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The taxonominal status of the nomina *Lesueuria* Milne Edwards, 1841 and Lesueuriidae Chun, 1880, and introduction of a new genus and a new family for *Lesueuria pinnata* Ralph & Kaberry, 1950, as well as an additional new species of the new genus (Ctenophora, Lobata)

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Contents

Abstract

The nomenclatural problems posed by the nomen of the ctenophore species *Lesueuria vitrea* Milne Edwards, 1841, type species of the genus *Lesueuria* Milne Edwards, 1841 which is type genus of the family *LESUEURIIDAE* Chun, 1880, and by a few other species long referred to this genus and family, are addressed, and new solutions are proposed for some of them. For the species *Lesueuria pinnata* Ralph & Kaberry, 1950, an unusual 'finned' lobate ctenophore from the southern Pacific Ocean, a new genus and a new family are introduced. It is shown that the nomenclatural problems discussed in this paper raise difficulties for four distinct reasons, related to four different basic concepts of zoological nomenclature: those of 'name-bearing type' or onomatophores, of 'type species' of genera or nucleospecies, of availability, validity and *nomen dubium*, and of 'nomenclatural stability'. The fact that specimens of this group are 'fragile' and difficult or impossible to fix and keep in collections requires recourse to indirect methods (detailed description, good iconography and molecular sequencing) applied to 'ephemeral' type specimens (holotypes or neotypes) to objectify and stabilize the nomenclature in this group.

Key words

Lesueuria, *LESUEURIIDAE*, *Bolina*, *Bolinopsis*, *BOLINOPSIDAE*, onomatophore, type specimen, type species, *nomen dubium*, nomenclatural stability, new species, new genus, new family.

1. Introduction

The genus *Lesueuria* Milne Edwards, 1841 (phylum **CTENOPHORA**, order **LOBATA**) has rarely been mentioned in the last one hundred years, but is listed both in the *World Register of Marine Species* (*WoRMS*; Anonymous 2022) and by Mills (2022), the source list from which the *WoRMS* **CTENOPHORA** list was established, as a valid genus with four species: *L. vitrea* Milne Edwards, 1841, *L. hyboptera* A. Agassiz, 1865, *L. tiedemanni* (Eschscholtz, 1825) and *L. pinnata* Ralph & Kaberry, 1950.

The family *Lesueuridae* (nomen that should be emended into *Lesueuriidae*) was established for this genus by Chun (1880), but more recently the genus has been listed in the family ***Bolinopsidae*** Bigelow, 1912 (Anonymous 2022; Mills 2022).

The first author of this paper decided to revisit and review the genus *Lesueuria* after recently identifying the little-known *L. pinnata* in some 2021 photographs from New Zealand that had been posted on the net (*iNaturalist.org*). Below, we deal with each of the four species nomina presently assigned to *Lesueuria*, in sequence. We show that Milne Edwards' (1841) species nomen *Lesueuria vitrea* is a *nomen dubium*, but not the genus nomen *Lesueuria* Milne Edwards, 1841, which should replace the genus nomen *Bolinopsis* L. Agassiz, 1860, unless the International Commission on Zoological Nomenclature ('the Commission' below) decides its suppression. We also discuss the statuses of the species nomina *L. hyboptera*, *L. tiedemanni* and *L. pinnata.* We erect a new genus and a new family for the latter, and we describe a new species of this genus.

Solving the taxonominal (both taxonomic and nomenclatural) problems raised by this work will require consideration of some of the basic Rules of the *International Code of Zoological Nomenclature* (Anonymous 1999, 2012; 'the *Code*' below). The taxonominal status of a nomen has two different dimensions: its nomenclatural and its taxonomic ones (Dubois 2017*a*: 35–37; Dubois *et al.* 2021: 387, 399, 403). To address correctly the questions raised in this paper, both these aspects will have to be considered.

2. Historical taxonomic survey

2.1. **Lesueuria vitrea** *Milne Edwards, 1841*

Lesueuria vitrea Milne Edwards, 1841: 199–207, pl. 2–4.

Lesueuria vitrea: Lesson 1843: 90; Gegenbaur 1856: 193; Sars 1857: 70; Carus & Gerstaecker 1863: 540; Spagnolini 1870: 61–63; Chun 1879: 202–203; Chun 1880: 291; Carus 1885: 55; M'Intosh 1888: 464–466; M'Intosh 1890: 43–47; Moser 1908: 42, 45–46; Moser 1909: 184; Mortensen 1912: 89–91; Trégouboff & Rose 1957: 412; Mills 1995: 3, 33; Anonymous 2022; Mills 2022.

2.1.1. History

Milne Edwards (1841) found in the Bay of Nice (French Mediterranean Sea coast) a great abundance of a ctenophore species, about 2 cm in length, with four ribbonlike auricles, but with only rudimentary oral lappets or lobes. He described them as a new lobate species *Lesueuria vitrea*, which he explicitly designated (Milne Edwards 1841: 199–200) as type species of his new genus *Lesueuria.*

Lesueuria vitrea was then listed by Lesson (1843), Gegenbaur (1856), Sars (1857), Carus & Gerstaecker (1863), Spagnolini (1870), Chun (1879, 1880), Carus (1885) and Moser (1908, 1909) as present in the Mediterranean. Chun (1879) wrote that he was not lucky enough to see *L. vitrea*, but since Sars and Spagnolini had mentioned it in the Neapolitan fauna, thought he should include it also (Chun 1879, 1880).

Spagnolini (1870: 61–63) had initially believed that his fisherman-collector had brought in three individuals of *Lesueuria vitrea*, but upon close examination and reading the literature, he concluded that what he had seen was actually the lobed *Mnemia norvegica* Sars, 1835, which is now known as *Bolinopsis infundibulum* (Müller, 1776). He specially noted that it is interesting that forms typical of northern seas are also found in the Bay of Naples. Chun (1879: 205) comments about Spagnolini's identification of this lobate as *Mnemia norvegica*, saying that it seems risky, based on Lesson's characteristics of *Bolina* (as *Alcinoe norvegica*, which is based on the old illustrations of Sars), and which are so general and apply to almost every lobed ctenophore, to identify a form that appears in the Mediterranean with an Arctic one.

M'Intosh (1888, 1890) reported having found in St. Andrews Bay, on the east coast of Scotland, great numbers of a ctenophore that agreed with the description of *L. vitrea*. He noted in both publications that, later in the summer, his *L. vitrea* specimens showed a much larger development of the principal lobes at the sides of the mouth than had been observed earlier in the season, but did not challenge the original description and the statement that possessing lobes was a normal condition of the animal.

Moser (1908, 1909) listed and described three known species of *Lesueuria*: *Lesueuria vitrea*, *Lesueuria hyboptera* and *Lesueuria tiedemanni*. Moser (1909: 178) speculated that although *L. vitrea* used to be very common in the Mediterranean near Nice and Naples, it is probably now completely extinct. Vanhöffen (1895) suspected that it is identical to *Bolina vitrea* A. Agassiz, common in the Tortugas and Florida Reefs, but Moser said that there is a lack of evidence for this.

Mortensen (1912: 89–91), in his report on the Danish Ingolf-Expedition, mentioned ctenophores near Iceland and Greenland, and provided a long discussion about the Mediterranean *Lesueuria vitrea*. He agreed with Vanhöffen (1895) to consider that the specimens reported by M'Intosh (1888, 1890) as *L. vitrea* belonged in fact to *B. infundibulum*. He concluded that *L. vitrea* is either a rare deep form only occasionally brought to the surface, or a *Bolina* in a "heteromorph condition": "In my opinion the *Lesueuria vitrea* is only a *Bolina infundibulum* (or perhaps some other lobate) which has lost its lobes through mutilation, and the same I think will prove to hold good of *Lesueuria hyboptera* A. Agassiz. I myself have observed such mutilated specimens of *B. infundibulum*, which were exactly like *Lesueuria* and which I would have regarded as such without the knowledge of the regenerative power of the *Bolina.* […] Leaving the question undecided, to which species the *Lesueuria vitrea* should be referred, it may be regarded as fairly certain that the genus *Lesueuria* cannot be maintained. It represents only mutilated specimens of *Bolina* (and perhaps also other Lobatae) which have lost their lobes."

Bigelow (1912: 390), in his study of ctenophores from the eastern Pacific, replaced the genus nomen *Bolina* Mertens, 1833, which was preoccupied by the molluscan nomen *Bolina* Rafinesque, 1815, by the nomen *Bolinopsis* L. Agassiz, 1860. He established a new family *BOLINOPSIDAE* for all species previously included in *Bolina*. He did not mention the genus *Lesueuria*, apparently because he thought he had not encountered it in his study.

Trégouboff & Rose (1957), in their compendium of Mediterranean plankton species, included *Lesueuria vitrea* with the note "non revue depuis"—'never seen again' [since its original description]. The species was similarly not identified from deep water near Nice and elsewhere along the French Mediterranean coast in more than 25 manned bathyscaphe dives in the 1950s to study the plankton, conducted by Trégouboff and others (e.g., Trégouboff 1958), nor was it seen during a series of eight manned submersible dives in April 1986 studying the plankton off the French coast near Nice (Laval *et al*. 1989), so it is unlikely that *Lesueuria vitrea* is a rarely-seen deep water Mediterranean species.

Trégouboff & Rose (1957) nevertheless reported *Bolinopsis hydatina* (see below) as present along the French coast. They never considered *L. vitrea* and *B. hydatina* to be the same species.

Based on a survey of the historic literature, Mills (1995) reported *Lesueuria vitrea* in a checklist of ctenophore species present in Italian waters and referred it to the family *BOLINOPSIDAE*.

Lesueuria vitrea was listed as a valid species in the family *BOLINOPSIDAE* in both *WoRMS* (Anonymous 2022) and Mills (2022).

2.1.2. Onomatophore

The nomenclatural status of the nomen *Lesueuria vitrea* is based on the specimens from the Bay of Nice that Milne Edwards (1841) had studied and used to write the description of this species, its syntypes. These syntypes, the number of which is unknown, appear to have been lost: Milne Edwards (1841) did not mention their whereabouts and no specimens of *L. vitrea* were deposited by Milne Edwards in the Paris Muséum National d'Histoire Naturelle, though specimens of *Beroe forskalii* Milne Edwards, 1841, also collected off Nice and described on the pages 207–217 of Milne Edwards' (1841) paper, were deposited and recorded in the Catalogue of acalephs of the MNHN (correspondence to C. E. Mills [CEM] from M. Castelin, head of the Cnidaria collection, November 2022). We presume that Milne Edwards was unable to preserve specimens of *L. vitrea* and thus did not deposit any.

2.1.3. Conclusions

That *Lesueuria vitrea* Milne Edwards, 1841 was a damaged *Bolinopsis* seems likely enough after reading the full literature, but especially Spagnolini's (1870) and Mortensen's (1912) arguments, and knowing that it has rarely (never?) been seen since its original description about 180 years ago. It seems not to be determinable whether in fact Milne-Edwards' Mediterranean material was *Bolinopsis infundibulum* (Müller, 1776) or another species, most likely *Bolinopsis vitrea* (L. Agassiz, 1860). Most *Bolinopsis* material identified in recent years in the Mediterranean has been identified as "*Bolinopsis vitrea* (L. Agassiz, 1860)" (see Shiganova & Malej 2009; Lučić *et al.* 2012), though Mills *et al.* (1996) reported both *Bolinopsis vitrea* (near the surface) and *Bolinopsis infundibulum* (between 274 and 831 metres deep, in colder water) in the Alborán Sea, the westernmost portion of the Mediterranean Sea.

In conclusion, the nomen *Lesueuria vitrea* Milne Edwards, 1841 must currently be considered a *nomen dubium* at species level, as it cannot be determined with certainty which Mediterranean species it is conspecific with, but not at genus level, as it most likely belongs in the genus *Bolinopsis*.

2.2.* Bolina vitrea *L. Agassiz, 1860

Bolina vitrea L. Agassiz, 1860: 268–269.

Bolina vitrea: A. Agassiz 1865: 19; Moser 1908: 53; Moser 1909: 185.

Bolinopsis vitrea: Mayer 1912: 22 .

Bolina hydatina Chun, 1879: 204. • ***Synonymy*** with *Bolinopsis vitrea*: Mayer (1912: 22).

Bolina hydatina Chun, 1880: 292–294; Moser 1908: 54; Moser 1909: 185; Mortensen 1912: 77.

2.2.1. History

L. Agassiz (1860: 268–269) briefly described and figured a species from Key West, Florida, that he called "BOLINA VITREA *Ag*.", thus claiming its authorship, and which he considered different from the Mediterranean *Lesueuria vitrea* (Milne Edwards, 1841). A. Agassiz (1865: 19) also mentioned this *Bolina vitrea* L. Agassiz, 1860 and reproduced the figure of L. Agassiz (1860).

Chun (1879, 1880) described a new lobate from the Mediterranean, *Bolina hydatina*, which he did not associate with *L. vitrea*. *B. hydatina* was synonymized with *Bolinopsis vitrea* by Mayer (1912: 25): "*B. hydatina* of Chun is evidently the immature *B. vitrea* from the Mediterranean". The same interpretation was later supported by Shiganova & Malej (2009).

2.2.2. Onomatophore

The nomen *Bolina vitrea* was supported by "only a few specimens" from Florida, illustrated by a drawing, which constitute the syntypes of this nominal species. Agassiz' syntypes, from which he wrote the description of *B. vitrea*, like *L. hyboptera*, would presumably have been deposited at the Museum of Comparative Zoology at Harvard University, where Agassiz worked, but no *B. vitrea* specimens are presently in the collection (correspondence to CEM from A. Baldinger, Collection Manager, May 2022), so they are presumed to be lost.

2.2.3. Conclusions

If this synonymy is adopted and if the nomina *Lesueuria vitrea* Milne Edwards, 1841 and *Bolina vitrea* L. Agassiz, 1860 are considered to apply to two different biological species of the genus *Bolinopsis* L. Agassiz, 1860, the latter is an invalid junior secondary homonym of the former and this species should bear the nomen *Bolinopsis hydatina* Chun, 1879.

2.3.* Lesueuria hyboptera *A. Agassiz, 1865

Lesueuria hyboptera A. Agassiz, 1865: 23–25, fig. 25–28.

Lesueuria hyboptera: Chun 1880: 291; Chun 1898: 22; Vanhöffen 1903: 4–5, fig. 10; Moser 1908: 42, 46; Moser 1909: 184; Mayer 1912: 19–20; Mortensen 1912: 90; Anonymous 2022; Mills 2022.

2.3.1. History

A. Agassiz (1865) described a new species *Lesueuria hyboptera* from Massachusetts Bay and Newport, Rhode Island, comparing it with *Bolina*, "mutilated specimens of which, when seen swimming in water, can easily be mistaken for this species". Agassiz believed the two species to be different, in fact belonging to different genera. Agassiz' syntypes, from which he wrote the description of *L. hyboptera*, would presumably have been deposited at the Museum of Comparative Zoology at Harvard University, where Agassiz worked and deposited other ctenophore specimens, but no *L. hyboptera* specimens are presently in the collection (correspondence to CEM from A. Baldinger, Collection Manager, May 2022), so they are presumed lost.

Chun (1880: xiv, 290–291) erected the new family *LESUEURIDAE* for the sole genus *Lesueuria* and the species *L. hyboptera* as an American (Atlantic) ctenophore species, in addition to the Mediterranean *L. vitrea*.

Chun (1898) mentioned again the family *LESUEURIDAE* with the species *L. hyboptera* as a western Atlantic species from Massachusetts Bay and Newport, Rhode Island.

Vanhöffen (1903) described and figured *L. hyboptera* for the North Atlantic, from A. Agassiz' (1865) description, without any new information. He noted that M'Intosh had observed a *Lesueuria* in the Bay of St. Andrews, Scotland, which is perhaps the same as A. Agassiz' species.

Moser (1908, 1909) listed three known species of *Lesueuria*: *Lesueuria vitrea*, *Lesueuria hyboptera* and *Lesueuria tiedemanni*.

Mayer (1912), while listing and thoroughly redescribing *L. hyboptera* for the east coast of the United States, commented that this species "must be a very rare and occasional visitor to our coast. A. Agassiz found it in great numbers in Massachusetts Bay and Newport Harbor about 1860, but it has never been seen since that time". Similarly, M'Intosh (1888) observed great swarms of *Lesueuria*, possibly *Bolinopsis*, off the coast of Scotland. At the end of his description of *Lesueuria hyboptera*, Mayer (1912: 20) wrote that A. Agassiz had been the "only observer of the American *Lesueuria*, and I am beginning to suspect that this so-called *Lesueuria* is only a *Bolinopsis infundibulum* with its oral lobes torn off and the edges healed over to produce a rounded contour, for I found many specimens of this Ctenophore in Halifax Harbour in such condition after a storm in September".

Mortensen (1912), after writing that he believed that *L. vitrea* will prove to be only a mutilated *Bolina infundibulum* (Müller, 1776), or perhaps some other lobate, suggested: "and the same I think will prove to hold good of *Lesueuria hyboptera* A. Agassiz".

Lesueuria hyboptera was listed as a valid species in the family *Bolinopsidae* in both *WoRMS* (Anonymous 2022) and Mills (2022).

2.3.2. Onomatophore

The nomen *Lesueuria hyboptera* was supported by an unstated number of specimens from Massachusetts and Rhode Island, illustrated by four figures, which constitute the syntypes, now lost, of this nominal species.

2.3.3. Conclusions

Mayer (1912) and Mortensen (1912) both suspected that *Lesueuria hyboptera* A. Agassiz, 1865 was likely only a damaged form of *Bolinopsis infundibulum* (Müller, 1776). No modern authors have reported finding this species and use of the nomen dropped out of the literature following their 1912 observations. *L hyboptera* A. Agassiz, 1865 should be regarded as a junior synonym of *Bolinopsis infundibulum*.

2.4.* Eucharis tiedemanni *Eschscholtz, 1825

Eucharis tiedemanni Eschscholtz, 1825: 742, pl. 5 fig. 12.

Eucharis tiedemanni: Eschscholtz 1829: 30–31, pl. 1 fig. 2; Lesson 1843: 87; Gegenbaur 1856: 193; L. Agassiz 1860: 291; Carus & Gerstaecker 1863: 540.

Lesueuria tiedemanni: Moser 1908: 42, 47; Anonymous 2022; Mills 2022.

Lesueuria (Eucharis) tiedemanni: Moser 1909: 184.

Leucothea (Eucharis) tiedemanni: Komai 1918: 457–458.

Leucothea tiedemanni: Matsumoto 1988: 309.

2.4.1. History

Eucharis tiedemanni Eschscholtz, 1825 was described as a new genus and new species from the North Pacific, east of Japan. This lobate ctenophore was incompletely described: we now understand that it was damaged and without lobes, though with four long and slender auricles; the body between the comb rows was densely covered with short cone-shaped projections. It was redescribed using the same nomen and a slightly different figure by Eschscholtz in 1829.

Lesson (1843), Gegenbaur (1856), L. Agassiz (1860) and Carus & Gerstaecker (1863) included *Eucharis tiedemanni* in their lists of all ctenophores known at the time.

Moser (1908) moved *Eucharis tiedemanni* to the genus *Lesueuria* following Eschscholtz's statement (1829) that it was distinguished from *Beroe multicornis* Quoy & Gaimard, 1824 (then referred to the genus *Eucharis* Eschscholtz, 1825, and now to the genus *Leucothea* Mertens, 1833) by its lobes entirely absent, with only four auricles developed. But Moser missed the point that the body surface of *Eucharis tiedemanni* was described as covered with unique conical projections (also called papillae by other authors), typical of the genus *Leucothea* (then *Eucharis*) and that the long and slender auricles of *E. tiedemanni* were different from those described by Milne Edwards (1841) and A. Agassiz (1865) for their two species of *Lesueuria*.

Komai's (1918) thoughtful reconsideration of Eschscholtz's (1829) description returned *E. tiedemanni* to the genus *Leucothea* (then *Eucharis*) based on its general, but incomplete anatomy. Komai described a new species, *Leucothea japonica*, from Misaki, Japan, because the original description of *L. tiedemanni* was not adequate to distinguish that species from the latter.

Matsumoto (1988), in describing an additional species of *Leucothea*, concurred with Komai that *L. tiedemanni* was best seen as a *Leucothea*, though its description was insufficiently detailed for further comparison.

The *World Register of Marine Species* (Anonymous 2022), which derived from Mills (2022)'s list of valid ctenophore species nomina, missed Komai's (1918) and Matsumoto's (1988) comments and thus continued to list *E. tiedemanni* as *Lesueuria tiedemanni*.

2.4.2. Onomatophore

The nomen *Eucharis tiedemanni* was supported by an unstated number of specimens from the North Pacific, illustrated by a figure, which constitute the syntypes, now lost, of this nominal species.

2.4.3. Conclusions

Current authors agree that *E. tiedemanni* Eschscholtz, 1825 belongs to the genus *Leucothea* Mertens, 1833, but as a dubious species, acknowledging that Eschscholtz's (1825) original description does not offer enough information for this species to be distinguished from *L. japonica* Komai, 1918.

2.5.* Lesueuria pinnata *Ralph & Kaberry, 1950

Lesueuria pinnata Ralph & Kaberry, 1950: 7–8.

Lesueuria pinnata: Mianzan *et al*. 2009: 52, 58; Anonymous 2021; Anonymous 2022; Mills 2022.

2.5.1. History

This species was collected in the Cook Strait, New Zealand, a few kilometres offshore of Island Bay on the exposed Wellington outer coast, in the autumn (March, April) 1935, during a year-long study from July 1934 to July 1935 (Ralph & Kaberry 1950; Mianzan *et al*. 2009). *L. pinnata* was common near the surface during periods of unusually calm weather with the absence of wind, which allowed observation and collection of these delicate animals, though they began disintegrating after an hour or so of confinement (Ralph & Kaberry 1950: 7). The authors remarked that this animal was very difficult to capture on account of its large size (to 290 mm in length) and delicate nature.

The unusually calm weather of the collection period may explain why this very large species has almost never been seen since its description. The species description was written about 15 years after the animals were collected, and is accompanied by a fairly cartoon-like illustration, which may have been drawn from memory, and which the first author has found difficult to interpret, until she saw photographs of purported *Lesueuria* from two locations in southern New Zealand, posted on *iNaturalist.org* (Anonymous 2021). The ctenophores in these two photographs have body proportions quite different from those of the drawing in Ralph & Kaberry (1950), but match the written description much more substantially.

Ralph & Kaberry (1950) revived the old genus *Lesueuria* for their new lobate species *Lesueuria pinnata*. "It is with hesitation that we revive the genus *Lesueuria* Milne-Edwards, 1841, to receive these New Zealand specimens of the *O. Lobata*, for Mortensen (1912) unhesitatingly concluded that *Lesueuria* is nothing else than a regenerating *Bolina* (Syn. *Bolinopsis* Mayer 1912). All the present specimens fall within the generic description of *Lesueuria* as defined by Mayer (1912). 'Lobatae with rudimentary oral lappets and with long, ribbon-shaped auricles. The peripheral gastrovascular system is simple, without complex windings.'" Ralph & Kaberry (1950) specifically mentioned that, in Cook Strait, "*Lesueuria* and *Bolinopsis* have been taken on the same day and can be readily distinguished one from the other." Their *Bolinopsis paragaster* has since been referred to the genus *Bathocyroe* (Madin & Harbison 1978: 562; Mianzan *et al*. 2009; Mills *et al*. 2023.)

Mianzan *et al*. (2009) reiterated Ralph & Kaberry's description of *L. pinnata*, which has apparently not been seen (or published, in any case) since Kaberry's 1934–1935 unpublished thesis collections.

Lesueuria pinnata was listed as a valid species in the family *BOLINOPSIDAE* in both *WoRMS* (Anonymous 2022) and Mills (2022).

Photographs of two lobate ctenophore specimens listed above were taken along the South Island and Stewart Island, New Zealand, in December, 2021. Without the benefit of observing the animals in life and under a microscope, they do appear to conform with Ralph & Kaberry's (1950) detailed description of *L. pinnata*.

2.5.2. Onomatophore

The nomen *Lesueuria pinnata* was supported by an unstated number of specimens from New Zealand, illustrated by a drawing, which constitute the syntypes, now lost, of this nominal species.

2.5.3. Conclusions

Lesueuria pinnata is currently considered a valid species of **LOBATA**, but, as shown above, its allocation to the genus *Lesueuria*, that rests on its type species *L. vitrea*, is not justified, and no other genus nomen is available for this species. This problem requires a nomenclatural solution, which is provided below.

2.6. Genus* Lesueuria *Milne Edwards, 1841

2.6.1. History

The genus *Lesueuria* was erected by Milne Edwards (1841) together with the species *Lesueuria vitrea.*

2.6.2. Onomatophore

The generic nomen *Lesueuria* was established for a single nominal species, *Lesueuria vitrea*, expressly designated as its type species by Milne Edwards (1841).

2.6.3. Conclusions

The two aspects of the taxonominal status of a nomen, its nomenclatural and its taxonomic statuses, often coincide, but sometimes disagree. This is the case here for the nomen *Lesueuria*.

Its nomenclatural status is clear: this nomen is based on the nominal species *Lesueuria vitrea* Milne Edwards, 1841, its type species, which means that it may potentially apply to any genus-series taxon including this species. Similarly, the nomenclatural status of the latter is also clear: it is based on the now lost syntypes of its type species.

The taxonomic status of this nomen therefore depends on the taxonomic interpretation given to the original description of *Lesueuria vitrea* by Milne Edwards (1841). If this interpretation is that it applies to organisms that have not yet been found again since 1841 and that, given the incomplete information we have about them, cannot be allocated to a known species or genus, the nomen *Lesueuria vitrea* must be interpreted as a *nomen dubium*, i.e. a nomen of completely unknown or doubtful application (Anonymous 1999), and by way of consequence this applies also to *Lesueuria*. Then, as long as this uncertainty persists, these two nomina must be treated as invalid and cannot be applied to any taxa. But if this interpretation is that the specimens observed by Milne Edwards were damaged specimens of a species of *Bolinopsis*, the nomen *Lesueuria* must be treated as applying to this genus, even if this species has not been collected again and remains very poorly known. Then the nomen *Lesueuria* must be accepted as a senior synonym of *Bolinopsis*, having priority over the latter.

2.7. Family **LESUEURIIDAE** *Chun, 1880*

LESUEURIDAE Chun, 1880: 290, 291.

LESUEURIDAE: Chun 1898: 22; Mortensen 1912: 91.

2.7.1. History

L. Agassiz (1860) and Carus & Gerstaecker (1863) included *Lesueuria* in the family *MNEMIIDAE* Eschscholtz, 1829, based on the genus nomen *Mnemia* Eschscholtz, 1825[1], while A. Agassiz (1865) moved this genus into the *BOLINIDAE* L. Agassiz, 1860.

Chun (1880: xiv, 290–291) erected a new family *LESUEURIDAE* for the species *L. vitrea* and *L. hyboptera*. This family nomen was incorrectly formed and should be emended into *LESUEURIIDAE*.

Chun (1898) again listed the family *LESUEURIDAE* with the species *L. hyboptera* as an Atlantic ctenophore species.

Moser (1908: 45, 1909: 184) placed *Lesueuria* in the family *BOLINIDAE*.

Mayer (1912), in his monograph of the ctenophores of the Atlantic coast of North America, listed 21 species of ctenophores, dividing them into the orders **CYDIPPIDAE**, **LOBATAE**, **CESTIDAE**, **BEROIDAE** and **PLATYCTENIDAE**, but did not use family nomina, so *Lesueuria* was listed only as belonging to the **LOBATAE**.

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[1] We will discuss elsewhere the statuses of the nomina *Mnenia* Eschscholtz, 1825 and *MNEMIIDAE* Eschcholtz, 1829.

Mortensen (1912) stated that, since the two *Lesueuria* species *L. vitrea* and *L. hyboptera* appear to be merely mutilated representatives of the genus *Bolina*, the family *Lesueuridae* cannot be maintained.

2.7.2. Onomatophore

The family nomen *Lesueuriidae* is based on its type genus *Lesueuria*, and therefore applies to any species including the type species of the latter, *Lesueuria vitrea* Milne Edwards, 1841.

2.7.3. Conclusions

The reasoning here is exactly the same for the taxonominal status of this family nomen as for its type genus *Lesueuria* Milne Edwards, 1841 discussed above under § 2.6.

3. Discussion

The nomenclatural problems discussed in this paper raise difficulties for four distinct reasons, related to four different basic concepts of zoological nomenclature: those of [A1] 'name-bearing type' or onomatophore, [A2] 'type species' of genera or nucleospecies, [A3] availability, validity and *nomen dubium*, and [A4] 'nomenclatural stability'.

3.1. The concept of onomatophore

The first basic concept to consider is that of 'name-bearing type' or onomatophore (Dubois & Ohler 1997; Dubois 2000, 2020). In zoological nomenclature, nomina are allocated to taxa through specimens, not through verbal descriptions or definitions. Species and subspecies nomina rely on 'name-bearing specimens' or onymophoronts (Dubois 2005), genus and subgenus nomina on 'name-bearing nominal species or subspecies' or nucleospecies (Dubois 2005), and nomina of taxa above genus on 'name-bearing nominal genera or subgenera' or nucleogenera (Dubois 2005, 2022). This objective connection between nomina and specimens allows the solution of most problems of allocation of nomina to taxa, but this requires that taxonomists rely on these 'name-bearers' for their work, i.e., in the end, on specimens preserved in permanent collections. It is also important to realize that the concept of onymophoront carries another important concept, that of 'type locality' (onymotope), which provides another important clue for the taxonomic allocation of species-series nomina (Dubois & Ohler 1997; Dubois 2000; Frétey *et al.* 2018).

In ctenophores, many taxonominal problems derive from the fact that few such specimens exist, and that allocation of many nomina is made merely through verbal descriptions and figures (drawings or photographs) of specimens, not through specimens themselves. This problem derives mostly from the impossibility to fix and preserve specimens of this group, which was stressed long ago. Thus, L. Agassiz (1850: 350) wrote about his *Bolina alata*: "It is a most delicate, transparent, and diffluent animal; so soft, that it readily decomposes under the least unfavorable circumstances. The admixture of a small proportion of fresh water in the bowls in which I used to preserve them caused not only their immediate death, but their almost instantaneous decomposition. All my efforts at preserving specimens in Goadby's liquor have entirely failed, and when, under identical circumstances, I succeeded in keeping for a long time specimens of *Pleurobrachia rhododactyla*, I failed in preserving specimens of *Bolina alata* longer than twenty-four hours." The reasons for this peculiarity of these specimens are presumably the very high water content and fragility of the tissues of many lobate and cydippid species. Differences in their biochemistry, including enzyme sequences (Winnikoff *et al*., 2019) and variations in cell membrane properties (Winnikoff *et al*., 2021), have recently been shown to vary with pressure, temperature and depth between ctenophore species, and likely also contribute to our inability to preserve some ctenophores with present methods.

In recent works, good morphological descriptions and illustrations can sometimes serve as acceptable proxies for specimens and allow reliable conclusions, but this is not the case in publications, especially ancient ones, which provide only poor descriptions and iconography. In such cases, taxonomic allocation of specimens can rely only on (sometimes highly) subjective interpretations, and cannot work as an acceptable basis for the validity of nomina or their relegation to the status of invalid synonyms. For this reason, Ceríaco *et al.* (2016) stated that "photography-based taxonomy is inadequate, unnecessary, and potentially harmful for biological sciences", and they recommended that the *Code* be modified in order to state that new species or subspecies nomina introduced without a material specimen deposited in a permanent institutional collection be denied nomenclatural availability. The Commission, without explaining its reasons to do so, refused to modify the *Code* in this respect, just adding some Recommendations (73G–73J), but keeping the Rules unchanged (Anonymous 2017).

The nomenclatural problems raised by the introduction of new nomina without reference vouchers in zoological groups where it is very difficult or impossible (at least nowadays) to collect or preserve specimens has already been pointed to in other zoological groups:

> "There may be various reasons for these difficulties: inaccessibility of specimens in their habitat, absence of appropriate methods of collection, size (too large or too small), problems of fixation and long-term preservation, etc. Garraffoni & Freitas (2017) highlighted the fact that, once fixed, specimens of some soft-bodied meiofaunal organisms (small invertebrates that live in marine and freshwater sediments, such as gastrotrichs) deteriorate and most of their 'diagnostic' characters vanish soon after preservation. They used this fact as an argument in favour of the description of such species based only on photographs and movies, without preserved specimens. In such cases, it certainly is fine and useful to provide photo and movie evidence in addition to preserved specimens (and of course this also applies to all other descriptions of animal taxa), but they won't replace the material evidence provided by a specimen (with its tissues, cells, nucleic acids, etc.), even if damaged. Furthermore, it can also be argued that the issue here lies with technological and scientific developments: namely that one should work for developing appropriate technological solutions for long terms preservation of such specimens with most of their characteristics. So the problem is (at least) as much not having devoted resources and ingenuity to the amelioration of preservation techniques of physical specimens. Some specimens that decades ago could not be preserved at all, like some mushrooms, can now be preserved using lyophilization, and certainly other 'new' techniques can and will be developed." (Dubois 2017*b*: 15).

The present work shows that ctenophores, or at least some of them, should be added to meiofaunal organisms as a group where nomenclatural problems derive from difficulties in the collection and preservation of specimens. Dubois & Nemésio (2007) and Dubois (2017*b*) have already proposed a possible solution to this problem, that could be compatible with a possible future requirement by the *Code* to deposit specimens in collections for the description of new species. They suggested that in such cases the problem be referred to a specific 'International Body' (IB), which could be the Commission, to give, or not, its agreement for such descriptions in exceptional cases, with the following addition to the *Code*:

> "[…] in the exceptional case where no specimen could or can be collected and/or preserved […], formal description and naming of the taxon should be postponed until one or several specimens can be collected and preserved; if it appears unlikely that any specimen will ever be collectable for deposition in a collection, the taxon may be described and named on the basis of indirect evidence (e.g., ancient document showing an illustration or presenting a description of the taxon, descriptions, photographs, molecular data) in a text submitted for evaluation to the IB, which will decide whether this description without nomen-bearer should be accepted as a publication as defined by the *Code* and the nomen at stake provided nomenclatural availability, as allowed by Article 10.1.
>
> […] in the case of a species-series nomen made available [through this procedure], a specimen complying with the qualifying conditions for neotype designation as defined in Article 75.3 is found to be preserved in a public collection, this specimen may be designated as neotype for the nominal taxon, just like in the case of name-bearers destroyed, lost or the accessibility for scientific study of which is denied by the persons in charge of their preservation." (Dubois 2017*b*: 28).

We support these proposals in the case of ctenophores. In many cases, it has proved so far impossible to fix and preserve specimens, because of the properties of these organisms. But an exceptional procedure could be used in such cases, which would be *Code*-compatible even without intervention of an IB, as long as the *Code* does not require the deposition of specimens in permanent collections for the availability of new nomina (which could possibly change in the future). This procedure would include the following steps: [B1] collection of new specimens which would clearly fit with either [B1a] the original description and the concept of the taxon used in the literature, and coming from a locality as close as possible to the original onymotope, or [B1b] the concept of a new taxon to be described; [B2] the designation of this specimen as either [B2a] neotype in the first case or [B2b] holotype in the second case; [B3] the gathering, immediately after collection of the specimen (possibly on the deck or laboratory of a boat or ship) of the following data from it: [B3a] its description, as accurate, detailed and complete as possible, [B3b] its iconography (photographs and/or drawings or paintings), as good and complete as possible, and [B3c] extraction from it, fixation and conservation, of tissues for future molecular sequencing. This being done, even if it decays and vanishes in the next hours, days or weeks, and that nothing remains of it, these data will be available as proxies for this specimen, allowing the use of the concept of nomen-bearer in ctenophore nomenclature.

Some of our proposals below are based on this rationale. This procedure could indeed be used to stabilize the status of all ctenophore species nomina, but this would be superfluous and useless in all the cases where there is a widespread, unchallenged consensus on the status of a nomen in the community—just like it is unnecessary to designate routinely neotypes for all species the type specimens of which have been lost but which raise no nomenclatural problems in all other zoological groups. But we propose below to use it in some cases of species nomina which are doubtful at species level, and we think it should become a standard in all future descriptions of new ctenophore species.

3.2. The concept of type species

The second problem to address is that it must be remembered that type species of genera are nominal species, not taxonomic species. In consequence, to be valid, a subsequent type species designation must mention a nominal species explicitly mentioned as included in the genus in the original designation, not one that did not appear there, even if it was later considered as a synonym of one of the originally included species (for details, see Dubois 2022).

3.3. The concepts of availability, validity and nomen dubium

The third important concept is that of *nomen dubium* (doubtful nomen), the proper understanding of which requires distinguishing the concepts of availability and validity in zoological nomenclature. A *nomen dubium* is a nomen of unclear taxonomic allocation, which can occur in three main different situations (Dubois 2011: 54–55): absence of onomatophore, heterogeneous onomatophore and onomatophore taxonomically unidentified. As long as these unclarities have not yet been cleared up, a *nomen dubium* cannot be used as valid, but it still remains available and cannot be rejected as permanently invalid.

Some authors (e.g., Dayrat 2005) consider *nomina dubia* as a major problem of zoological nomenclature, but this attitude derives from an misinterpretation of the nature of type specimens and a misunderstanding of the distinction between nomenclature and history of science.

Nomenclatural Rules appeared rather early in the history of biological taxonomy, simply because of the high numbers of taxa that were soon recognized by taxonomists and of the need to avoid miscommunication about these taxa. This was done through building a system allowing to establish unambiguously the unique valid nomen for each of these taxa within the frame of a given classification. In zoological nomenclature, in most cases, these Rules (relying upon specific technical concepts and tools such as availability, onomatophore or priority) allow reaching this goal rather straightforwardly and without possible discussion or disagreement between specialists, but this is not the case in a minority of cases. Among them are the situations where a nomen is a *nomen dubium*, as defined above. The nomenclatural and taxonomic status of such a nomen may often be clarified through a nomenclatural solution, e.g., a restriction (lectotype) among syntypes or a replacement (neotype) by onymotopic specimen(s) of lost or unidentifiable type specimens(s). The ideal situation is when the original information provided in the work which rendered the nomen available allows for a fairly good hypothesis about the taxon that was the basis for the erection of the new taxon and introduction of the new nomen. This allows to designate a well identified specimen (ideally associated with tissues or nucleic acid sequences) as lectotype or neotype. The purpose here is not to try to guess what was the species actually present in the hands of the author of a nomen, a question which belongs in the realm of history of nomenclature, but to fix and stabilize the status of the nomen, in order to remove the nomenclatural uncertainty resulting from the dubious status of this nomen. This practice allows solution of most nomenclatural problems linked to the existence of *nomina dubia*. Unfortunately, it seems largely ignored in ctenophore nomenclature.

There are several 'levels' for a nomen to be 'doubtful'. It may be so at species, but not at genus or higher level, as is the case for the genus *Lesueuria*, and this has nomenclatural consequences, as we have seen above.

Finally, when a nomenclatural problem of this kind cannot be solved by individual taxonomists, the possibility exists to call on the Commission for a 'suppression' (or better invalidation; see Dubois 2000) of nomina, but this should remain an exceptional, not routine, approach of the problems—especially given the very long delays from the date of submission of applications to the Commission to its final decision, when it indeed occurs.

3.4. The concept of 'nomenclatural stability'

Following changes brought to the *Code* in its 1999 edition, many taxonomists nowadays consider the concept of 'nomenclatural stability' as a very important one in zootaxonomy, although it is a poorly defined one (see Dubois 2005) and is contradictory and incompatible with the Principle of Priority which is the basis on which the validity of millions of nomina has been established during the long history of zoological nomenclature:

> “Given the gigantic number of ‘objects’ that the nomenclatural system has to manage, a simple system based on a single binding and automatic Principle will doubtless be more efficient in the long run than a dual system based on two contradictory and incompatible Principles. Furthermore, the new approach raises several kinds of problems […]: (1) it weakens the binding value and strength of the *Code*; (2) it encourages useless or destructive personal debates among taxonomists; (3) it sends a wrong message to non-taxonomists; (4) it acts as a threat against natural history museums.” (Dubois 2011: 28).

Among many others, Dickinson *et al.* (2011) also provided well-founded arguments to sticking to priority as the basic principle for the validity of zoological nomina. For this reason, the *Linz Zoocode Committee* (LZC) made the following proposals:

> “The plea for **nomenclatural stability** does not answer a scientific, but a practical need, and it should not take the lead on **nomenclatural accuracy**: ***Priority*** should be reinstated as the only **basic Principle** of validity of nomina, and usage should be called upon only for **very-well-known nomina**, objectively defined.” (Dubois *et al.* 2019: 9).
>
> “The LZC does not adhere to the current worship for so-called nomenclatural stability. We consider that Priority should be reinstated as **the basic Principle** of validity of nomina, and that usage should be called upon only for very-well-known nomina. The formula ‘very-well-known nomina’ points to nomina that have been used as valid **hundreds or thousands of times** in the general scientific (and even non-scientific) literature, like *Drosophila melanogaster*, *Homo neanderthalensis* or *Tyrannosaurus rex*. The protection against Priority should be limited to such nomina, and in all other cases the normal Rules should apply. The so-called ‘nuisance’ caused by nomenclatural instability exists only for these well-known nomina. In all other cases, the ‘nuisance’ comes instead not from nomenclatural instability but from those who do not want to follow the *Code* and who will engage our community into endless discussions to establish whether or not the normal Rules should be circumvented in order to protect an ‘obscure’ nomen (used, and even known, by only a handful of persons) against another ‘obscure’ one. Such sterile discussions have already been the cause of the loss of hundreds of working hours and of printed pages in the last century and, in the century of extinctions, it is time for this to stop, in order to free up a lot of time for genuine taxonomic work.” (Dubois *et al.* 2019: 22).

The LZC (Dubois *et al.* 2019: 71) proposed to replace the statements concerning stability in the *Code* (in particular, but not only, in its Article 23.9) by a new ‘Principle of Sozoidy’. The latter requires, to validate a nomen found to be in conflict of priority with a senior nomen to designate the same taxon, that the junior one has appeared in the ***titles*** of at least 100 publications after 31 December 1899, whereas the senior one has never been used as valid in any title. This objective Rule is much stricter than those of the *Code* and it should limit the endless discussions which currently appear in the literature around such problems, such as that potentially caused by the disputed taxonomic status of the nomen *Lesueuria vitrea* Milne Edwards, 1841.

So far, however, such a Rule is not present in the *Code*, and Articles 23.9.1–2 cannot be used to solve the nomenclatural problem described above, as both nomina *Lesueuria* and *Bolinopsis* have been used as valid in the literature after 1899 (see Dubois & Ohler 2018). The only Article that could be used in this case is Article 23.9.3, which reads:

> “If the conditions of 23.9.1 are not met but nevertheless an author considers that the use of the older synonym or homonym would threaten stability or universality or cause confusion, and so wishes to maintain use of the younger synonym or homonym, he or she must refer the matter to the Commission for a ruling under the plenary power […].” (Anonymous 1999: 28).

As this Article relies on what a taxonomist 'considers', it is not really an operational Rule having an universal value as it allows opposite interpretations (see also Dubois & Ohler 2018). We will discuss this point in more detail below.

4. Conclusions

4.1. New proposals

The data and discussions above led us to a few conclusions, which require complementary reflections and actions: [C1] the type species of *Lesueuria* Milne Edwards, 1841, *Lesueuria vitrea* Milne Edwards, 1841, described from the Mediterranean Sea, as well as *Lesueuria hyboptera* A. Agassiz, 1865, described from the northwest Atlantic, share features with the genus *Bolinopsis* L. Agassiz, 1860, to which they have been transferred by some authors, whereas others regarded their nomina as *nomina dubia*; [C2] *Eucharis tiedemanni* Eschscholtz, 1825 is now considered to be an insufficiently characterized species of *Leucothea* Mertens, 1833; [C3] as for *Lesueuria pinnata* Ralph & Kaberry, 1950, a species from an ocean different from that where *Lesueuria* Milne Edwards, 1841 had been described, and having unique features within the lobate ctenophores, it is here interpreted as belonging to a still undescribed genus, for which a nomen needs to be provided.

Below, we review the taxonomic and nomenclatural consequences of these findings for the nominal species above and for a few related nominal taxa.

The nomen *Beroe infundibulum* Müller, 1776 was one of the first species of **CTENOPHORA** ever described, which explains why it has several synonyms. For reasons given above, here we consider the nomen *Lesueuria hyboptera* A. Agassiz, 1865 as an invalid junior subjective synonym of *Beroe infundibulum* Müller, 1776, and the nomen *Bolina vitrea* L. Agassiz, 1860 as a senior synonym of *Bolina hydatina* Chun, 1879.

As we have seen above (§ 2.6.3), the nomenclatural statuses of the nomina *Lesueuria vitrea* Milne Edwards, 1841, *Lesueuria* Milne Edwards, 1841 and *LESUEURIIDAE* Chun, 1880 are clear, but their taxonomic statuses depend on the taxonomic interpretation of the description of *Lesueuria vitrea* by Milne Edwards (1841). Let us remember the two possible interpretations of this description: [D1] if this description is considered to point to an 'unknown', or at least poorly known, species whose generic allocation is dubious, these three nomina will have to be considered *nomina dubia* and therefore provisionally invalid—but this situation may change if new information allowing to clarify the taxonomic status of the specimens at stake is found later; [D2] if this description is considered to apply to a, still undeterminate, species, but that this species is considered to be clearly a member of the genus *Bolinopsis*, *Lesueuria vitrea* will remain a *nomen dubium* at species level, but this will not be the case of *Lesueuria* and *LESUEURIIDAE*.

Let us note that, nowadays, the recourse to molecular techniques (nucleic acid sequencing, barcoding) could allow to clarify the taxonomic allocation of specimens newly collected at or close to the type localities of all these nominal species and fitting their original descriptions, including *Lesueuria vitrea*. This has not been done so far, but should such work be carried out, and should it confirm that specimens fitting the original description of the latter are members of the genus currently known as *Bolinopsis* L. Agassiz, 1860 (situation [D2]), then the nomen *Lesueuria* Milne Edwards, 1841 would have priority over the latter and should replace it as the valid nomen of the genus. As both nomina *Lesueuria* and *Bolinopsis* have been used as valid in the scientific literature after 1899, Article 23.9 of the *Code* on reversal of precedence cannot be called upon to 'save' *Bolinopsis*. In such a case, the same logic would apply among family nomina: *LESUEURIIDAE* Chun, 1880 would have to replace its junior subjective synonym *BOLINOPSIDAE* Bigelow, 1912.

Which of these two solutions would be the best in this case?

It should be pointed out that most specialists of these animals who have so far examined in detail the available (morphological) data concerning *Lesueuria vitrea* have come to the conclusion that the specimens originally described under this nomen were damaged specimens of *Bolinopsis*, not a new, unknown genus different from all known and well studied genera of **LOBATA**.

The solution [D1], preserving the validity of *Bolinopsis* and *BOLINOPSIDAE*, would clearly be the most cautious one, as it would not rely on assumptions, but it would be liable to be refuted as soon as molecular data are available. If these data confirmed the assumptions reviewed above, this would result in nomenclatural instability, these two nomina having to be replaced by *Lesueuria* and *LESUEURIIDAE*. This instability would be all the more worrying that a long time would have elapsed before this molecular confirmation of hypotheses shared by most authors.

The solution [D2], which would result in this replacement being implemented right now, before molecular confirmation, would appear more 'radical' today, but would have apparently much more chance to be confirmed by molecular data, and therefore to lead to longer nomenclatural stability.

Besides long term stability, another argument in favour of solution [D2] is parsimony. The interpretation [D1] creates the hypothesis of the existence of an 'unknown', or at least insufficiently described and characterized, genus that would have escaped the attention of all authors and naturalists until now, whereas [D2] does not require this gratuitous hypothesis and is therefore more parsimonious. This case is reminiscent of a famous one dating from the beginnings of scientific natural history, concerning the mammal genus *Giraffa* Brünnichius, 1772.

Let us recollect the basic facts of this affair, which qualifies as one of the first 'pages' of the then nascent discipline of comparative anatomy. A very large bone of unknown origin which had been kept in the natural history cabinet of Gaston d'Orléans, brother of the French king Louis XIII, was transferred in 1670 to the Jardin du Roy, the ancestor of the Paris Museum of Natural History. It was then believed to be a tibia of a giant and was the pride of the marquise de Pompadour, favorite of Louis XV. In 1762, the naturalist Louis Jean-Marie Daubenton (1716–1800) presented and published a report where he stated that this bone was in fact a radius of giraffe, although he had not seen any skeleton of this animal which was then known only from travellers' tales. His reasoning was as follows: as we know that such a giant animal exists in Africa, and as we have a very large bone that does not fit with any of the many skeletons of large mammals that we have in our collections, the hypothesis that this bone comes from this animal is simpler (we would now say 'more parsimonious') than that according to which it would come from an unknown animal, which would then require an additional hypothesis. Daubenton had confirmation of his hypothesis only in 1795, when he finally had the possibility to examine a complete skeleton of a giraffe (Poplin 1981: 102–105; Dufay 2009: 39–43).

The present paper is co-signed by two authors. It happens that they disagree on the best solution to this nomenclatural problem. Although this is not a very common situation in science, nothing impedes two authors having different opinions about the best solution to a problem requiring a choice between two possibilities to co-sign a paper explaining their respective rationales. In the present case, the first author thinks that we cannot be sure of what species was in the hands of Milne Edwards, whose description does not fit with any species currently known, and for this reason favours the solution [D1]. The second author acknowledges that this uncertainty exists but thinks that nomenclatural problems are distinct from historical ones: while it is clear that we will never know which species was in the hands of Milne Edwards, the duty of taxonomists now is to fix the taxonomic status of his nomen *Lesueuria*, which can be done through the designation of a neotype for this nominal taxon.

Given this disagreement between the two authors of the present paper, we suggest this case should be submitted to the arbitration of the Commission, and both authors declare that they will abide by it. Such an external arbitration is necessary because there is no objective fact allowing to choose between the two genus nomina as the valid one for the species described by Milne Edwards (1841). Both interpretations have been adopted since 1899, the threshold fixed by Article 23.9, to designate it: while Vanhöffen (1903), Moser (1908, 1909), Trégouboff & Rose (1957) and Mills (1995, 2022) used for it the generic nomen *Lesueuria*, Vanhöffen (1895) and Mortensen (1912) referred it to the genus *Bolina* or *Bolinopsis*.

Below we present the synonymic lists (*sensu stricto*, i.e., not mentioning aponyms and chresonyms: see Dubois 2000) and the taxonominal statuses of all the ctenophore nomina addressed here. Regarding the nomenclatural status of the nomen *Lesueuria vitrea* Milne Edwards, 1841, which is at the root of several of the nomenclatural problems discussed above, we present these lists under two different rationales, [D1] according to which this nomen applied to an 'unknown', or at least poorly known, species whose characters and generic allocation is dubious, and [D2] according to which this nomen was based on specimens of a species being a member of the genus *Bolinopsis* as currently understood.

In the second hypothesis, we go a little further in the disambiguation of the nomenclatural situation through proposing that, whenever available, a specimen clearly referred to the species originally described as *Beroe infundibulum* Müller, 1776~~:~~ be designated as neotype for *Lesueuria vitrea* Milne Edwards, 1841, under the three-step procedure reviewed below (§ 4.2).

A further consequence of the choice between [D1] and [D2] is that, according to it, the nomen *Bolina vitrea* L. Agassiz, 1860 will be either an invalid junior secondary homonym of *Lesueuria vitrea* Milne Edwards, 1841 under [D2], and then will have to be replaced by *Bolina hydatina* Chun, 1879 as valid nomen of the species, or not under [D1], and then standing as the valid nomen of this species (which may be a source of confusion with Milne Edwards' nomen).

In parallel with the present paper, we will address an application to the *Bulletin of Zoological Nomenclature* asking the Commission to choose between the options [D1] and [D2].

4.2. Proxies for type specimens

We discussed above (§ 3.1) why the difficulties for the preservation of many ctenophores require use of a peculiar procedure for the fixation of their type specimens, using proxies to replace the vanishing specimens on which the original description was built. We described a three-step process, [B1] to [B3], which could be used for this purpose. It is true that in its current version the *Code* does not require the deposition of specimens in collections for the promulgation of new nomina, and just provides Recommendations (73G–73J) in this respect. But this situation might change in the future, especially considering the overwhelming majority of taxonomists who expressly supported the statement that the availability of new nomina should require such a deposition: just compare the 493 signatories of the paper by Ceríaco *et al.* (2016) with the 40 signatories altogether of the papers by Pape *et al.* (2016) and Krell *et al.* (2016). This striking fact was fully ignored by the Commission in its decision on this matter (Anonymous 2017). We think the *Code* should be modified again in this respect by incorporating in it the explicit three-step procedure above. This would provide a solution for the problems raised by the few groups of organisms, including meiofauna and ctenophores, for which it is currently impossible to preserve specimens—while prohibiting the promulgation of new nomina proposed without type specimens based on neglect (specimens escaped from captivity before having been fixed or dead and decayed in captivity and not preserved) or other spurious reasons such as reluctance to euthanize specimens or so-called 'conservation' arguments (see in this respect the detailed discussions in Dubois & Nemésio 2007 and Dubois 2009).

We think this three-step procedure should become a standard in all future descriptions of new ctenophore species, and some of our proposals below are based on this rationale.

4.3. Synonymic lists

We present below synonymic lists of some of the taxa of ctenophores discussed in this paper, excluding those currently referred to the families *Leucotheidae* Lesson, 1843 and *Mnemiidae* Eschscholtz, 1829 which will be discussed elsewhere. The formats of these lists follow those used recently by Dubois (2021), Frétey (2022) and Dubois *et al.* (2022). Synonymies are presented by families, listed by alphabetical order.

Some of these synonymies differ according to the choice made between [D1] and [D2] above, here renamed Options 1 and 2, regarding the status of the nomen *Lesueuria vitrea* Milne Edwards, 1841, presented respectively under 4.3.1.1 and 4.3.1.2. The other synonymic lists are not affected by this choice: they are presented in 4.3.2.

4.3.1. Synonymic lists resulting from choice between Options 1 or 2 for the taxonomic status of Lesueuria vitrea *Milne Edwards, 1841*

4.3.1.1. Option 1. The nomen *Lesueuria vitrea* Milne Edwards, 1841 is a *nomen dubium*

F1. Family ***Bolinopsidae*** Bigelow, 1912

Bolinidae L. Agassiz, 1860: xi, **200** [family]. • ***Type genus***, by implicit etymological designation: *Bolina* Mertens, 1833: 513. • ***Comment***: Permanently invalid nomen for being based on a genus nomen being an invalid junior homonym. • ***Synonymy***: *Hoc loco*.

Bolinopsidae Bigelow, 1912: 390 [family]. • ***Type genus***, by implicit etymological designation: *Bolinopsis* L. Agassiz, 1860: 199. • ***Comment***: Although Bigelow (1912: 390) explicitly presented this new nomen as a 'nom. nov.', this is incorrect, because he did not mention the nomen *Bolinidae*, and because *Bolinopsis* is not a *nomen novum* for *Bolina*.

G1. Genus ***Bolinopsis*** L. Agassiz, 1860

Bolina Mertens, 1833: 513 [nec *Bolina* Rafinesque, 1815: 144]. • ***Originally included nominal species*** (2): *Bolina elegans* Mertens, 1833: 513; *Bolina septentrionalis* Mertens, 1833: 515. • ***Type species***, by present designation: *Bolina elegans* Mertens, 1833: 513. • ***Synonymy***: Mayer (1912: 2). • ***Comments***: [1] Permanently invalid nomen for being a junior homonym (Mayer 1912: 2). [2] To the best of our knowledge, no type species has ever been designated for this nominal genus, which was erected with two originally included nominal species. L. Agassiz (1860: 249) wrote: "I have also pointed out generic differences between *Bolina elegans* Mert. and *Bolina septentrionalis* Mert., which will require their separation; but I would retain the name of *Bolina* for the type to which *B. septentrionalis* Mert., our *B. alata*, and Sars's *Mnemia norvegica* belong." Although this sentence only cites one of the two originally included species, this is not an unambiguous type species designation as its mentions three nominal species as types. Later, in the same year, both Mortensen (1912: 76) and Mayer (1912: 21) independently considered *Bolina septentrionalis* as a subjective synonym of *Beroe infundibulum* Müller, 1776: 232. The latter was the first to refer this species to the genus *Bolinopsis* L. Agassiz, 1860, where it still stands according to recent authors (Anonymous 2022; Mills 2022). For this latter reason, we chose *Bolina elegans*, which is still considered a valid species according to the same sources, for type species of this nominal genus. The second reason of this choice is that *Bolina* Mertens, 1833 and *Bolinopsis* L. Agassiz, 1860 are now objective synonyms, although the latter is not a *nomen novum* for the former.

Bolinopsis L. Agassiz, 1860: 290. • ***Type species***, by original monotypy: *Bolina elegans* Mertens, 1833: 513. • ***Included species considered valid here*** (10): *Bolinopsis ashleyi* (Gerschwin, Zeidler & Davie, 2010); *Bolinopsis chuni* (von Lendenfeld, 1885); *Bolinopsis elegans* (Mertens, 1833); *Bolinopsis hydatina* (Chun, 1879); *Bolinopsis indosinensis*

(Dawydoff, 1946); *Bolinopsis infundibulum* (Müller, 1776); *Bolinopsis microptera* A. Agassiz, 1865; *Bolinopsis mikado* (Moser, 1907); *Bolinopsis ovalis* (Bigelow, 1904); *Bolinopsis rubripunctata* (Tokioka, 1964). • ***Comments***: [1] L. Agassiz (1860: 290) erected this genus and wrote about it: "This genus differs from *Bolina* in having its anterior and posterior rows of locomotive flappers extending to the bend of the chymiferons tubes, and the abactinal direction of the medial anastomosis of the latter, which trend in the opposite direction in *Bolina*. The spherosome is papillate, while that of *Bolina* is smooth. The large lobes are deeply indented." This nomen was therefore not proposed as a *nomen novum* for *Bolina* Mertens, 1833 on account of the fact that the latter was an invalid homonym. However, starting with Bigelow (1912: 390), all authors have considered both nomina as synonyms. In order to follow L. Agassiz's opinion, *Bolina septentrionalis* Mertens, 1833 should be designated as type species of *Bolinopsis*, as suggested by L. Agassiz (1860: 249) himself in the ambiguous sentence cited above. But then these two nomina would be subjective, not objective synonyms. In case later these two nominal species would be placed in different genera, this might be a source of confusion and ambiguity regarding the allocation of the nomen *Bolina* Mertens, 1833, and we prefer the solution making both nomina objective synonyms. [2] *Bolinopsis microptera* A. Agassiz 1865 was removed from synonymy with *B. infundibulum* by Johnson *et al*. (2022) whose population genomic study of *Bolinopsis* from many locations in the world revealed a genetically distinct species of *Bolinopsis* present along the west coast of the United States, including the type locality of *Bolinopsis microptera* A. Agassiz in Rosario Strait, Washington State.

S1. Species ***Bolinopsis vitrea*** (L. Agassiz, 1860)

Bolina vitrea L. Agassiz, 1860: 268 [nec *Lesueuria vitrea* Milne Edwards, 1841: 199]. • ***Name-bearing type***: Series of "only a few" syntypes of unknown number, lost. • ***Type locality***: Key West, Florida, USA.

Bolina hydatina Chun, 1879: 204. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Gulf of Naples, Italy. • ***Synonymy***: Mayer 1912: 25.

S2. Species ***Bolinopsis infundibulum*** (Müller, 1776)

Beroe infundibulum Müller, 1776: 232. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Spitzbergen, Norway.

Bolina septentrionalis Mertens, 1833: 513, **515**. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Saint Matthew Island in Bering Sea [Insel Mathaei in Behringischen Meere], USA. • ***Synonymy***: Both Mortensen (1912: 76) and Mayer (1912: 21), independently.

Mnemia norvegica Sars, 1835: x, 14, **32**. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Bergen, Norway. • ***Synonymy***: Mortensen (1912: 75).

Cydippe quadricostata Sars, 1835: x, 15, **36**. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Floröen, Norway. • ***Synonymy***: Mortensen (1912: 75).

Bolina alata L. Agassiz, 1850: 350. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Coast of New England, northeastern USA. • ***Synonymy***: Both Mortensen (1912: 75) and Mayer (1912: 21), independently.

Lesueuria hyboptera A. Agassiz, 1865: 23. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Massachusetts Bay, Massachusetts, and Newport, Rhode Island, USA. • ***Synonymy***: Mortensen (1912: 75).

G2. Genus ***Lesueuria*** Milne Edwards, 1841 ***nomen dubium***

Lesueuria Milne Edwards, 1841: 199. • ***Type species***, by original designation: *Lesueuria vitrea* Milne Edwards, 1841: 199. • ***Included species considered doubtful here*** (1): *Lesueuria vitrea* Milne Edwards, 1841: 199 ***nomen dubium***.

S3. Species ***Lesueuria vitrea*** Milne Edwards, 1841 ***nomen dubium***

Lesueuria vitrea Milne Edwards, 1841: 199. • ***Name-bearing type***: Series of syntypes of unknown number, lost. Neotype in need of designation. • ***Type locality***: Bay of Nice, France.

4.3.1.2. Option 2. The nomen *Lesueuria vitrea* Milne Edwards, 1841 refers to a species congeneric with *Beroe infundibulum* Müller, 1776

F2. Family ***LESUEURIIDAE*** Chun, 1880

BOLINIDAE L. Agassiz, 1860: xi, **200** [family]. • ***Type genus***, by implicit etymological designation: *Bolina* Mertens, 1833: 513. • ***Comment***: Permanently invalid nomen for being based on a genus nomen being an invalid junior homonym. • ***Synonymy***: *Hoc loco*.

LESUEURIDAE Chun, 1880: xiv, 290, **291** [family]. • ***Emended spelling*** (*hoc loco*): *LESUEURIIDAE*. • ***Type genus***, by implicit etymological designation: *Lesueuria* Milne Edwards, 1841: 199. • ***Included genus*** (1): *Lesueuria* Milne Edwards, 1841. • ***Comment***: The original spelling of this nomen was incorrect, and is here corrected.

BOLINOPSIDAE Bigelow, 1912: 390 [family]. • ***Type genus***, by implicit etymological designation: *Bolinopsis* L. Agassiz, 1860: 199. • ***Comment***: Although Bigelow (1912: 390) explicitly presented this new nomen as a 'nom. nov.', this is incorrect, because he did not mention the nomen *BOLINIDAE*, and because *Bolinopsis* is not a *nomen novum* for *Bolina*. • ***Synonymy***: *Hoc loco*.

G3. Genus ***Lesueuria*** Milne Edwards, 1841

Lesueuria Milne Edwards, 1841: 199. • ***Type species***, by original designation: *Lesueuria vitrea* Milne Edwards, 1841: 199. • ***Included species considered valid here*** (10): *Lesueuria ashleyi* (Gerschwin, Zeidler & Davie, 2010); *Lesueuria chuni* (von Lendenfeld, 1884); *Lesueuria elegans* (Mertens, 1833); *Lesueuria hydatina* (Chun, 1879); *Lesueuria indosinensis* (Dawydoff, 1946); *Lesueuria infundibulum* (Müller, 1776); *Lesueuria microptera* (A. Agassiz, 1865); *Lesueuria mikado* (Moser, 1907); *Lesueuria ovalis* (Bigelow, 1904); *Lesueuria rubripunctata* (Tokioka, 1964).

Bolina Mertens, 1833: 513 [nec *Bolina* Rafinesque, 1815: 144]. • ***Originally included nominal species*** (2): *Bolina elegans* Mertens, 1833: 513; *Bolina septentrionalis* Mertens, 1833: 515. • ***Type species***, by present designation: *Bolina elegans* Mertens, 1833: 513. • ***Synonymy***: First tentatively synonymised with *Lesueuria* by Mortensen (1912: 91). • ***Comments***: [1] Permanently invalid nomen for being a junior homonym (Bigelow 1912: 390). [2] To the best of our knowledge, no type species has ever been designated for this nominal genus, which was erected with two originally included nominal species. L. Agassiz (1860: 249) wrote: "I have also pointed out generic differences between *Bolina elegans* Mert. and *Bolina septentrionalis* Mert., which will require their separation; but I would retain the name of *Bolina* for the type to which *B. septentrionalis* Mert., our *B. alata*, and Sars's *Mnemia norvegica* belong." Although this sentence only cites one of the two originally included species, this is not an unanbiguous type species designation as its mentions three nominal species as types. Later, in the same year, both Mortensen (1912: 76) and Mayer (1912: 21) independently considered *Bolina septentrionalis* as a subjective synonym of *Beroe infundibulum* Müller, 1776: 232. The latter was the first to refer this species to the genus *Bolinopsis* L. Agassiz, 1860, where it still stands according to recent authors (Anonymous 2022; Mills 2022). For this latter reason, we chose *Bolina elegans*, which is still considered a valid species according to the same sources, for type species of this nominal genus. The second reason of this choice is that *Bolina* Mertens, 1833 and *Bolinopsis* L. Agassiz, 1860 are now objective synonyms, although the latter is not a *nomen novum* for the former.

Bolinopsis L. Agassiz, 1860: 290. • ***Type species***, by original monotypy: *Bolina elegans* Mertens, 1833: 513. • ***Synonymy***: First tentatively synonymised with *Lesueuria* by Mortensen (1912: 89–91). • ***Comments***: L. Agassiz (1860: 290) erected this genus and wrote about it: "This genus differs from *Bolina* in having its anterior and posterior rows of locomotive flappers extending to the bend of the chymiferons tubes, and the abactinal direction of the medial anastomosis of the latter, which trend in the opposite direction in *Bolina*. The spherosome is papillate, while that of *Bolina* is smooth. The large lobes are deeply indented." This nomen was therefore not proposed as a *nomen novum* for *Bolina* Mertens, 1833 on account of the fact that the latter was an invalid homonym. However, starting with Bigelow (1912: 390), all authors have considered both nomina as synonyms. In order to follow L. Agassiz's opinion, *Bolina septentrionalis* Mertens, 1833 should be designated as type species of *Bolinopsis*, as suggested by L. Agassiz (1860: 249) himself in the ambiguous sentence cited above. But then these two nomina would be subjective, not objective synonyms. In later case these two nomial species would be placed in different genera, this might be a source of confusion and ambiguity regarding the allocation of the nomen *Bolina* Mertens, 1833, and we prefer the solution making both nomina objective synonyms.

S4. Species ***Lesueuria hydatina*** (Chun, 1879) ***comb. nov.***

Bolina vitrea L. Agassiz, 1860: 268 [nec *Lesueuria vitrea* Milne Edwards, 1841: 199]. • ***Name-bearing type***: Series of 'only a few' syntypes of unknown number, lost. • ***Type locality***: Key West, Florida, USA. ***Synonymy***: Mayer, 1912: 25. • Invalid nomen in the genus *Lesueuria* Milne Edwards, 1841 for being a junior secondary homonym of *Lesueuria vitrea* Milne Edwards, 1841: 199.

Bolina hydatina Chun, 1879: 204. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Gulf of Naples, Italy.

S5. Species ***Lesueuria infundibulum*** (Müller, 1776) ***comb. nov.***

Beroe infundibulum Müller, 1776: 232. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Spitzbergen, Norway.

Bolina septentrionalis Mertens, 1833: 513, **515**. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Synonymy***: Both Mortensen (1912: 76) and Mayer (1912: 21), independently. • ***Type locality***: Saint Matthew Island in Bering Sea [Insel Mathaei in Behringischen Meere], USA.

Mnemia norvegica Sars, 1835: x, 14, **32**. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Bergen, Norway. • ***Synonymy***: Mortensen (1912: 75).

Cydippe quadricostata Sars, 1835: x, 15, **36**. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Floröen, Norway. • ***Synonymy***: Mortensen (1912: 75).

Lesueuria vitrea Milne Edwards, 1841: 199. • ***Name-bearing type***: Series of syntypes of unknown number, lost. Neotype in need of designation. • ***Type locality***: Bay of Nice, France. • ***Synonymy***: Vanhöffen (1903); Mortensen (1912: 89–91), although with doubt; *hoc loco*. • ***Comment***: [1] The taxonomic allocation of this nomen is currently doubtful at species level but not at genus level and above. Its taxonominal status should be stabilised, which can be done through the designation for it of a neotype from the Bay of Nice belonging to the species long known under the epithet *infundibulum* Müller, 1776. If preservation of this neotype proves impossible, publication of its detailed and good description and iconography, as well as data from its molecular sequencing, could serve as proxies for this specimen. This solution will preserve the nomenclatural stability of this species at species level but will require a change in the generic nomen of this and 8 other species. [2] The recognition that *Lesueuria* is the valid senior synonym of *Bolinopsis* makes the nominal species *Bolina vitrea* L. Agassiz, 1860 an invalid junior secondary homonym of *Lesueuria vitrea* Milne Edwards, 1841.

Bolina alata L. Agassiz, 1850: 350. • ***Name-bearing type***: Series of syntypes of unknown number, lost. • ***Type locality***: Coast of New England, northeastern USA. • ***Synonymy***: Both Mortensen (1912: 75) and Mayer (1912: 21), independently.

Lesueuria hyboptera A. Agassiz, 1865: 23. • ***Name-bearing type***: Series of syntypes of unknown number, deposited in the Museum of Comparative Zoology at Harvard in Boston, currently lost (Adam Baldinger, May 1922, personal comunication to CM). • ***Type locality***: Massachusetts Bay, Massachusetts, and Newport, Rhode Island, USA. • ***Synonymy***: Mayer (1912: 20), Mortensen (1912: 75).

4.3.2. Synonymic lists that do not depend on choice between Options 1 or 2 for the taxonomic status of Lesueuria vitrea *Milne Edwards, 1841*

F3. Family ***PTERYGIOCTENIDAE fam. nov.***

PTERYGIOCTENIDAE ***familia nova***. • ***Type genus***, by present designation: *Pterygiocteis* gen. nov. • ***Etymology***: Formed from the stem of *Pterygiocteis*, "Pterygioctein-". • ***Included genus*** (1): *Pterygiocteis* ***gen. nov.*** • ***Diagnosis***: See the characters of its only genus. • ***Comment***: In agreement with our morphological conclusions that this should be established as a new family, published lobate ctenophore sequences (Christianson *et al*. 2022, Johnson *et al*. 2022) were used with BLAST to retrieve COI, 18S and 28S fragments from transcriptome data in the NCBI Sequence Read Archive (SRX3058265) deposited for "Lobata species Punta Arenas" by Whelan *et al*. (2017). New plots with approximately 25 other species of **Lobata** indicate that *Pterygiocteis nigrolimbatus* ***sp. nov.*** is widely different from other **Lobata** species (S. B. Johnson and S. H. D. Haddock, personal communication to CEM October 2023). The illustration of "Lobata species Punta Arenas" in Whelan *et al*. (2017) in the phylogenetic tree shown in their Figure 3 shows the same specimen as the photograph provided to us by L. L. Moroz, shown in our Figure 2d and used as holotype of *Pterygiocteis nigrolimbatus* ***sp. nov***.

G4. Genus ***Pterygiocteis gen. nov.***

Pterygiocteis ***genus novum***. • ***Grammatical gender***: Masculine. • ***Type species***, by present designation: *Lesueuria pinnata* Ralph & Kaberry, 1950: 1, 7–8, Text Figure 4. • ***Etymology***: From the Greek πτερύγιον, *pterygion*, (n.), 'fin', and κτείς, κτενός, *kteis*, *ktenos*, (m.), 'comb', referencing the two or four pairs of narrow fins that run down most of the length of the body that are unique to this genus. Grammatical gender: masculine. • ***Included species*** (2): *Pterygiocteis pinnatus* (Ralph & Kaberry, 1950) ***comb. nov.***; *Pterygiocteis nigrolimbatus* ***sp. nov.*** • ***Diagnosis***: Lobate ctenophores, highly compressed in the tentacular axis; with four flat, flexible, roughly elongate-triangular auricles; with a pair of aboral, roundly-pointed, gelatinous appendages extending below the statocyst and the aboral end of the animal, aligned in the tentacular plane and curved slightly inward in larger specimens; the four subtentacular comb rows extending down the gelatinous aboral processes nearly to their tips; statocyst sunken into a broad cavity at the aboral end of the body; all comb rows with broad and fairly tightly-spaced comb plates; gonads developing in the broad outpocketings of the meridional canals directly beneath the comb plates; with four or eight slender fins forming on the body surface on the interradial sides of the comb rows (primarily on the substomodaeal comb rows), mostly below the lobes, but continuing as they taper up the lower portions of the lobes—the somewhat irregular fin crests being adorned with a row of closely-spaced, tiny papillae. • ***Comment***: Ralph & Kaberry's (1950) fairly detailed description and drawing of "*Lesueuria pinnata*" were sufficient to recognize it in photographs taken in New Zealand in 2021. More ctenophores that we have identified as *Pterygiocteis* were photographed and posted on *iNaturalist.org* in 2021–2023 from Southern Chile and Tierra del Fuego in southern Argentina, and some subantarctic islands. Additionally, our colleagues G. I. Matsumoto and L. L. Moroz have offered their photographs of lobate ctenophores from the Antarctic Peninsula and Punta Arenas, Strait of Magellan for study and we have identified these also as *Pterygiocteis*.

S6. Species ***Pterygiocteis pinnatus*** (Ralph & Kaberry, 1950) ***comb. nov.***

Lesueuria pinnata Ralph & Kaberry, 1950: 1, 7–9, text figure 4. • ***Name-bearing type***: Ralph & Kaberry (1950: 7) referred to a 'preserved specimen', presumably collected in 1935, that would have been left in the possession of the Zoology Department, Victoria University College, now Victoria University of Wellington. Correspondence between CEM and M. Dohner, Victoria University of Wellington Laboratory Technical Officer, in November 2022, revealed that no ctenophores remain in the collection, so the original specimen is presumed lost. • ***Type locality***: Off Island Bay, a suburb of Wellington, bordering Cook Strait, New Zealand. • ***Etymology***: the epithet *pinnatus* derives from the Latin adjective *pinnatus*, 'winged or feathered', presumably in reference to the unique fins located along the interradial sides of each of the substomodaeal comb rows.

History

The species was named by Patricia Ralph and C. Kaberry (1950) with no explanation. It was subsequently referred to as *Lesueuria pinnata* by Mianzan *et al*. (2009: 52 including text figure, 58), to *Eurhamphaea* sp. by Mianzan *et al*. (2009: 58; with doubt) and Schiariti *et al*. (2021: 286, 292 Fig. 2B, 293 Table 3, 296–297), and to *Lesueuria pinnata* by Mills *et al.* (2023).

Material examined

This ctenophore can not be preserved. The redescription below is based on Ralph & Kaberry's (1950: 7–9 including Text Fig. IV on p. 8) original description and figure, and recent photographic images posted on *iNaturalist.org*. We have not had access to living specimens.

Diagnosis

With lobes about 1/4–1/3 of the total body length; overall body shape an elongated oval in the stomodaeal plane, very compressed in the tentacular axis; body generally translucent, with the extensively-winding canals on the inside surfaces of the lobes not discernable from the outside; with four (eight?) slender fins forming on the interradial sides of the substomodaeal (and also subtentacular?) meridional comb rows, ending on the lower portions of the lobes—the degree of exaggeration of these fins seemingly under the control of the animal; with a pair of elongate, roundly pointed gelatinous aboral processes that point aborally, usually curving slightly inward at their extremity; black (or infrequently, brick-red) pigment, if present, may be diffusely lining the inside surfaces of the lobes and auricles, to a lesser extent in the stomodaeum, and often in streaks along the perradial-, or less often also along the interradial-, sides of the comb rows, and sometimes as a pale blackish line on the edges of the fins.

Redescription

Body and oral lobes. • The body is to at least 30 cm in total length, on average much less, in the general shape of an elongate oval about 2.5 times as long as wide when viewed in the stomodaeal plane, but highly compressed in the tentacular axis. The very delicate lobes comprise about the oral 1/4–1/3 of the body length and are generally fairly opaque; even when open, these lobes do not flare usually beyond the general elongate oval of the body profile and when contracted, the lobes may fold up over one another, like crossed fingers, or simply overlapping—these are characteristic postures when cruising forward with the lobes leading. The auricles (visible in Figure 1b) are medium-long, flat, very flexible and broadly triangular and lanceolate, typically held up or folded within the lobes. This species bears a set of four fins (Figures 1c–d) that run most of the length of the body from nearly the aboral end onto the lower portions of the lobes; the fins arise on the interradial sides of the substomodaeal comb rows (the sides facing the subtentacular comb rows), seemingly supported by the diverticula on that side of the substomodaeal meridional canals, which run to the sharp crest of each fin; this somewhat irregular crest of each fin is adorned with a row of closely-spaced, tiny papillae along its entire length (Figures 1c–d), which may also be somewhat darkly-pigmented. It is possible that, like in *Pterygiocteis nigrolimbatus* ***sp. nov.*** (Figure 2c), the interradial sides of the subtentacular comb rows may form another four, smaller, less distinct fins. The temporal existence and attitude of these fins appears to be somewhat controllable by the animal. The aboral end is characterized by a pair of roundly pointed, gelatinous processes aligned in the tentacular plane, which may become longer and slightly recurved towards each other in some specimens. Unlike *P. nigrolimbatus* ***sp. nov.***, this species is usually fairly opaque so that the details of the internal anatomy cannot be well distinguished through the body wall. Most individuals have some black pigment on the body, often diffusely lining the inside surface of the lobes and auricles, to a lesser extent in the stomodaeum, and often in streaks along the perradial- (Figure 1a), or less often also along the interradial-, sides of the comb rows, and sometimes as a pale blackish line on the edges of the fins; a few of the individuals photographed in Chile and Argentina had brick-red pigment in place of the black pigment and the most-pigmented individual also had general brick-red color on some of the mesogloea, especially at the aboral end; the aboral processes were always colorless.

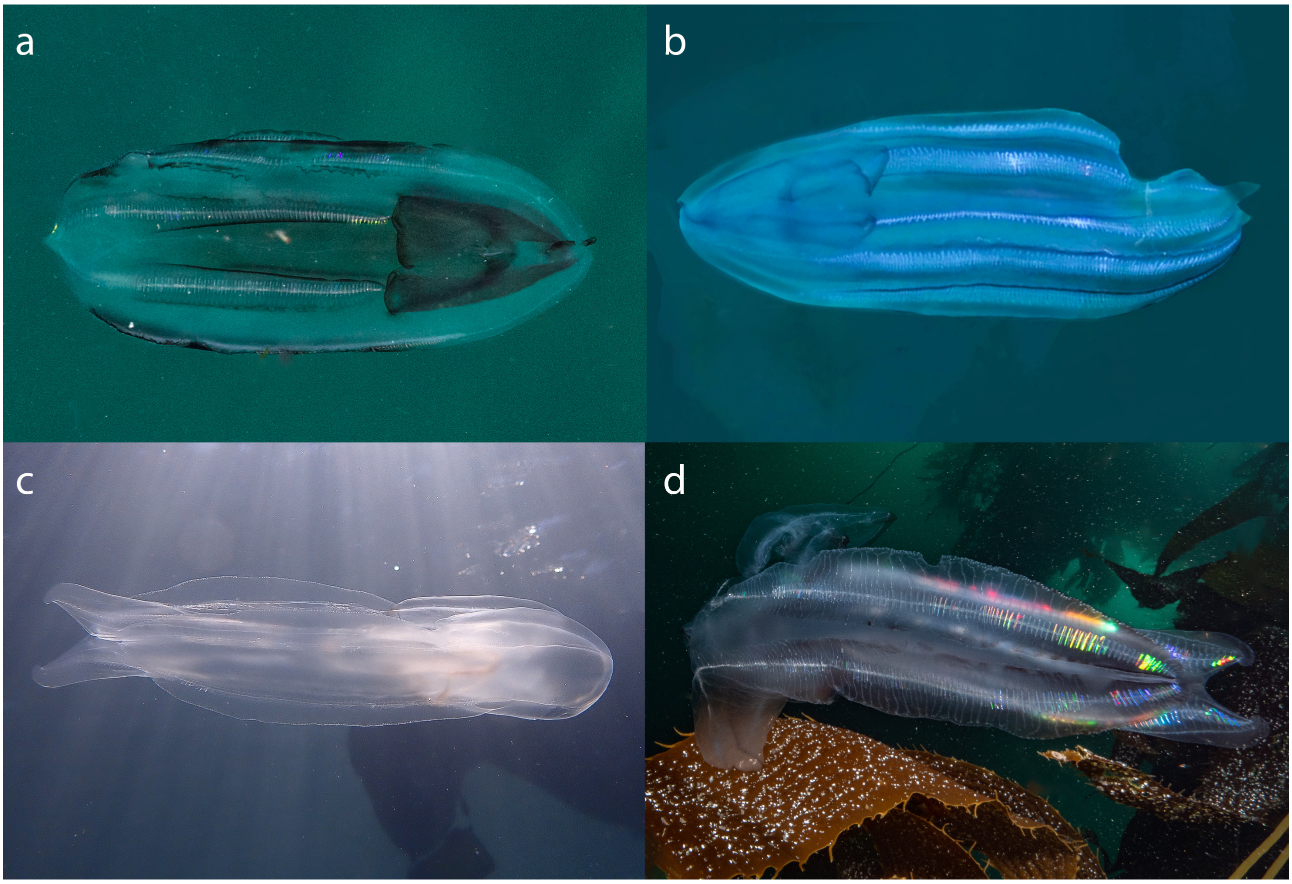

FIGURE 1. *Pterygiocteis pinnatus* **comb. nov.** (a) View in the stomodaeal plane, length approximately 20–25 cm. *In situ* photograph by Tom Driscoll, Pargua, Chile, just north of Chiloé Island, 13 February 2012. (b) View in the stomodaeal plane, length 25–30 cm. *In situ* photograph by Izumi Schmidt Uchida, Deborah Bay, Port Chalmers, Otago, New Zealand, 29 December 2021. (c) View in the tentacular plane, showing lateral compression, the pair of aboral processes, and transparent side fins edged with a row of tiny papillae or granules, length ~ 25 cm. *In situ* photograph by Mariano Rodríguez—@argentinasubmarina, Baliza Escarpados, Beagle Channel, Tierra del Fuego, Argentina, 10 February 2021. (d) Oblique side view in the tentacular plane, note pair of aboral processes and irregularly-edged, prominent side fins, length 15–20 cm. *In situ* photograph by Patrick Webster, Puerto San Juan del Salvamento, Isla de los Estados, Tierra del Fuego, Argentina, 11 March 2023.

Comb rows. • The comb rows are approximately the same length, but offset, because the four subtentacular comb rows extend down the gelatinous aboral processes nearly to their tips and then run up to the bases of the lobes, while the substomodaeal comb rows begin at the rounded aboral end of the body and then continue up a short distance up onto the lobes. The comb plates are broad with short cilia, and tightly spaced; the cilia of the subtentacular comb rows continue out onto the auricles, where they align end-to-end in a single row, around the edge of each auricle.

Statocyst and pole plates. • The statocyst is sunken several millimetres into a broad cavity at the aboral end of the body, further concealed in the tentacular plane by the pair of aboral processes. No images revealed the pole plates.

Tentacular apparatus. • Because this species is fairly opaque, the tentacular apparatus usually could not be seen, but in one photograph, a bright white elongate spot at the center of the mouth edge between the lobes was presumably the tentacular apparatus.

Gastrovascular system. • The mouth is located above and between the bases of the lobes, opening out into a very long, stomodaeum. The infundibular canal is very short—only a few millimetres. As stated by Ralph & Kaberry (1950) in their original description, the gastrovascular system including the meridional canals could not be seen because the mesogloea was too opaque; although the stout diverticula bearing the gonads all along the meridional canals under the comb rows do show through the body wall (Figures 1a–b,d), the longer diverticula that extend beyond these gonadal regions mostly cannot be seen. We presume that the canal system in *P. pinnatus* is similar to that of the much more transparent *P. nigrolimbatus* ***sp. nov.***, described below, and can confirm from a couple of photographs at least that *P. pinnata* has the same, complex open-loop winding canals that completely cover the inner surfaces of its two lobes.

Gonads. • The gonads develop in the broad outpocketings of the meridional canals directly beneath the comb plates.

Geographic distribution

In New Zealand off Wellington, Cook Strait (Autumn 1935) (Ralph and Kaberry, 1950) and near Port Chalmers, Otago on the South Island (December 2021), Stewart Island (December 2021) and Campbell Island (December 2022) and Tasmania, Australia (November 2019)—all reported at *iNaturalist.org*.

In South America along the southern coast of Chile near Chiloé Island (February 2012, May 2021), in the Beagle Channel, in Patagonia, Chile and Tierra del Fuego, Argentina (January 2015, May 2015, December 2018, December 2020, January 2021, February 2021, December 2022), and Isla de los Estados, Argentina (March 2023), South Georgia and the South Sandwich Islands (January 2020)—all reported at *iNaturalist.org*. It appears that *Pterygiocteis pinnatus* is an austral summer species, probably with a circum-subantarctic distribution, presumably carried by the Antarctic Circumpolar Current.

Vertical distribution and behavior

Known only from near-surface waters, this species can be present as isolated individuals or numerous (“common during calm weather in autumn” 1935, near Wellington, but very fragile and subject to fragmenting when handled “on account of its size and delicate nature”; Ralph & Kaberry 1950: 7) A three-minute video filmed by scuba diver Patrick Webster of one 15–20 cm long individual beside a kelp forest at Isla de los Estados, Tierra del Fuego, Argentina and shared with CEM in March 2023, showed this species to be a smooth and strong swimmer, but fragile and easily damaged unintentionally by the photographers.

Remarks

Ralph & Kaberry’s (1950) choice of the genus *Lesueuria* was never really appropriate for this ctenophore, since the primary character of *Lesueuria* is “Lobate with rudimentary oral lappets” (Mayer 1912: 19) and the New Zealand animal they described and figured had substantial, well-formed oral lobes (“lappets”). Nevertheless, they were apparently reluctant to create a new genus.

> “Ralph and Kaberry’s 1950 description-drawing of *Lesueuria pinnata* must have been made from memory of specimens collected years earlier. While not drawn with much skill, it also lacks basic and important features of this animal: in reality, the statocyst is sunken well within a broad funnel, not at the aboral surface of the body as they drew it, and the aboral end is further characterized by a distinctive pair of fleshy, conical projections in line in the tentacular plane. These aboral projections are substantial and unusual and show in nearly every one of the photographs … that we have examined. They are mentioned in the text of the original description, but are not drawn into the accompanying figure. Similarly, the two pairs of unusual gelatinous fin-like flaps (apparently the source of the species name, *pinnata*) running from the aboral end out onto the base of the lobes flanking the substomodaeal comb rows were very difficult to conceptualize from the original drawing. These remarkable fins cause us to wonder how they function in the ciliary swimming of this large lobate ctenophore.” (Mills *et al*. 2023).

Note that the animal shown in our Figure 1b is damaged in its lower quarter, which in a perfect animal would be symmetrical in outline, and the animal shown in Figure 1d has torn lobes, barely visible, which occurred during the *in situ* photo session.

S7. Species ***Pterygiocteis nigrolimbatus sp. nov.***

Pterygiocteis nigrolimbatus **species nova**. • ***Name-bearing type***: Holotype, specimen photographed by Leonid L. Moroz, in Punta Arenas, Strait of Magellan, Patagonia, Chile, in November 2013, shown here in figure 2d, of which a small tissue sample only was preserved (see 'Material examined' below). • ***Type locality***: Punta Arenas, Magallanes, Chile (at the surface, 53°10'11.1"S, 70°54'24.8"W). • ***Etymology***: The specific epithet derives from the Latin adjectives *niger*, 'black' and *limbatus*, 'bordered', in reference to the narrow black outline usually (but not always) present around the auricles and outer edge of each lobe.

History

This species was first reported from New Zealand as *Bolinopsis* sp. by Mianzan *et al.* (2009: 53, 54 including text figures C–D, 58), then from Tasmania as *Bolinopsis* sp. A by Gershwin *et al.* (2010: 22–23 text and figure 3A), then from Southern Chile as "Lobata Punta Arenas, Argentina" [*sic*] by Whelan *et al.* (2017: 1741 figure 3 including photograph, 1742 figure 4, 1743 figure 5, Table S1), and finally as *Lesueuria* **sp. nov.** from New Zealand by Mills *et al.* (2023: in press).

Material examined

This ctenophore can not be preserved. The first author examined and made drawings from three specimens approximately 7 cm long, collected in a 1/4 m diameter, 225 µm plankton net in four, 5-minute tows about 20 cm below the surface in front of the University of Canterbury Kaikoura Marine Laboratory, New Zealand, on 24 December 1981 about noon local time (CEM's unpublished field notebook). These drawings provided a basis for comparison with: [1] six photographs taken *in situ* on 18 October 2022 in Taputeranga Marine Reserve, Wellington, New Zealand, by Luca Davenport-Thomas (see Figure 2a) and posted on *iNaturalist.org*; [2] thirteen *in situ* photographs taken in the austral summer 1984–1985 at the American Palmer Station in the Antarctic Peninsula, Antarctica, by George I. Matsumoto (see Figures 2b–c); [3] about 25 *in situ* photographs taken in the Beagle Channel near Ushuaia, Argentina by Mariano S. Rodríguez 2015–2023; [4] additionally, a genetic sequence from Punta Arenas, Chile, used to make phylogenetic trees in Whelan *et al.* (2017) and deposited with the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRX3058265) Biosample SAMN07426143. This sample is frozen and presently deposited at the University of Florida, Lobata sp. UF-2017, collector Leonid L. Moroz. This sequence has proved to be taken from *P. nigrolimbatus* by comparing the photograph taken in November 2013 of UF-2017 on shipboard in the Strait of Magellan, Patagonia, Chile, by Leonid L. Moroz, reproduced in Whelan *et al.* (2017: 1741) and reproduced here in our Figure 2d, with others in our study set. The latter specimen is hereby designated as holotype of *Pterygiocteis nigrolimbatus* **sp. nov.** because both the photograph and the sequence serve as proxies for this specimen, of which only a small tissue sample remains (see § 4.2 above).

Diagnosis

With lobes about 1/2 of the total body length; overall body shape more or less an oval in the stomodaeal plane if the lobes are closed, very compressed in the tentacular axis; body generally transparent, with the extensively-winding canals on the inside surfaces of the lobes visible from the outside; with four or eight slender fins forming on the interradial sides of the substomodaeal and (less so) subtentacular meridional comb rows, ending on the lower portions of the lobes—the degree of

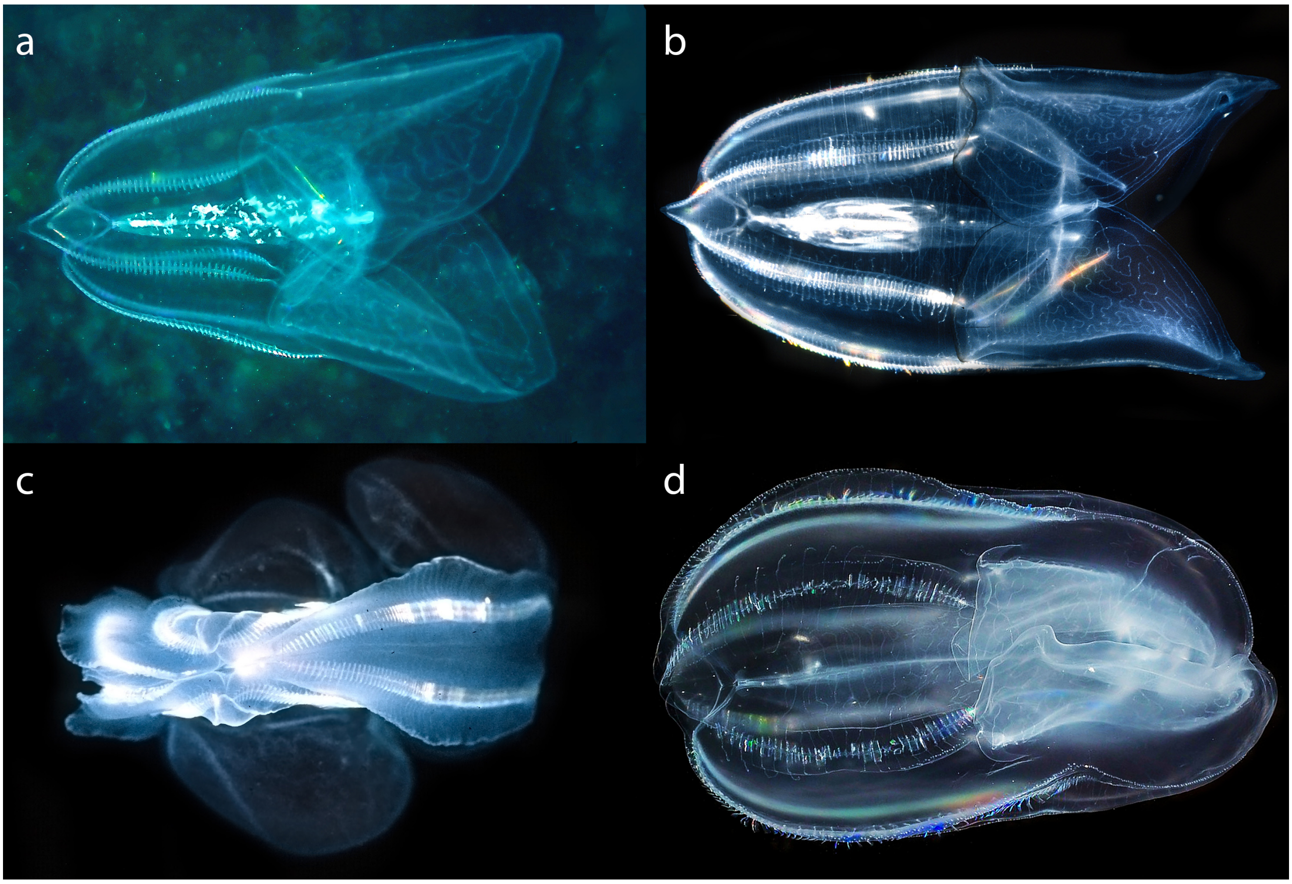

FIGURE 2. *Pterygiocteis nigrolimbatus* ***sp. nov.*** (a) View in the stomodaeal plane, note unidentified small partially-digested contents in gut, body length ~ 8 cm. *In situ* photograph by Luca Davenport-Thomas, Taputeranga Marine Reserve, Wellington, New Zealand, 18 October 2022. (b) View in the stomodaeal plane, note partially-digested ctenophore *Callianira cristata* in gut, body length approximately 16–20 cm. *In situ* photograph by George I. Matsumoto, Palmer Station, Antarctic Peninsula, austral summer 1984–1985. (c) View of the aboral end with open oral lobes showing in the background, note fins on the body associated with each comb row, body width approximately 7–10 cm. *In situ* photograph by George I. Matsumoto, Palmer Station, Antarctic Peninsula, austral summer 1984–1985. (d) View in the stomodaeal plane, note fins edged with tiny papillae extending onto the lobes, aboral processes held in within the general oval body shape, body length ~ 10 cm. Shipboard photograph by Leonid L. Moroz, Punta Arenas, Strait of Magellan, Patagonia, Chile, November 2013.

exaggeration of these fins seemingly under the control of the animal; with a pair of short, roundly pointed gelatinous aboral processes that may be held up within the general oval outline of the animal, or may at other times point aborally, distinctly breaking up the oval outline; black pigment, if present, usually as a distinctive black outline of the lobes and auricles.

Description

Body and oral lobes. • The body to at least 20–25 cm in total length, on average much less, in the general shape of an oval about two times as long as wide when viewed in the stomodaeal plane and the lobes are closed, but highly compressed in the tentacular axis. The very delicate lobes comprise about the oral 1/2 of the body, and can flare broadly open beyond the oval of the body profile. This species is typically a little smaller and relatively shorter and rounder than *P. pinnatus*, as well as much more transparent. The auricles (Figures 2a–b) are medium-long, flat, flexible, narrow, lanceolate triangles, typically held up within the lobes. This species also bears the set of four fins (Figure 2c) described above for *P. pinnatus*, that run most of the length of the body from nearly the aboral end to the lower portion of the lobes; the primary fins arise on the interradial side of the substomodaeal comb rows (the side facing the subtentacular comb rows), seemingly supported by the diverticula on that side of the substomodaeal meridional canals, which run to the sharp crest of each fin—this somewhat irregular fin crest is adorned with a row of tiny papillae or granules along its entire length (Figure 2d) —these granules continue up the body surface overlying the substomodaeal meridional canals to the top of the lobes. In some images, another set of fins can be seen along the interradial sides of the subtentacular comb rows (see Figure 2c) and these lesser fins also bear a row of tiny papillae along their crests (Figure 2d). The aboral end of the body is characterized by a pair of short, roundly pointed, fleshy processes aligned in the tentacular plane (Figures 2a–b), and which may become longer and slightly recurved in some specimens; these aboral processes may be pointed aborally, outside of the overall oval outline of the body or may be held in, over the depression containing the statocyst, and barely discernable (Figure 2d). Like *P. pinnatus*, when not feeding with lobes expanded, this species contracts its lobes for forward-swimming, lobes first, sometimes folding the lobes over one another, a little like crossed fingers. This species is quite transparent, so the windings of the canals on the insides of the lobes can be discerned from the outside, and it usually has a distinct, narrow black band of pigment outlining the outer edge of the two lobes and sometimes the auricles (see Figures 2a–b).

Comb rows. • The substomodaeal comb rows are somewhat longer than the subtentacular comb rows, but the difference in length appears to be exaggerated because the pairs are offset—the four subtentacular comb rows extend down the gelatinous aboral processes nearly to their tips and then run up to the bases of the lobes, while the substomodaeal comb rows begin at the rounded aboral end of the body and then continue up a short distance onto the lobes. The comb plates are broad with short cilia and tightly spaced; the cilia of the subtentacular comb rows continue out onto the auricles, where they align end-to-end in a single row, around the edge of each auricle.

Statocyst and pole plates. • The statocyst is sunken several millimetres into a broad cavity at the aboral end of the body, further concealed in the tentacular plane by the pair of aboral processes. No images revealed the pole plates.

Tentacular apparatus. • In photographs of fairly transparent mature specimens from the Antarctic Peninsula and the Beagle Channel, the tentacular apparatuses appear as a pair of bright-white patches a couple of millimetres long at the edge of either side of the mouth (Figure 2b), and many tentacles can sometimes be seen streaming from the oral groove down over the upper 1/4–1/2 of the body surface. A tentacular canal could could be traced, running up near the paragastric canal, from the infundibulum to the tentacular apparatus in one photo of an individual from the Beagle Channel.

Gastrovascular system. • This species is quite transparent and its gastrovascular system can be seen quite clearly in good, well-focused photographs. The mouth is located above and between the bases of the lobes, opening out into a very long, stomodaeum. The infundibular canal is very short (Figures 2a–b,d). The four substomodaeal meridional canals extend to nearly the lowest aboral point of the mesogloeal body wall, where they are met inline at their aboral ends by four adradial canals descending from the infundibulum (Figures 2b,d). The four subtentacular meridional canals terminate lower, two each running to the tips of the pair of elongate aboral processes; these are fed by adradial canals running down from the infundibulum and joining the subtentacular meridional canals obliquely at approximately the level of the statocyst, well above their blind ends on the aboral processes. At their oral end, below the lobes, each subtentacular meridional canal continues beyond the subtentacular comb rows, running along the edge of each auricle and then arching up along the edges of both lobes as a wavy line, joining at the top. The oral ends of the substomodaeal meridional canals continue straight up the lobes to the top, just a couple of millimetres below the edge-loop of the subtentacular canals, where they run out in both directions parallel to that loop canal before running through the mesogloea and forming a series of many tens of complex open-loop windings that completely cover the inner surfaces of the two lobes. Where they run underneath the comb rows, all eight meridional canals have outpocketings where the gonads develop beneath each comb plate; longer, more slender diverticula extend beyond these stout outpockets, alternating longer and short every other comb plate along the comb rows (Figure 2b). A pair of pharyngeal canals run up the midline of the stomodaeum, and these canals also have diverticula branching off both to the left and to the right every few millimetres—these diverticula are quite long and slender, passing through the mesogloea towards the diverticula coming off the perradial sides of the subtentacular meridional canals, and inter-digitating with them. A tentacular canal runs from the infundibulum to the tentacular apparatus at the edge of the mouth.

Gonads. • The gonads develop in the broad outpocketings of the meridional canals directly beneath the comb plates (Figure 2b).

Geographic distribution

In New Zealand off Kaikoura, South Island (CEM personal observations December 1981) and near Wellington Harbor (October 2022) and Auckland Island (January 2023)—reported at *iNaturalist.org*. In Tasmania, Australia (Gershwin *et al*. 2010: 22, Figure 3A). In South America in the Strait of Magellan, Patagonia, Chile (November 2013, L. L. Moroz, personal communication to CEM), and in the Beagle Channel, Tierra del Fuego, Argentina (November 2017, December 2018, January–February 2020, December 2020, February 2021, December 2022)—all reported at *iNaturalist.org*. Antarctic Peninsula at the American Palmer Station, austral summer 1984–1985 (G. I. Matsumoto, personal communication to CEM, June 2023); South Georgia (January 2020) and South Shetland Islands, Deception Island (December 2021)—reported at *iNaturalist.org*. Like *Pterygiocteis pinnatus*, *P. nigrolimbatus* ***sp. nov.*** appears to have a circum-subantarctic distribution and is likely a resident species of the Antarctic Circumpolar Current. This current is driven by the Westerlies of the Southern Ocean, apparently spinning off in vortices into high latitude subantarctic islands and even temperate regions including New Zealand and Tasmania.

Vertical distribution and behavior

Known only from near-surface waters, this species can be present as isolated individuals or in the hundreds (Strait of Magellan November 2013, L. L. Moroz, personal communication to CEM, October 2023; "common" in the austral summer 1984–1985 on the Antarctic Peninsula, G. I. Matsumoto, personal communication to CEM, June 2023).

Specimens observed along the Antarctic Peninsula were frequent predators on the relatively large Antarctic cydippid ctenophore *Callianira cristata* Moser, 1909, seen in the gut of the individual in Figure 2b (G. I. Matsumoto, personal communication to CEM, June 2023). Their very fragile nature and unliklihood of surviving conventional oceanographic collecting techniques, combined with the apparent impossibility of preserving this species, probably explains why this apparently common species was not reported by Moser (1909) in her monograph on the ctenophores collected by the German South Pole Expedition of 1901–1903, though she described the more robust Antarctic cydippid *Callianira cristata* as a new species from that series of samples.

Remarks

Professional diver/photographers in Tierra del Fuego have in the past identified this new species as "*Mnemiopsis*", while they identified *P. pinnatus* as "*Eurhamphaea*", confirming that the two species of *Pterygiocteis* look basically different (M. S. Rodríguez, personal communication to CEM, July 2023). Our colleague G. I. Matsumoto saw many *P. nigrolimbatus* ***sp. nov.*** on the Antarctic Peninsula at the American Palmer Research Station, scuba diving to about 20 m during the Austral summer 1984–1985 and shared his many, well-focused photographs, which allowed CEM to visualize and describe the gastrovascular system and other features described here.

It seems that this species can appear to be with or without the fin-like flaps that run beside the substomodaeal comb rows, and are characteristic of both species of *Pterygiocteis*, and we wonder if the fins can be inflated or deflated to some extent depending on the physiological status of the animal. We note that the angle of the fins relative to the body is not the same in all individuals, and appears also to be variable depending on conditions.

Acknowledgments

Luca Davenport-Thomas brought the genus *Lesueuria* to the attention of the first author with regard to two *iNaturalist.org* ctenophore images from New Zealand in 2021, which set her off on this examination of the history of the genus. CEM had observed an unknown ctenophore in New Zealand in 1981 which she assumed was a species of *Bolinopsis* prior to conversations with Davenport-Thomas. A 2023 conversation with George Matsumoto revealed that he had seen and photographed a species of "*Bolinopsis*" while scuba diving at the Palmer Research Station on the Antarctic Peninsula in the austral summer of 1984–1985, which has proven to be the same species, now *Pterygiocteis nigrolimbatus*. Another 2023 conversation with Gustav Paulay led to the discovery that Leonid Moroz had not only photographed this species in Punta Arenas, Chile in 2013, but that he had also sequenced it and published the data. Shannon Johnson retrieved the "Lobata Punta Arenas" sequence from NCBI and constructed several phylogenetic trees using other published and unpublished **LOBATA** data, and confirming that *Pterygiocteis* deserves erection of a new family of **LOBATA**. Submission of an earlier version of this manuscript led to Alain Dubois joining CEM in order to solve both nomenclatural and taxonomic problems within the **CTENOPHORA** that were revealed by this study. During the course of developing this manuscript, images of an additional ~ 25 specimens in the genus *Pterygiocteis* were posted on *iNaturalist.org* from New Zealand, Chile, Argentina, several subantarctic islands and the Antarctic Peninsula. We are grateful to the citizen scientists who post their images on *iNaturalist.org*, which has enabled us to conduct an armchair field study in order to understand the two species described in this paper. We are grateful to our colleagues who shared their photos that were used for study in writing the descriptions and in Figures 1 and 2. Nick Bezio produced Figures 1 and 2 from photographs selected by CEM from those available to us.

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