 3577; (E) *P. typha* NHM1986.154-157; (F) *P.* sp B. USNM 90532-3; (G) *P. australis* NHM 1986.74-91; (H) *P. mediterranea* KGB 50/22; (I) *P. wui* NMC 1986-0057; (K) *P. unibranchia* MNCN 1782. All uncini from TU1. All scale bars 50 μm.

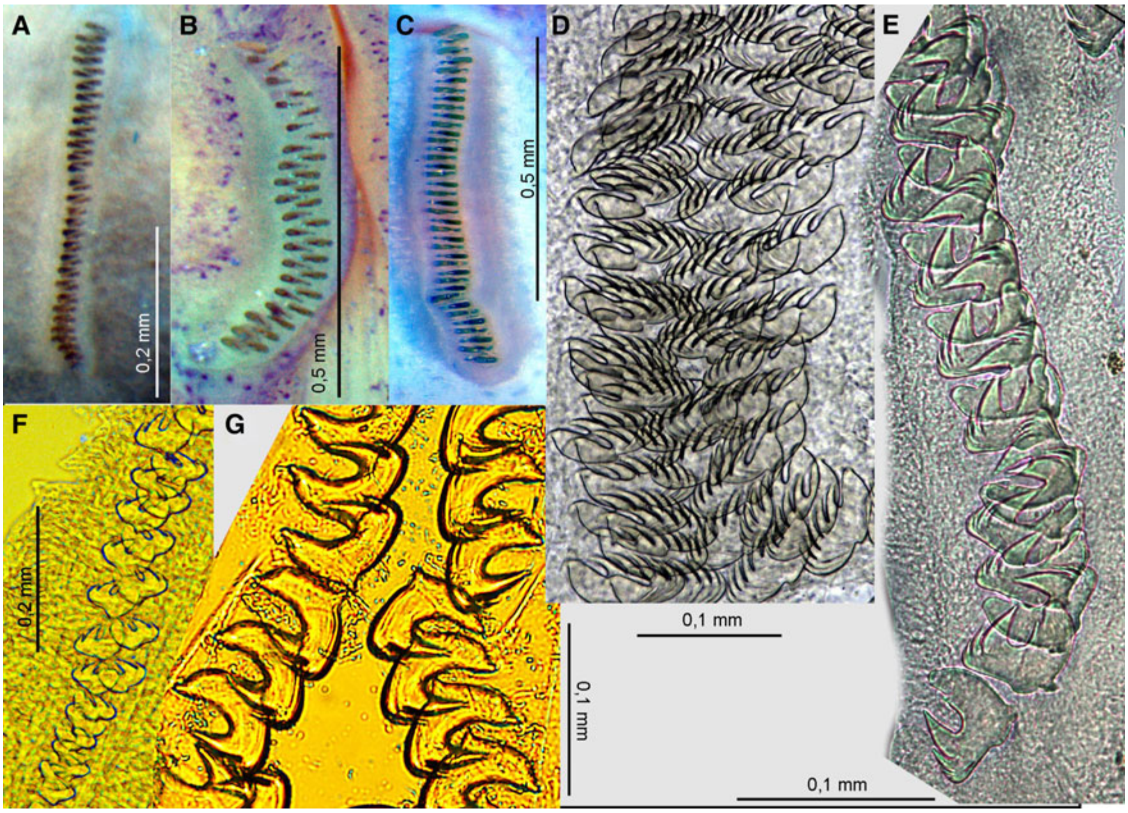

Fig. 8. Double rows uncini of *Axionice* and *Pista* and TU1 uncini of *Scionella vinogradovi* and type species of *Loimia* and *Lanice.* (A) *Pista cristata* TU8 KGB Ronsfjord; (B) *Axionice maculata* KGB R/V Alaid 30.8; (C) *Pista mediterranea* MNCN5801; (D) *Axionice medusa* (formerly *Loimia medusa*) APEM 55109 TU11; (E) *Axionice cretacea* TU7 MNCN1744; (F) *Axionice flexuosa* uncini TU11 Maslov_33; (G) *Axionice conchilega* (formerly *Lanice conchilega*) TU7 Neaples H – TU7.

Axionice are given below to support our opinion. Updated diagnoses for all the genera we consider to be valid are also given below.

Holthe (1986b) placed both *Pista* and *Axionice* in one tribe: Pistini. This cannot be accepted, due to significant differences between them.

Species with and without manubria are scattered between the *Axionice* and *Pista* (Figure 11B), so this character cannot be used for separation of genera; this opinion has been accepted by many authors (see above). So the diagnoses of *Axionice* and *Pista* do not require the obligatory presence or absence of an uncinal manubrium: it may be present or absent; but, if a manubrium is present, its origin is different between *Axionice* and *Pista*. The manubrium of *Axionice* develops as an extension of the uncinus. Figure 15 presents different stages of this development from the single neuropodium of several *Axionice* species. The manubrium develops either as prolongation of the base of the uncinus (*A. elongata* Figure 15A) or as prolongation behind it (most other *Axionice* Figure 15B–F). Its development starts in a special sac under the body surface, above the dorsal margin of the uncinal row. Figure 16 shows prepared TU1 neuropodia of *A. alata* showing the sac where uncini form. If the manubrium is broken, the break may occur at any point along the manubrium, usually far from the uncinal body (Figure 15F). This kind of development agrees perfectly with hypotheses about the possible origin of the manubrium in Terebellinae (Garraffoni & Lana, 2010). The manubrium of *Pista* originates quite differently: as a more or less chitinized tendon. The point of attachment is obvious and, if the manubrium is broken, it almost always happens at this point.

Obviously, the plesiomorphic shape of the uncini in *Axionice* and *Pista* and closely related genera is avicular uncini without a manubrium, as in *Axionice flexuosa* (Figure 6A) and *Pista cristata* (Figure 7A). The uncinus goes through this stage during development (see Figure 15C). So, the manubria of *Axionice* and *Pista* are homoplasies. Manubria probably have independent origins even within *Axionice*, but this requires further investigation.

The plesiomorphic state of lateral lobes is poorly developed lobes or absence of lobes. The apomorphic state of lobes in *Axionice* is very large lobes on S1, and it is a synapomorphy for the group. Other segments may or may not have lobes; S3 has well-developed lobes, while S2 usually has no lobes at all, but they are sometimes present or even well-developed. In contrast, *Pista* has poorly developed lobes on S1. *Scionella* has a quite different structure on anterior segments, which should be treated as an apomorphy.

The synapomorphy of *Pista* is pompom-like branchiae.

SYSTEMATICS

Order TEREBELLOMORPHA Hatschek, 1893
Family TEREBELLIDAE Johnston, 1846
Genus *Pista* Malmgren, 1866
Type species *Amphitrite cristata* Müller, 1776

WoRMS: 129708. Lobes of S1 not the largest, usually the smallest or absent; other lobes of various sizes and shapes,

Fig. 9. Ventral pads of *Axionice*. (A) *A. flexuosa* KGB R/V Maslov 10.33; (B) *A. elongata* BCPM 974-305-2; (C) *A. maculata* KGB R/V Alaid 30.8; (D) *A. diabranchiata* (formerly *Eupistella diabranchiata*) NHM 1928.4.26.15; (E) *A. sinusa* NHM 1986.92; (F) *A. palmata* USNM 496; (G, H) *A. herpini* NHM 133.7.10.285 and 1928.4.26.31.

some large; largest lobes on S2 or S3. Branchiae pompom-like (bottle-brush, club-shaped, plumose – branching filaments in a spiral arrangement); sometimes the whole plume is in an apical position like a brush. Dorsal crest absent. Ventral pads divided into posterior and anterior parts, with different colours. Uncinal manubrium, if present, always develops from the uncinal tendon. Uncini in double rows arranged face-to-face. Notochaetae laterally smooth.

The genus, as defined above, includes 29 species (Appendix 1).

We have some doubt concerning the position of *P. penicillibranchiata*. In contrast to all other known species of the *Axionice*/*Pista* group, its ventral pads are not subdivided and, whilst its branchiae are definitely not arborescent, their pompom-like structure is reduced to a *Penicillus*-like tuft (Figure 14); however, all calculations place this species within *Pista*.

Pista cristata (Müller, 1776)
Figures 4A, 7A, 8A & 10A

Amphitrite cristata Müller, 1776: 216; type locality Christianfjord, Norway ≈ 58°06′N 8°00′E, type material 'probably lost or never designated' (Holthe, 1986a: 112).
Pista cristata – Malmgren, 1866: 382–383 (partim), non Tab. XXII f. 59 (*P. mediterranea*); Jirkov, Leontovich & Saphronova, 2001: 521–522, textfig – non auctuorum.

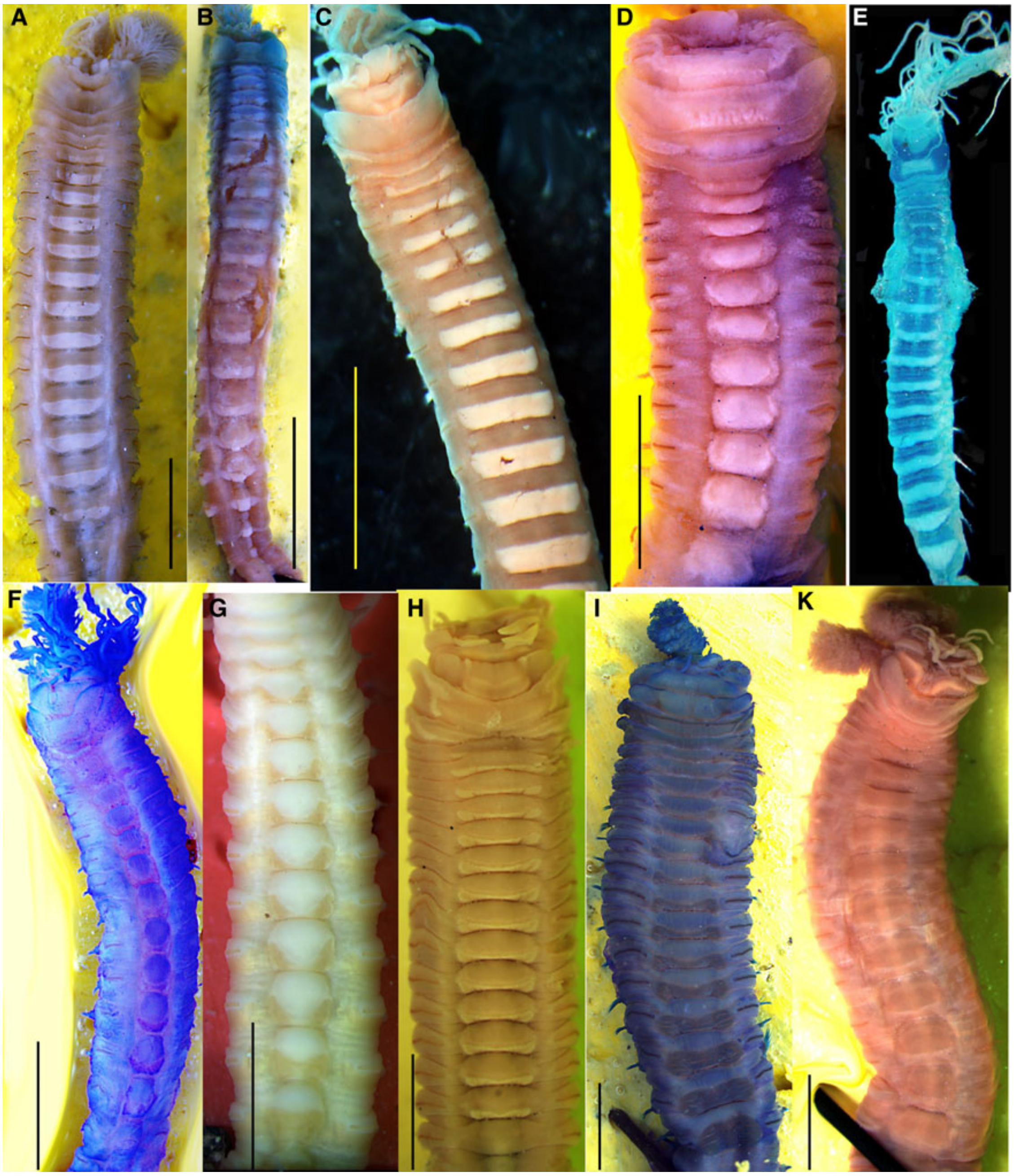

Fig. 10. Ventral pads of *Pista*. (A) *P. cristata* KGB Slettholmen; (B) *P. bansei* KGB R/V Sevastopol 1086; (C) *P. unibranchia* MNCN 1782; (D) *P. paracristata* IORAN R/V Vitjaz 3577; (E) *P. papillosa* after Londoño-Mesa (2009); (F) *P. mediterranea* KGB 50/22; (G) *P. typha* NHM 1986.154-157; (H) *P. grubei* NHM 1953.3.1.506/504; (I) *P. wui* NMC 1986-0057; (K) *P. australis* NHM 1986.74-91. All scale bars 2 mm.

Scionella lornensis Pearson, 1969: 509–513, fig. 1, 2, type locality Loch Linnhe, Loch Creran and Firth of Lorne, Scotland, holotype BMNH ZB 1968 15; Holthe, 1986a: 114–115, fig. 50;
Pistella lornensis – Hartmann-Schröder, 1996: 520.
Pista lornensis – Saphronova, 1988: 890–891, fig. a, b.
Pista sp. II – Banse, 1980: 31, fig. 4j–k.
WoRMS: 131516

MATERIAL EXAMINED

Slettholmen 12.09.1979 (10 ex., det. as *Scionella lornensis* by E. Oug), Ronsfjord, 58°06′30″N 8°06′E (very close to the type locality); 25.08.1979 (4 ex., det. as *Scionella lornensis* by E.Oug); Kattegat Frederikshavn Hirsholm, 25–30 m 21.06.1960 57°29′30″N 10°37′30″E (1 ex., det. as *Scionella lornensis* by M. Petersen) collection of ZMMGU; 15 ex. Islas Chafarinas, between Cabo de San Antonio and Puerto de Valencia, Cala Uruguay MNCM; type of *Scionella lornensis* BMNH ZB 1968 15.

DIAGNOSIS

Length up to 60 mm, width 3 mm. Upper lip small. S1 reduced, without lobes. S2 with large semi-rounded ventro-lateral lobes, covering S1, their upper margin on the level of the upper end of the uncinal row of S5, maximum length of lobes at their centre, lobes poorly developed ventrally, S1 visible through broad incision. Lobes of S3, if present,

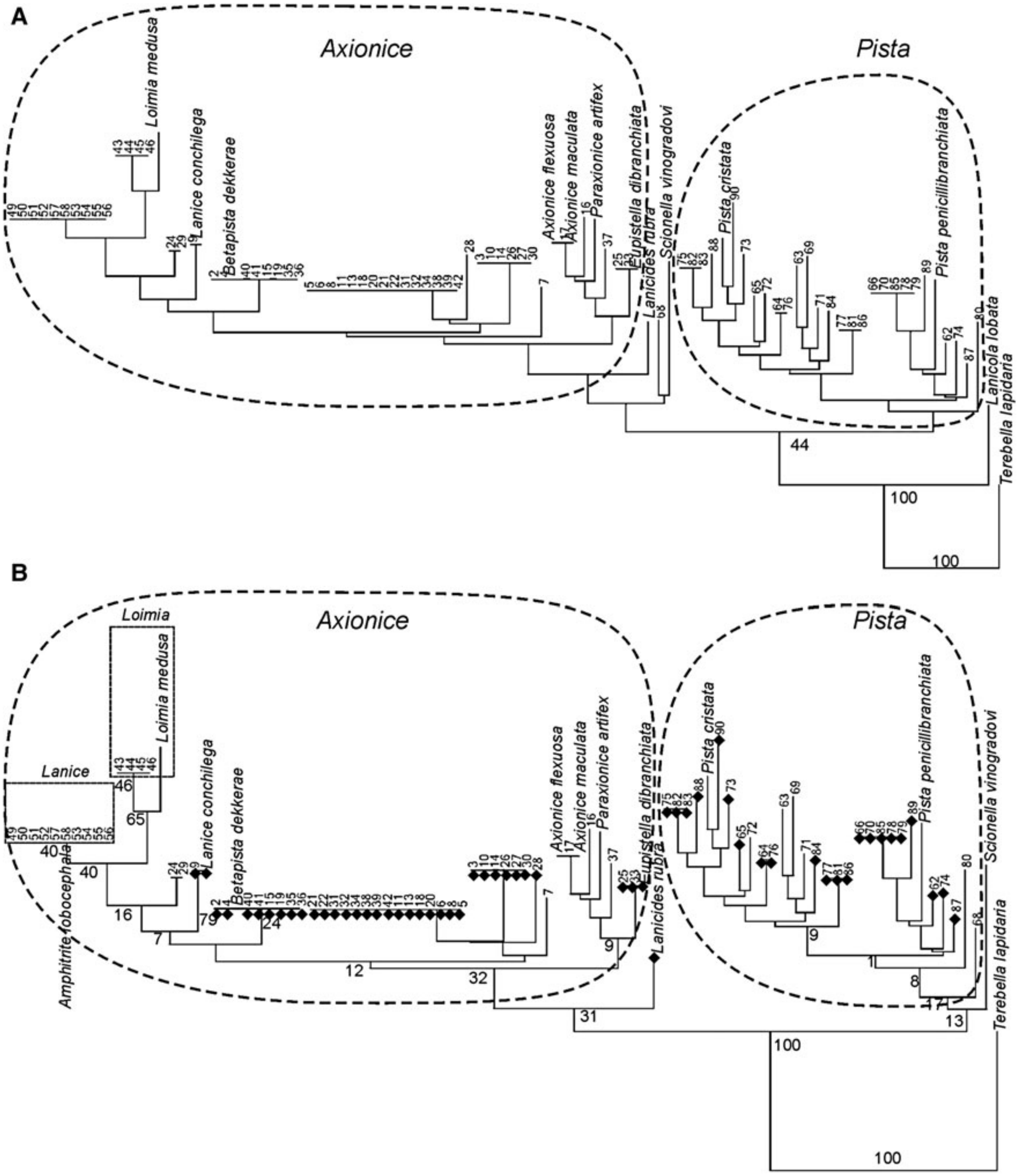

Fig. 11. Cluster tree, characters 1–9. (A) with *Lanicola lobata*; (B) without. Black rhombus – species with long-handled uncini on TU1. Used binomens valid on 1 April 2017. Horizontal number – bootstrap, vertical – number of species (Table 1).

distinctly smaller, their upper margin lower than upper margin of the lobes of S2, ventrally not developed. S4 without lobes or small variably developed thickening below notopodia. One pair of branchiae on transverse fold, branchiae pompom-like, usually left and right of different sizes. Notopodia start from S4, extending for 17 S (17TS), short, cylindrical, 1st pair on the same level as others, or slightly higher. Neuropodia start from S5, uncini in double rows arranged face-to-face on S11–S20 (up to the end of the thorax). All thoracic neuropodia are tori, all abdominal neuropodia are pinnuli, about 50 AU. Rows of thoracic uncini of similar length, those of abdominal region 2 to 3 times shorter. Nephridial papillae on S6 and S7, usually invisible. Ventral pads start from S4–S6, not developed on preceding segments, at first semicircular, then as transverse rectangles, absent on last 1–2 TU, middle pads are the largest. Ventral pads divided into posterior and anterior parts, with different colours: anterior parts of the same colour as other parts of the body, posterior half white. All uncini avicular, in double rows, neuropodia face-to-face, flexible tendon attached to the back of uncini, tendons easily separated from uncini while preparing slides. Tube of dense detritus, with inlaid shells and their fragments, oriented transversely.

Species range. Records almost worldwide, but all reports refer to *Pista* with two pairs of branchiae, i.e. to different species. Confirmed distribution from the North and Mediterranean Seas.

Biology. Shallow water, not deeper than 25 m.

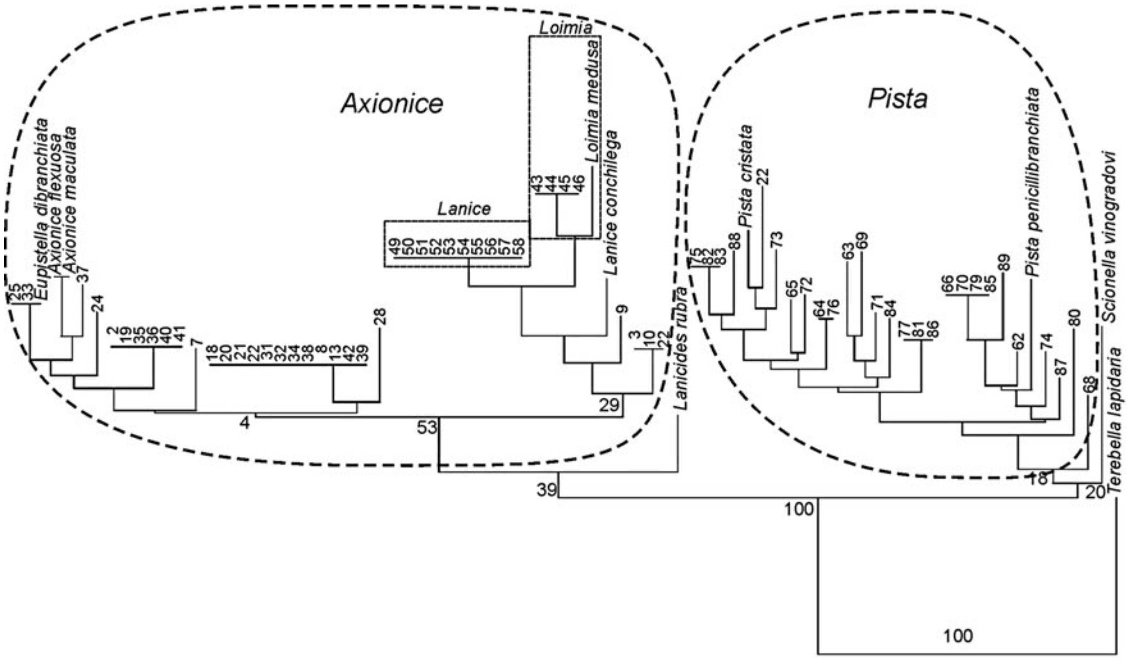

Fig. 12. Cluster tree, characters 1–10. Used binomens valid on 1 April 2017. Horizontal number – bootstrap, vertical – number of species (Table 1).

Genus *Axionice* Malmgren, 1866
Type species *Terebella flexuosa* Grube, 1860

WoRMS: 129689. Lobes of S1 are the largest, usually at least twice as large as the largest lobes of other segments, directed anteriorly and covering the upper lip; lobes of S3 smaller, but still large; lobes of other segments much smaller or absent; a usual trait is small or absent lobes on S2. Branchiae arborescent. Dorsal crest absent. Ventral pads not subdivided. Uncinal manubrium, if present, develops as an extension of the uncinus. Uncini in double rows arranged face-to-face. Notochaetae laterally smooth.

Axionice in sense proposed here includes 94 species (Appendix 1). It is interesting that all of them have been described outside *Axionice*. The re-description of the type species is given below.

Taxonomic remarks on generic synonymy.

Betapista Banse, 1980. WoRMS: 325246. Banse (1980) stated that the main reason for establishing the new genus was branchiae starting from S3 instead of S2. However, he noticed that counting segments is difficult and that the

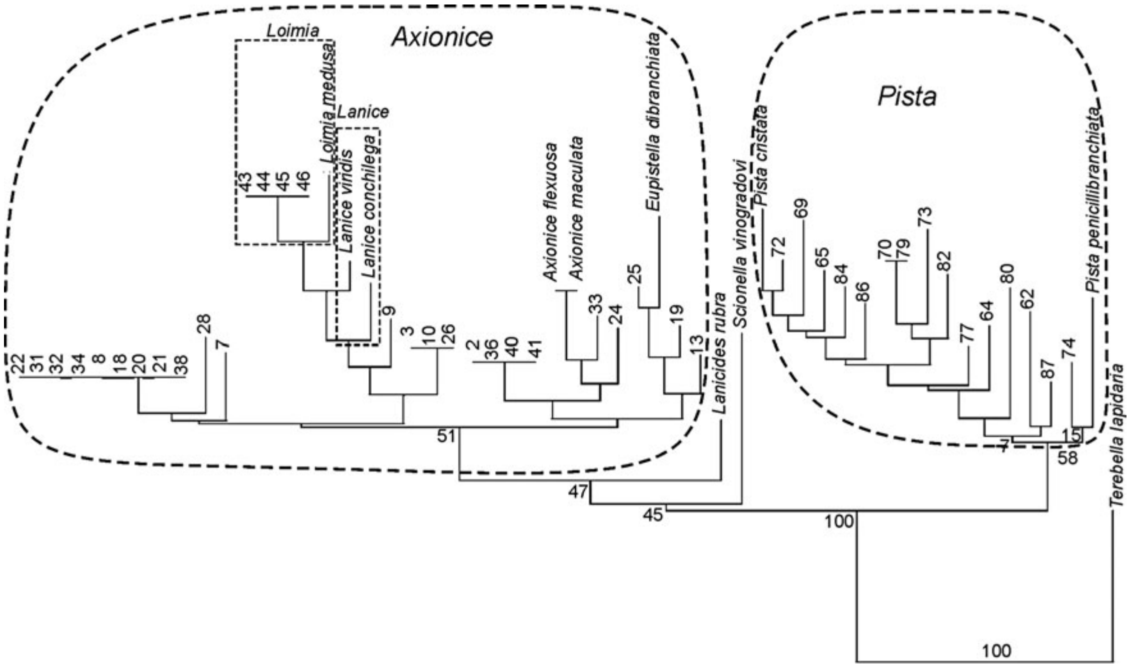

Fig. 13. Cluster tree, characters 1–11. Used binomens valid on 1 April 2017. Horizontal number – bootstrap, vertical – number of species (Table 1).

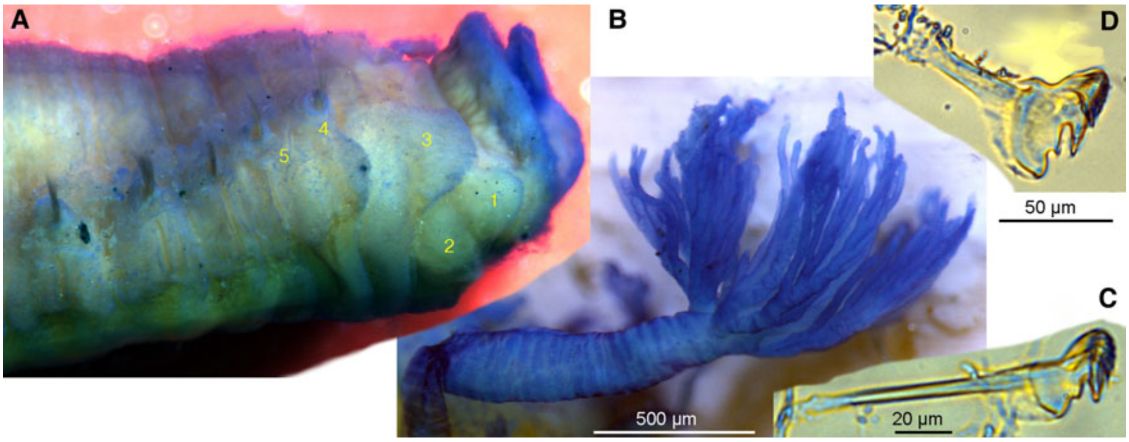

Fig. 14. Morphology of *Pista penicillibranchiata*. (A) lateral view; (B) tip of branchia; (C) uncinus TU1; (D) uncinus TU16. (A) NHM, (B–D) IORAN. All from the same station RV 'Vitjaz 618'.

genus could be based on several other characters that seemed stable. He defined the first of these characters as: double rows of uncini beginning on segment 11, a diagnostic character at the subfamily level (see Hessle, 1917: 145; Caullery, 1944). While it is true that double rows of uncini usually start from TU7 (=TC8=S11), the character is not as stable as the authors supposed. We have found *Axionice elongata* with double rows of uncini starting two segments earlier: from TU5 (=TC8=S9) (Figure 17). We consider the difference to be only individual variation as, in all other characters, this worm did not differ from other *Axionice*; it showed, however, that the starting point of double rows of neuropodial uncini is a variable character (though not commonly so) and not a real basis for the accepting *Betapista* as valid, at least not before variation within a species has been investigated.

Euscione Chamberlin, 1919. WoRMS: 882063. Chamberlin (1919) proposed *Euscione* as a replacement for the junior homonym *Scione* Malmgren. The type species of *Scione* (*Scione lobata*), presently accepted as *Axionice maculata* is so similar to *Axionice flexuosa* (Figures 2A, C, 6A, B & 9A, C), that there is no doubt that *Euscione* should be accepted as a junior synonym of *Axionice*.

Eupistella Chamberlin, 1919. WoRMS: 129692. Unfortunately only the type of *E. dibranchiata* was available. Contrary to the original description, branchiae are clearly dichotomous. So, at least this species should be transferred to *Axionice*. The validity of the genus should be clarified after investigation of McIntosh's species types; unfortunately, they were not available during the course of our study. However, the presence of cirriform instead of arborescent branchiae is not accepted as enough to differentiate genera in Terebellidae; for example, within *Amphitrite*, the type species has cirriform branchiae, while most others have more or less branched branchiae (some of them are sometimes transfered to *Neoamphitrite*).

Lanice Malmgren, 1866. WoRMS: 129697. There is remarkable similarity in the development of lateral lobes (compare Figures 2 and 3 with Figure 5B) and uncini of TU1 (Figure 6) between *Lanice* and *Axionice*. The only difference between them is that the uncini in double rows are arranged back-to-back (Figure 8G), rather than face-to-face (Figure 8B, F). However this difference can appear if two rows are well separated or at least not completely 'zipped'. However it is not always the case: in some species, such as *Pista mediterranea* (Figure 8C) and *Axionice cretacea* (Figure 8E), uncini of different orientations form a single row and they cannot be named either back-to-back, or face-to-face, but only side-to-side. The existence of such species makes the difference between *Lanice* and *Axionice* insignificant or, at least, cannot be enough to accept the feature as valid for the separation of genera. Also, it is necessary to mention that the type species of *Lanice* (*L. conchilega*), contrary to previous descriptions, differs from other members of the genus in that it has a short but distinct manubrium. This manubrium seems to have an origin similar to that of *Axionice* (Figure 15). Also, the tube with a branched, fine-meshed fan attached to the opening is not characteristic for the genus: we have seen very similar tubes built by *Thelepus*.

Loimia Malmgren, 1866 (Figure 8). WoRMS: 129700. As in *Lanice*, the lateral lobes of *Loimia* are remarkably similar to those of *Axionice* (compare Figures 2 and 3 with Figure 5A). *Loimia* is defined by a unique generic character: adults with pectinate uncini, but juveniles of some species have the usual avicular uncini in the posterior abdomen (Wilson, 1928; Hutchings & Glasby, 1988). This seems to be an apomorphy and the group seems to be monophyletic. However, there is great variation in uncini within *Axionice* and the difference between, for example, *A. elongata* (Figure 6C) and the type species *A. flexuosa* (Figure 6A) is much greater than between *A. flexuosa* and *Loimia* (Figure 6R). Probably, detailed investigation of *Axionice* s. lato will show that there are several groups of species, but an evaluation of such a group is beyond the goal of the present investigation. It would require much deeper investigation of their morphology than is currently possible and cannot be completed using literature data alone. Also, *Loimia* differs from all other genera of the investigated group except for *Lanice* in that the uncini are arranged in a back-to-back position, but we already considered that this is not enough for accepting a genus as valid.

Paraxionice Fauchald, 1972. WoRMS: 325264. The original description states: 'It has sixteen thoracic setigers and a single pair of branchiae; both the other genera mentioned [*Axionice* and *Pista* IJ] have seventeen thoracic setigers and two or three pairs of branchiae' (p. 319). However, this is not true: the type species of *Axionice* has only 15 thoracic chaetigers and one

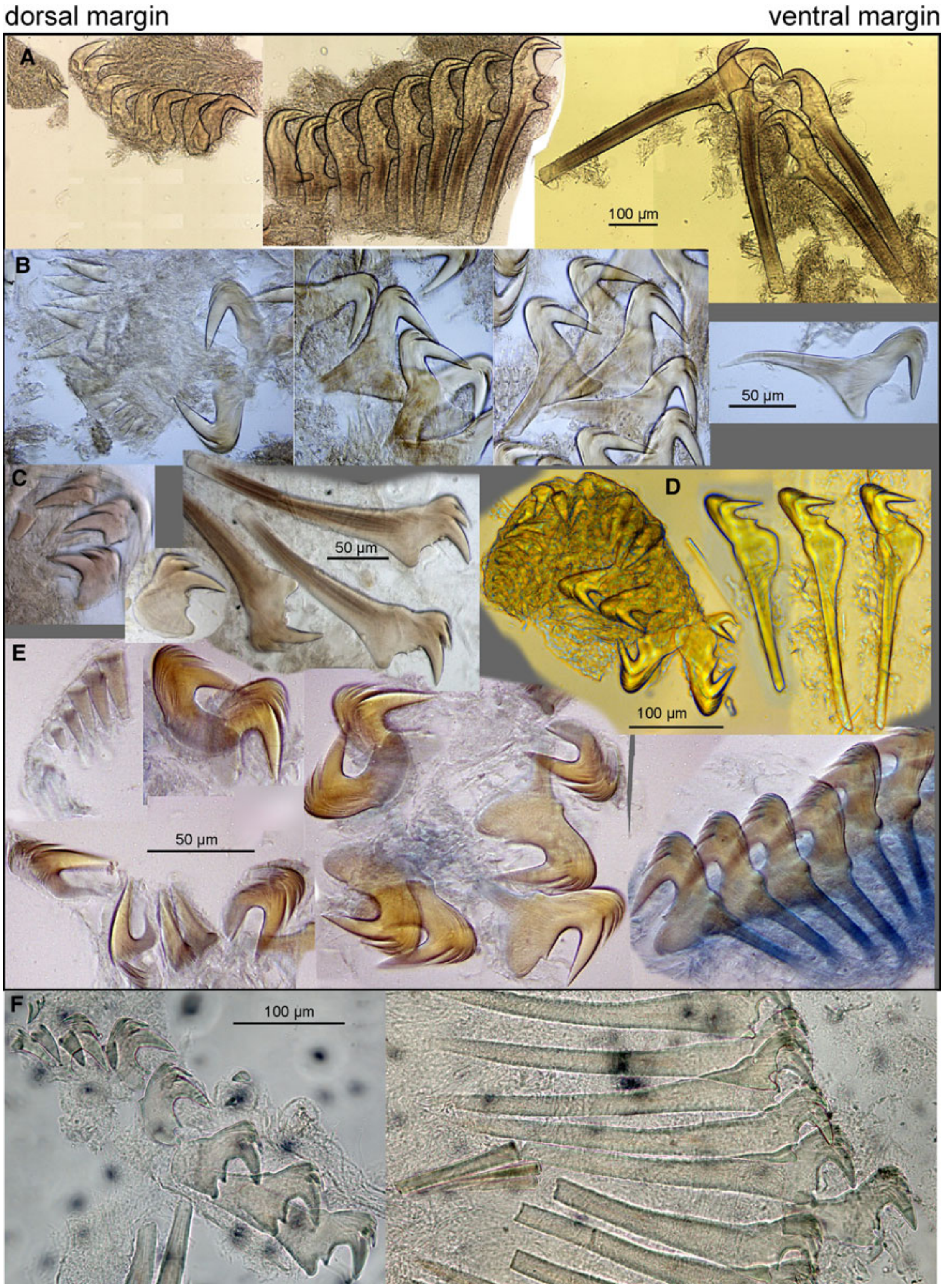

Fig. 15. Development of uncini in different *Axionice* species. (A) *A. elongata* BCPM 974-305-2; (B) *A. alata* NHM; (C) *A. foliigera* NHM 1961.19.1227/1232; (D) *A. incarrientis* IORAN RV 'Vitjaz 1790'; (E) *A. sinusa* NHM 1986.92; (F) *A. cretacea* MNCN5801. All uncini from TU1 except (F), which are from TU3.

pair of branchiae (see re-description above). The number of TC in *Pista* and *Axionice* varies from 15 to 20 and the number of branchiae varies from one to three. So, Fauchald's reasons for establishing the new genus are not valid and *Paraxionice* should be accepted as a junior synonym of *Axionice*. This was also indicated by our calculations.

Axionice flexuosa (Grube, 1860)

Figures 2A, 6A, 8F & 9A

Axionice flexuosa – Holthe, 1986a: 118–120, fig. 52, map 51.
Pista flexuosa – Uschakov, 1955: 386; Jirkov, Leontovich & Saphronova, 2001: 522, textfig.
WoRMS: 131483

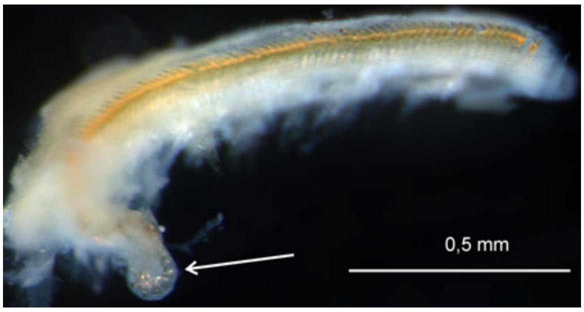

Fig. 16. Row of uncini of TU1 of *Axionice alata*. Sac with juvenile uncini is arrowed.

MATERIAL EXAMINED

Ninety samples (307 specimens) from collections KGB, IORAN and ZIN, 9–263 m from the Barents Sea to the northern parts of the Sea of Japan.

DIAGNOSIS

Length up to 60 mm. Eyespots absent. Lobes S1 are the largest, ventro-lateral, ventrally fused and cover prostomium. Lobes absent from S2. Lobes on S3 large, lateral, covering S2 completely and partly covering S1. One pair of arborescent branchiae on S2. Notopodia from S4 extending for 15 S. Neuropodia start from S5, uncini in double rows arranged face-to-face on S11–S16, thus uncini are single rows on neuropodia of last two thoracic segments. All thoracic neuropodia (including last single row) are tori, all abdominal neuropodia are pinnuli. Ventral pads uniform. Uncini avicular, without manubrium. Notochaetae laterally smooth. Tube distinctive and peculiar to this species: flat and undulating, sandy.

Species range. From the Barents Sea to the northern parts of the Sea of Japan.

Biology. Shallow water, mainly shallower than 100 m.

Remark. Although we have not investigated type material, all characters perfectly fit Holthe's (1986a) re-description with one exception: Holthe reported this species as having double-rows of neuropodia up to the end of the thorax. In reality, although all thoracic neuropodia are tori and all neuropodia starting from AU1 are pinnuli, the last two TU have neuropodia with uncini in single rows. As far as we know, all other Terebellinae have neuropodia with uncini in double rows at least to the end of the thorax and often on some (occasionally numerous) abdominal neuropodia. Nevertheless, as there are no similar species in the Arctic that can be confused with *A. flexuosa*, we suppose that Holthe's description is partly inaccurate.

Genus *Scionella* Moore, 1903
(Figure 5C–F)
Type species *Scionella japonica* Moore, 1903

WoRMS: 147148.

Lobes of S1–S4 well developed, equal in size. Branchiae spirally wound arising from a transverse dorsal fold on S4. Ventral pads not subdivided. Uncinal manubrium absent. Uncini in double rows arranged face-to-face. Notochaetae with serrated tips.

Saphronova (1991) considered this genus to be distinctive in its dorsal crest and the arrangement of its lateral lobes, not by the absence of a manubrium, as thought by Pearson (1969); we agree with her conclusions.

Fig. 17. Double rows start in *Axionice elongate*. BCPM 974-305-2.

Genus *Lanicides* Hessle, 1917 sensu Nogueira *et al.* (*2015*).
Type species *Terebella* (*Phyzelia*) *bilobata* Grube, 1878
according to Nogueira *et al.* (2015).

WoRMS: 174905.

S1 reduced, S2 and S3 with lobes of variable size. Branchiae arborescent or plumose. Serrated notochaetae present. Uncini avicular; manubrium in some anterior segments.

Remark. We have not investigated any species of this genus; data in Table 1 based on the best description of the species of the genus given by Nogueira *et al.* (2015) – *Lanicides rubra*.

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APPENDIX 1

Proposed taxonomic status of species of the genera *Axionice*, *Betapista*, *Eupistella*, *Lanice*, *Lanicides*, *Loimia*, *Paraxionice*, *Pista* and *Pistella*

Axionice agassizi (Hilbig, 2000) as *Pista*
Axionice alata (Moore, 1910) as *Pista*
Axionice alonsae (Santos *et al.*, 2010) as *Pista*
Axionice amphelisso (Hutchings, 2007) as *Lanice*
Axionice annulifilis (Grube, 1872) as *Terebella*
Axionice arakani (Hissmann, 2000) as *Lanice*
Axionice arborea (Moore, 1903) as *Loimia*
Axionice armata (Carrerette & Nogueira, 2015) as *Loimia*
Axionice artifex (Fauchald, 1972) as *Paraxionice*
Axionice atypica (Hessle, 1917) as *Pista*
Axionice auricula (Hutchings, 1990) as *Lanice*
Axionice bandera (Hutchings, 1990) as *Loimia*
Axionice batilla (Hutchings & Glasby, 1988) as *Loimia*
Axionice bermudensis (Verrill, 1900) as *Loimia*
Axionice bidewa as (Hutchings & Glasby, 1988) *Lanice*
Axionice brasiliensis (Carrerette & Nogueira, 2015) as *Loimia*

Axionice breviuncinata (Hartmann-Schröder, 1965) as *Pista*
Axionice caulleryi (Holthe, 1986a, b) as *Lanice*
Axionice cetrata (Ehlers, 1887) as *Terebella*
Axionice chloroplokamia (Nogueira *et al.*, 2015) as *Pista*
Axionice conchilega (Pallas, 1766) as *Nereis*
Axionice contorta (Ehlers, 1908) as *Terebella (Loimia)*
Axionice corrientis (McIntosh, 1885) as *Pista*
Axionice crassifilis (Grube, 1878) as *Terebella*
Axionice cretacea (Grube, 1860) as *Terebella*
Axionice darwini (McIntosh, 1885) as *Eupista*
Axionice decora (Pillai, 1961) as *Loimia*
Axionice dekkerae (Banse, 1980) as *Betapista*
Axionice dibranchiata (Fauvel, 1909) as *Eupista*
Axionice digitibranchia (Caullery, 1944) as *Eupista*
Axionice elongata (Moore, 1909) as *Pista*
Axionice expansa (Treadwell, 1906) as *Lanice*
Axionice fasciata (Grube, 1870) as *Dendrophora*
Axionice fauveli (Day, 1934) as *Lanice*
Axionice flabellum (Baird, 1865) as *Terebella*
Axionice flexuosa (Grube, 1860) as *Terebella*
Axionice foliigera (Caullery, 1915) as *Pista*
Axionice foliigeraformis (Annenkova, 1937) as *Pista*
Axionice gibbauncinata (Saphronova, 1984) as *Pista*
Axionice godfroyi (Gravier, 1911) as *Scione*
Axionice grubei (Holthe, 1986a, b) as *Loimia*
Axionice grubei (McIntosh, 1885) as *Eupista*
Axionice haitiana (Augener, 1922) as *Lanice*
Axionice harrissoni (Benham, 1916) as *Scione*
Axionice hataam (Londoño-Mesa, 2012) as *Pista*
Axionice herpini (Fauvel, 1928) as *Pista*
Axionice incarrientis (Annenkova, 1925) as *Pista*
Axionice ingens (Grube, 1878) as *Terebella*
Axionice juani (Nogueira, Hutchings & Carrerette, 2015) as *Loimia*
Axionice keablei (Nogueira, Hutchings & Carrerette, 2015) as *Loimia*
Axionice kristiani (Nogueira *et al.*, 2015) as *Pista*
Axionice lizae (Londoño-Mesa, 2012) as *Pista*
Axionice macrolobata (Hessle, 1917) as *Terebella*
Axionice maculata Dalyell, 1853 as *Scione*
Axionice marionensis (Branch, 1998) as *Lanice*
Axionice medusa (Savigny in de Lamarck, 1818) as *Terebella*
Axionice medusa angustescutata (Willey, 1905) as *Loimia*
Axionice megaoculata (Carrerette & Nogueira, 2015) as *Loimia*
Axionice minuta (Treadwell, 1929) as *Loimia*
Axionice mirabilis (McIntosh, 1885) as *Pista*
Axionice montagui (Grube, 1878) as *Terebella* (nomen dubium)
Axionice moorei (Berkeley & Berkeley, 1942) as *Pista*
Axionice nigrifilis (Caullery, 1944) as *Loimia*
Axionice ochracea (Grube, 1878) as *Terebella (Loimia)*
Axionice pachybranchiata (Fauvel, 1932) as *Pista*
Axionice pacifica (Berkeley & Berkeley, 1942) as *Pista*
Axionice palmata (Verrill, 1873) as *Scionopsis*
Axionice parapacifica (Hartmann-Schröder, 1965) as *Pista*
Axionice pegma (Hutchings & Smith, 1997) as *Pista*
Axionice pseudotriloba (Nogueira, Hutchings & Carrerette, 2015) as *Loimia*
Axionice qolora (Day, 1955) as *Pista*
Axionice quadrilobata (Augener, 1918) as *Nicolea*
Axionice robustiseta (Caullery, 1915) as *Pista*
Axionice salazari (Londoño-Mesa & Carrera-Parra, 2005) as *Loimia*
Axionice savignyi (McIntosh, 1885) as *Loimia*
Axionice savignyi trussanica (Annenkova, 1925) as *Loimia*
Axionice seticornis (McIntosh, 1885) as *Terebella (Lanice)*
Axionice sinata (Hutchings & Glasby, 1990) as *Lanice*
Axionice sinusa (Hutchings & Glasby, 1988) as *Pista*
Axionice socialis (Willey, 1905) as *Polymnia*
Axionice sp. A Kritzler, 1984 as *Pista*
Axionice spinifera (Ehlers, 1908) as *Scione*
Axionice symbranchiata (Ehlers, 1913) as *Nicolea*
Axionice triloba (Hutchings & Glasby, 1988) as *Loimia*
Axionice trunca (Hutchings, 1977) as *Pista*
Axionice tuberculata (Nogueira, Hutchings & Carrerette, 2015) as *Loimia*
Axionice turawa (Hutchings & Glasby, 1988) as *Pista*
Axionice turgida (Andrews, 1891) as *Loimia*
Axionice variegata (Grube, 1870) as *Terebella*
Axionice verrucosa (Caullery, 1944) as *Loimia*
Axionice violacea (Hartmann-Schröder, 1984) as *Pista*
Axionice viridis (Moore, 1903) as *Loimia*
Axionice viridis (Nogueira, Hutchings & Carrerette, 2015) as *Lanice* HOMONYM
Axionice wollebaeki (Caullery, 1944) as *Lanice*
Pista abyssicola McIntosh, 1885
Pista anneae Nogueira *et al.*, 2015
Pista anthela Hutchings & Glasby, 1990
Pista australis Hutchings & Glasby, 1988
Pista bansei Saphronova, 1988
Pista brevibranchia Caullery, 1915
Pista cristata (Müller, 1776) as *Amphitrite*
Pista curtiuncata Hartmann-Schröder, 1981
Pista dibranchis Gibbs, 1971
Pista disjuncta Moore, 1923
Pista estevanica (Berkeley & Berkeley, 1942) as *Scionella*
Pista franciscana (Nogueira *et al.*, 2015) as *Pistella*
Pista grubei Augener, 1918
Pista gwoyarrma Hutchings, 1997
Pista kimberliensis Hutchings & Glasby, 1990
Pista microlobata Hessle, 1917
Pista mediterranea de Gaillande, 1970
Pista ortodoxa Saphronova, 1984
Pista papillosa Tourtellotte & Kritzler, 1988
Pista paracristata Safronova, 1988
Pista patriciae Hartmann-Schröder & Rosenfeldt, 1989
Pista pencillibranchiata Saphronova, 1984
Pista sp. B Kritzler, 1984
Pista torquata Hutchings, 2007
Pista typha aequibranchia Caullery, 1944
Pista typha Grube, 1878
Pista unibranchia Day, 1963
Pista vossae Londoño-Mesa, 2012
Pista wui Saphronova, 1988

Invalid species

Pista percyi Hilbig, 2000. Original description does not allow differentiation of this species from *Axionice incarrientis.*

Pista brevibranchiata Moore, 1923. Never described, see Hilbig (2000) for taxonomic explanation = *Axionice agassizi.*

Pista zachsi Annenkova, 1925. Indeterminable, fide Leontovich, Jirkov (2011).

Pista shizugawaensis Nishi & Tanaka, 2006 = *Axionice agassizi* fide Leontovich & Jirkov (2011).

Scionella lornensis Pearson, 1969 = *Pista cristata* s. str. fide Jirkov, Saphronova & Leontovich (2001).

Taxonomic remarks

1. *Pista shizugawaensis*. This species has been considered as a junior synonym of *A. brevibranchiata* by Leontovich & Jirkov (2011) based on re-investigation of paratypes. Choi *et al.* (2015) did not agree and wrote: '*P. shizugawaensis* differs from *P. brevibranchiata* referred by Leontovich and Jirkov (2011) in terms of the detailed shape of notosetae. *P. shizugawaensis* has broadly or narrowly winged capillary notosetae, while *P. brevibranchiata* has capillary notosetae bearing only small denticles on the surface. Also, *P. shizugawaensis* lacks shafts or has short-handled shafts that appear additionally in the uncini on the posterior thoracic segments, but *P. brevibranchiata* has only long handled shafts (Leontovich & Jirkov, 2011)' (p. 156). The differences described by Choi *et al.* (2015) in the notochaetae between their specimens and ours is no more than the difference seen through the compound microscope used by them and seen in the SEM used by us. Uncini without a manubrium in *Axionice* are normally present as a stage of development (see above), so the uncini without a manubrium reported by Choi *et al.* (2015) are either juvenile uncini or, more probably, uncini with broken manubria (it happens often and is not easily distinguishable). So we propose that *Pista shizugawaensis* should be accepted as a junior synonym of *A. brevibranchiata* or, more correctly, of *A. agassizi* (Hilbig, 2000), as *A. brevibranchiata* has never been described as required by the Code (see Hilbig, 2000 for taxonomic discussion).

2. *Amphitrite lobocephala* Hsieh, 1994. According to characters mentioned in the original description (shape of branchiae, arrangement of lateral lobes, uncini arranged back-to-back and others, see Table 1), this species agrees well with species formerly belonging to *Lanice*; we do not understand why it was described as *Amphitrite*. Our calculations (Figures 11 & 12) show that it should be transferred to *Axionice* as we consider that *Lanice* should be accepted as its junior synonym. Nogueira *et al.* (2013) came to the same conclusion, but did not make the necessary taxonomic amendments.