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History of the *Clio pyramidata*-complex (Mollusca, Gastropoda, Euthecosomata, Cliidae) in the Atlantic Ocean, restoring its original concept

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'*My heart is down, my head is turning around*'
(Harry Belafonte, *Jamaica Farewell,*1956)

An extensive overview of the historical use of the genus *Clio* and its type species *Clio pyramidata* Linné, 1767 (described from the Caribbean: Jamaica) during the last two and a half centuries demonstrates the current incorrect use of the species name and the junior synonymy of the taxon *Hyalea lanceolata* Lesueur, 1813 (described from the Mediterranean). The latter taxon was incorrectly considered to be a shell-morphologically different form of *C. pyramidata*. A neotype is designated for *C. pyramidata* from the original type locality to stabilise nomenclature. We examined the relationship of two shell forms of that species, viz. the form with straight carinae or shell sides (occurring in the northern Atlantic Ocean and so far considered to represent typical *C. pyramidata*) and the (neo)typical form with strongly concave carinae (occurring in the (sub)tropical Atlantic, inclusive of the Caribbean and Mediterranean) currently indicated as forma or subspecies *lanceolata* Lesueur, 1813. Based on combined morphological and genetic analyses of specimens from the Atlantic Ocean and the Caribbean we found that there are intermediates between the two shell forms and that they have different, but overlapping distributions. Moreover, there was no molecular evidence to separate the two forms as distinct species. Hence, we consider the name *C. pyramidata* appropriate for the different shell forms within this taxon. For the form with straight carinae the name *angusta* Boas, 1886, is available, but may be applied at subspecific rank only. A lectotype for *angusta* is selected, and a type species is designated for *Flabellulum* Bellardi, 1873.

Key words: systematics, nomenclature, distribution, type locality, neotype, lectotype, barcoding, Jamaica.

Introduction

The euthecosomatous pteropod *Clio pyramidata* Linné, 1767, is one of the more abundant holoplanktic mollusc species with a very wide distribution in almost all oceans and seas (e.g., van der Spoel, 1967). The species is, generally speaking, easily recognisable, although its wide distribution in cold as well as warm waters has led to the introduction of a number of forms and/or subspecies, or even species, based on shell morphology. In the Atlantic two different shell forms are present, distinguished by the shape of the carinae (shell sides) in dorsal and ventral views: straight in the North Atlantic, more concave in the (sub) tropical Atlantic, the Caribbean and Mediterranean. Over the course of time, erroneous interpretations have changed the original species concept, resulting in the current incorrect application of the name. Here we provide a historical survey of the taxon and, in the absence of syntype material, restore its original definition by designation of a neotype from its type locality Jamaica. Furthermore, we examined the different forms occurring in the northern and central Atlantic Ocean by means of combined analyses of shell form and DNA sequencing.

Abbreviations: NHMD = Natural History Museum of Denmark, Copenhagen; RGM = Rijksmuseum van Geologie en Mineralogie, collection now in Naturalis Biodiversity Center, Leiden, The Netherlands.

Historical notes on the genus *Clio*

Linné (1767: 1094), when formally introducing the genus *Clio*, a name borrowed from Browne (1756: 386), diagnosed the genus as '*Corpus natans, oblongum; Alis duabus, membranaceis, oppositis*', which describes the pelagic way of life, the shape of the body and the presence of two opposite, membranaceous parapodia, but does not mention the presence of a shell. Linné, however, included only the three-shelled species already described but unnamed by Browne (1756: 386), for which he introduced the names *Clio caudata, C. pyramidata* and *C. retusa*. For each of these a shell (Latin: *'vagina*') is described, following Browne's earlier descriptions. For *C. caudata*, diagnosed as *'C. vagina compressa caudata*', a taxon currently considered to be a synonym of *C. pyramidata*, Linné not only referred to Browne's (1756) description, but also included a suggestion ('*Conf.*' = compare) to Martens (1675: 128, pl. P fig. f), adding the remark '*qui nullam vaginam in sua delineavit*', which seems to mean 'who did not mention a shell in his text'.

Martens' illustration (copied here as Fig. 1) of his '*See Gots-Pferd*' (translated as 'sea may-flye' in Phipps, 1774: 195) indeed does not at all represent a species with a compressed shell (which is Linné's description of *C. caudata*), but is a completely different pteropod species, without a shell and belonging to the Gymnosomata, but very much agreeing with Linné's diagnosis of the genus *Clio.* Linné's diagnosis and the reference to Martens' paper led to much confusion as several later authors decided to include the same or similar shell-less pteropod species in the genus *Clio.*

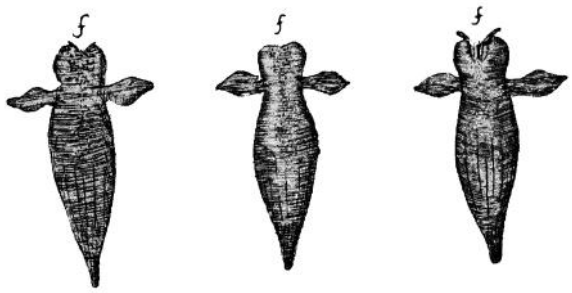

Fig. 1. Martens' (1675: 128, pl. P figs f) 'See Gots-Pferd' = *Clione limacina* (Phipps, 1774). Size not indicated (maximum body length up to 40 mm).

Martens' species was, shortly after Linné, formally described as *Clio limacina* Phipps, 1774, and also as *Clione borealis* Pallas, 1774, of which the former name has priority (MolluscaBase, 2018a). Müller (1776: 226, nr 2742), however, apparently not aware of Phipps' and Pallas' papers, used Linné's name *Clio retusa* for this species. He added to the confusion by including the short Latin description of the shell given by Browne and repeated by Linné ('*vagina triquetra, ore horizontali*'), but he also added the reference to Martens (1675) and the Greenlandic vernacular names of the species described by Martens ('*Ataurfak, Augurfak*'). Also Fabricius (1780: 334) used the name *Clio retusa* for this gymnosome species and gave an extensive description, but realising that this is a shell-less species, he left *'vagina triquetra'* out of his diagnosis. Fabricius referred to Pallas' 1774 description, but cited for that reference the incorrect name *Clione papilionacea*, not used by Pallas.

Gmelin (1791) also included *Clio limacina* Phipps and *Clione borealis* Pallas in the genus *Clio*, and transferred the reference to Martens from *Clio caudata* to *Clio limacina*, while retaining the description of the *C. caudata* shell as given by Browne and Linné, adding references to Müller and Fabricius. This mixing up of completely different species has caused even further confusion in later literature.

Bruguière (1792: xi) included the genus *Clio* in his '*Tableau systématique des vers*, Ordre III – *Les vers mollusques*, section II - *Avec tentacules'*, containing exclusi-

vely shell-less species. On pages 505-508 he discussed the genus *Clio*, considering the genus *Clione* Pallas, 1774, to be a synonym of *Clio* Linné, 1767, and accepting only *Clio borealis* Pallas, 1774, and *C. australis* Bruguière, 1792, both belonging to the Gymnosomata, and currently part of the genus *Clione* (fide van der Spoel, 1976: 110, 115). Bruguière excluded the shelled species of Browne and Linné from the genus *Clio*, as according to him they belonged to another group, namely his 'Ordre V – *les vers testacés*' and announced their future description '*dans la suite au mot* fissurelle [*'in a next part under the word* fissurelle']'.

Cuvier (1802: 242-244) described this '*chaos*' and stated that the species described as *Clione borealis* by Pallas had become the most commonly known and had to be considered the type species of the genus *Clio*. This statement, however, cannot be taken as valid, as the taxon *C. borealis* Pallas was not included in Linné's description of *Clio.* Such taxonomic ruling, however, did not yet exist in the early nineteenth century.

Probably it was Cuvier's unchallenged authority that also led Péron & Lesueur (1810: 65) to arrange the genus *Clio* among the group of pteropods without a shell, which at the same time necessitated them to introduce a new genus, *Cleodora* Péron & Lesueur, 1810, for the shelled species described by Browne and Linné. They included a single species in the new genus, indicated with the vernacular name 'Cléodore Pyramidale' (their pl. 2 fig. 14) (see next chapter). The illustration is rather poor and schematic, but recognisable as *Clio pyramidata* as interpreted until that time, and showing a triangular shell form with completely straight carinae.

After 1810, the name *Clio* was predominantly applied to the shell-less gymnosome species, and *Cleodora* was commonly used for the shell-bearing species. Herrmannsen (1847: 247-250) gave many references for the use of the names *Clio* and *Cleodora*. Bruguière's 1792 promise to describe Browne's and Linné's shelled species later was only realised in 1830, in the second volume of the *Histoire naturelle des vers*, and then under the authorship of Deshayes. In the meantime the genus *Cleodora* was introduced and one might have expected that the shelled species were discussed there. However, only Lesueur's 1813 species *Hyalea lanceolata* was included there with the name *Cleodora lanceolata*, not a word on Browne's and Linné's species. In that publication the genus *Clio*, is still used for the gymnosome species only.

At last Gray (1847: 203) synonymised *Cleodora* Péron & Lesueur, 1810, with *Clio* Linné, 1767, and designated *Clio pyramidata* as the type species of *Clio*. Thereafter several authors (e.g., Adams & Adams, 1853: 52; Philippi, 1853: 291; Jeffreys, 1869: 118; Pelseneer, 1888: 42; Norman, 1890: 62; Meisenheimer, 1905: 20, etc.) indeed applied the genus *Clio* for the shelled species, but other authors (e.g., Gegenbaur, 1855: 210; Conti, 1864: 26; Seguenza, 1867: 9; Weinkauff, 1868: 425-426; Bellardi, 1873: 30; Fol, 1873: 177; Fischer, 1883: 435; Boas, 1886: 54; Friele & Grieg, 1901: 122; Collins, 1934: 200) retained the name *Cleodora* as valid.

Bonnevie (1913: 20) introduced the subgenus *Euclio* in *Clio* for three species, among which also *Clio pyramidata.* This makes *Euclio* an objective junior synonym of *Clio*.

Thiele's (1931: 401) *'Handbuch der systematischen Weichtierkunde*' listed *Clio* as a valid genus in the Cavoliniidae, with *Cleodora*, *Balantium* Children, 1823, and *Euclio* as synonyms, and *Clio pyramidata* as type species. Tesch (1946: 13-14), however, retained *Euclio*, and although he was well aware of 'the rules of priority' (Tesch, 1946: 14) also wrote 'seems to me preferable to Pelseneer's *Clio* (*s. str.*)'.

Hubendick (1951: 3) introduced the genus *Proclio* for the species *P. subteres* Hubendick, 1951, that was subsequently synonymised with *Clio pyramidata* f. *antarctica* Dall, 1908, by van der Spoel (1967: 72; see also van der Spoel, 1962), which made *Proclio* a subjective junior synonym of *Clio.* However, *Clio pyramidata* f. *antarctica* was found to be genetically distinct from *C. pyramidata* by Burridge et al. (2017, fig. S1), which makes the name *Proclio* available again.

Zilch (1959: 51 fig. 169) also placed *Cleodora* and *Euclio* in synonymy with *Clio*, together with *Balantium* and some taxa introduced by Bellardi (1873) for fossil species (*Poculina, Flabellulum*). That author, however, retained the genus *Proclio* as valid. His illustration is copied from Sowerby (in Reeve, 1878, Pteropoda pl. 4 fig. 25a-b) and represents a specimen of *Clio pyramidata* with concave carinae. As type species of *Clio* Zilch erroneously mentioned *Clio 'pyramidalis* Linnaeus', obviously a lapsus calami for *pyramidata*. The same error occurs in the caption of his fig. 169. Also Bowdich (1822) had described a '*Cleodora pyramidalis*'. Confusingly, the name *Clio pyramidalis* had also validly been introduced for a gymnosome pteropod by Quoy & Gaimard (1832), see next chapter.

In van der Spoel (1967: 65-66) the names *Cleodora, Balantium, Euclio* and also *Proclio* are considered synonyms of *Clio.* Also an extensive synonymy is given for this genus This author accepted nine species in the genus *Clio* and additionally seven formae.

The application of subgenera in the genus *Clio* was discussed by Janssen (2000: 44), who observed that in the various recent as well as fossil species not only considerable differences in adult shell morphology occur, but also in the details of the protoconchs. He suggested the use of *Clio* s. str. and *Balantium* as subgenera, but noted that other Recent species do not

conform to the morphology of these two. Later (Janssen, 2005) the subgenus *Bellardiclio* was introduced for *C. cuspidata* Bosc, 1801, and a related fossil species. Assigning most fossil cliids to subgenera, however, is problematic as in many of the species described from the fossil record the protoconchs are still unknown. Currently (e.g., in WoRMS) such subgenera in *Clio* are not accepted, which may be changed once sufficient molecular data have become available, which may lead to accepting these taxa at full genus level. The genus *Clio* was one of the genera that was not found to be monophyletic in molecular phylogenetic analyses of Corse et al. (2013) and Burridge et al. (2017).

Only in 2006 the International Commission on Zoological Nomenclature ruled that the name '*Clio* Linnaeus, 1767' is placed on the Official List of Generic Names in Zoology, with its type species '*Clio pyramidata* Linnaeus, 1767', by subsequent designation of Gray (1847). Currently eight recent *Clio* species are accepted (MolluscaBase 2018b). Subgenera are not used. The various earlier distinguished formae have no official status, as ruled by ICZN (1999).

The species *Clio pyramidata* in the eighteenth and nineteenth century

The species *Clio pyramidata*, together with *C. caudata* and *C. retusa*, were formally introduced by Linné (1767: 1094), who obviously had no specimens before him but based the names on the descriptions of Browne (1756: 386), who had only illustrated *C. pyramidata* in his pl. 43 fig. 1 (reproduced herein as Fig. 2). Syntypes are not available either. The short descriptions of Browne, repeated by Linné, leave no doubt that all three names represent shelled species.

Fig. 2. Browne's (1756) illustration of *Clio pyramidata*, from Jamaica (enlarged, the size was indicated as 'length seldom exceeds half an inch'.

From the illustration it is clear that the artist had seen a live animal, as the parapodia are drawn in life position. Several later authors, however, criticised the representation of the animal's head. The shell is drawn as a regular triangle, with completely straight carinae and, agreeing with Browne's description, an obliquely positioned triangular aperture. However, a form of *C. pyramidata* with such straight carinae does not occur in the type area (here all specimens would have concave sidelines). We have arrived at the inevitable conclusion that it is especially this picture, together with several follow-ups of later authors, that have initiated an erroneous interpretation of the species *Clio pyramidata* that has generally been accepted for more than 250 years, as we will explain, and for which we introduce a solution, below.

A second early illustration was published, as an unnamed 'insect', by La Martinière (1787a: 207, pl. 11 figs 1-3), observed during the unhappy voyage of De la Pérouse, near Notka (Vancouver Island, Canada; Fig. 3). Also these drawings are apparently based on the observation of a live animal, and although showing several differences compared to Browne's drawing, it unambiguously represent the same species.

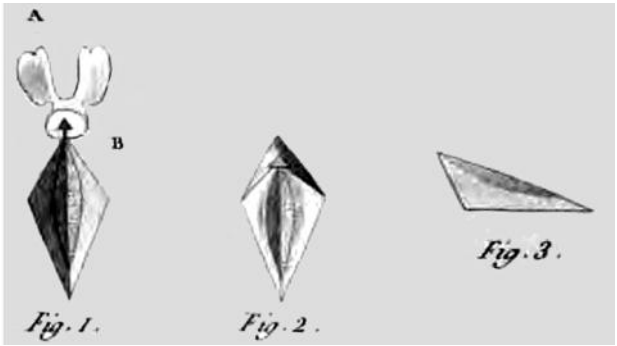

Fig. 3. Unnamed 'insect', after La Martinière, 1787a, from 'près de Notka' (Vancouver Island, British Columbia, Canada). Size not indicated.

Gmelin (1791: 3148) followed Linné (1767) in including the same three species in the genus *Clio* that were adopted from Browne (1756), but adding references for *Clio retusa* to Müller (1776) and Fabricius (1780), which both, however, concerned unshelled gymnosome species, and giving a rather long Latin description for that species, at least partly based on Fabricius' even longer description. Apart from the three Linnean species, Gmelin furthermore included *Clio borealis* Pallas, *C. limacina* Phipps, which again are unshelled gymnosomes, and *C. helicina* Phipps. For the latter Gmelin referred also to Martens (1675: 129, pl. Q fig. e), where a so-called '*Schnecken Rotzfisch*' ('sea slimefish' in an English translation, White, 1855) was de-

scribed and illustrated. These three drawings (here reproduced in Fig. 4), however, evidently represent a shelled, sinistrally coiled pteropod in apical view, with the parapodia indicated. This species is currently known as *Limacina helicina* (Phipps, 1774) and has nothing to do with *Clio*. Martens' illustrations may be the earliest recognisably published euthecosomatous pteropod.

Fig. 4. Martens' (1675, pl. Q fig. e) illustrations of '*Schnecken Rotzfisch*' = *Limacina helicina* (Phipps, 1774).

Gmelin (1791: 3148) also included a reference to La Martinière (1787b: 366, pl. 2 figs 15-16) for *Clio limacina*, where again an unnamed 'insect' was described. La Martinière's illustration (Fig. 5 herein), however, does represent not even a pteropod, but a pelagic nudibranch, *Glaucus atlanticus*, already described (but not illustrated) by Forster (1777: 49) and so beautifully pictured on the cover of Lalli & Gilmer's (1989) book. Gmelin's decision to incorporate it in the genus *Clio* is explained by a footnote in La Martinière (1787b: 366) saying '*Il paroit se rapprocher du genre des* clios' [it seems to be close to the genus *clio*]. Although the genus *Glaucus* was known to Gmelin (1791: 3025), he did not recognise La Martinière's figures to belong to it.

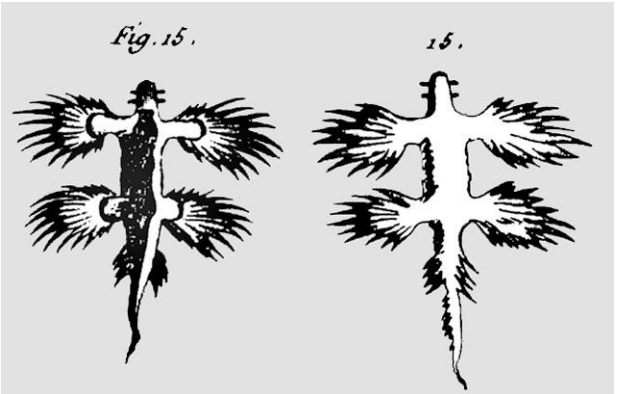

Fig. 5. Unnamed 'insect' in La Martinière (1787b, pl. 2 figs 15-16) from Baschi (?) Islands = *Glaucus atlanticus* Forster, 1777 (Nudibranchia).

Ten years after its first publication, the same paper of La Martinière (1787a) was republished posthumously and almost unchanged in volume 4 of the '*Voyage de la Pérouse*' (La Martinière, 1797: 61, pl. 20 figs 1-3), but with redrawn, even more unrealistic illustrations (Fig. 6).

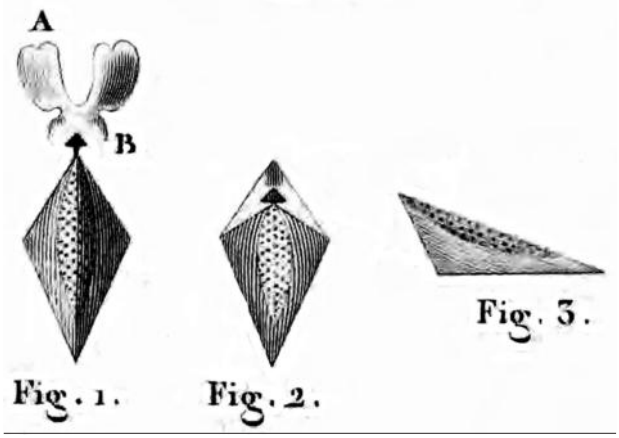

Fig. 6. Unnamed 'insect', after La Martinière, 1797, from Nootka (Vancouver Island, British Columbia, Canada).

Bosc (1801: 241, pl. 9 figs 1-3; Fig. 7 herein) recognised La Martinière's (1787a) illustrations as the species earlier figured by Browne and described as *Clio pyramidata* by Linné. Bosc included it in the genus *Hyalæa* Lamarck (1799: 89), a monotypic genus introduced for *Anomia tridentata* Forsskål in Niebuhr, 1775, which currently is included in the genus *Cavolinia*. He gave new figures that evidently are based on the earlier published drawings of La Martinière, but have again been changed and further deviate from reality. Several later authors also preferred to use the genus name *Hyalæa*, but see the extensive description and discussion in de Blainville (1821).

To the description of their new genus *Cleodora*, Péron & Lesueur, 1810, pl. 2 fig. 14, reproduced herein as Fig. 8, added an illustration of the only included species of that genus, indicated as 'Cléodore Pyramidale', a schematised drawing very much resembling the original figure of Browne (1756).

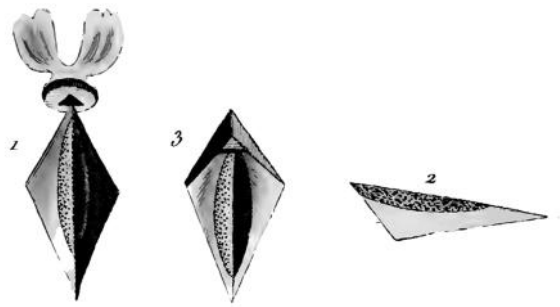

Fig. 7. *Hyalæa pyramidata*, after Bosc (1801), from 'les mers d'Amérique'.

Fig. 8. Péron & Lesueur's (1810) illustration of 'Cléodore pyramidale'.

From the Mediterranean, off Nice, Lesueur (1813: 284, pl. 5 fig. 3) introduced a new species, described as *Hyalea lanceolata*. Curiously, the author did not include his new species in the genus *Cleodora*, introduced few years earlier (1810) by Péron and himself. The drawings (copied herein as Fig. 9) show a *Clio* resembling the earlier illustrations of *C. pyramidata*, but differing by the strongly diverging, concave carinae of the shell, ending in short lateral spines at the aperture.

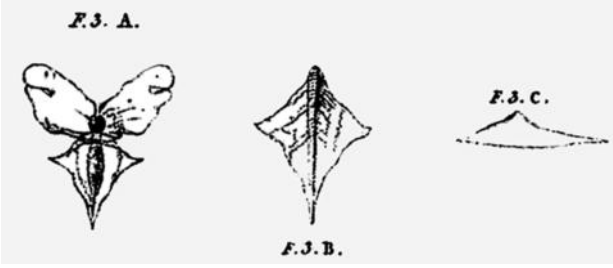

Fig. 9. *Hyalea lanceolata* Lesueur, 1813. After Lesueur (1813: 284, pl. 5 fig. 3A-C).

Bowdich (1822: 23, 56, pl. 5 fig. 2) attributed the genus *Cleodora* to Péron (not Péron & Lesueur) and included it, together with some other genera, in a new division 'Vaginaceae' of his 'Univalve shells'. The division name is based on the fossil pteropod genus *Vaginella* Daudin, 1800, that Bowdich, however, renamed *Vaginellites*, as was frequently done for fossils. He described *Cleodora 'pyramidalis'* (lapsus calami)[1] as 'cartilo-gelatinous; like a reversed truncated pyramid', and gave its distribution as 'Seas of warm climates'. His illustration of the 'envelope' of this species is rather schematic, showing a shell with completely straight sidelines, that seems to be based on the early drawing in Browne (1756) . Bowdich's illustration is copied here in Fig. 10.

[1] This author appears to have been rather shabby in his namings, as he also illustrated (pl. 5 fig. 1) a *Hyalea* '*tricuspidata*', where obviously '*tridentata*' is meant. In WoRMS (Gofas, 2014) this Bowdich citation is, erroneously and with the incorrect year 1820, interpreted as *Clio cuspidata* (Bosc, 1801).

Fig. 10. The 'envelope' of *Cleodora 'pyramidalis'*, after Bowdich (1822, pl. 5 fig. 2). Enlarged, size and locality not mentioned.

A new taxon was introduced by de Blainville (1824: 272; 1825: 481; 1827, pl. 46bis figs 1, 1a-b) with the name 'Cléodore de Browne, *Cleodora Brownii*', obviously based on Browne's (1756) illustration. He gave a short description and referred to Péron & Lesueur (1810, pl. 3 fig. 14) (error for pl. 2), which is 'Cléodore pyramidale' - *Clio pyramidalis*. He described the *Cleodora* shell as '*une sorte d'étui gélatineux à ouverture antérieure fort grande, et non échancrée latéralement* [sort of a gelatinous case with a very large anterior opening, without lateral slits]. His drawings are reproduced here as Fig. 11.

Van der Spoel (1967: 68) synonymised *Cleodora brownii* with *Clio pyramidata*, but this seems to be a bit doubtful because of the rather strong lengthwise curvature of the shell as seen in de Blainville's fig. 1.a (Figure. 11 herein). In *Clio pyramidata* the shell is virtually straight.

From the voyage of the 'Astrolabe' Quoy & Gaimard (1832: 386, pl. 27 figs 7-13) gave a description and illustrations of *Cleodora pyramidata* from the southern Atlantic Ocean, referring to *Hyalea lanceolata* Lesueur as a synonym. In their description they give a number of anatomical soft part details. Their illustration represents a shell with concave sidelines. Rather confusingly, however, they also (Quoy & Gaimard, 1832: 371, pl. 27 fig. 37) introduced from '*la rade d'Amboine*' the new (gymnosome) species *Clio pyramidalis* (not a homonym of *Clio pyramidata* Linné, 1767). The name *Clio pyramidalis* was later on discussed by Souleyet, in Rang & Souleyet (1852: 80, pl. 11 fig. 13) and also by Pruvot-Fol

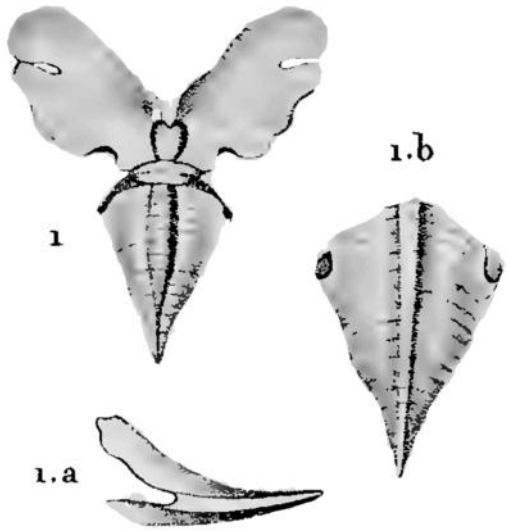

Fig. 11. De Blainville's 1827 illustrations of *Cleodora brownii*.

(1932: 508), who both expressed some doubts about the validity of that species. Tesch (1913: 130) did not give a clear opinion on this taxon, but referred to it without comments at the end of his text on the genus *Clione*.

According to van der Spoel (1976: 130), however, Quoy & Gaimard's name *Clio pyramidalis* is a synonym of the gymnosome species *Clione limacina* (Phipps, 1774) or its f. *antarctica* (Smith, 1902). This seems doubtful, as according to van der Spoel's (1976 fig. 221) distribution map of that colder water species neither *C. limacina*, nor its f. *antarctica* occurs in the tropics near Amboina. See above for Bowdich's (1822) and Zilch's 1959 erroneous use of the name *Clio pyramidalis*.

D'Orbigny (1834: 113; 1836, pl. 7 figs 25-32), in his '*Voyage dans l'Amérique méridionale*', described the present species as '*Hyalæa pyramidata* Linn.', interpreting the genus *Hyalæa* in a very wide sense (1834: 77), including a number of earlier names in it as synonyms, among which also *Clio*, *Carolina* [sic], *Creseis* and *Cleodora*, but accepting several of these as a subgenus. For *Hyalæa* (*Cleodora*) *pyramidata* a number of earlier references are given, among which also La Martinière's 1797 illustrations. D'Orbigny distinguished for *Hyalæa pyramidata* the varieties A ('*très élargie latéralement*') and B ('*presque pyramidale*') and gave different geographical distributions, but mentioned his var. B (p. 115) exclusively from '*le grand Océan austral*'. Of the earlier illustrations of Browne (1756; which d'Orbigny considered to represent a juvenile specimen) and La Martinière (1797) d'Orbigny wrote '*C'est évidemment la variété B*'. Although he gave (1834: 114) the reference to Lesueur's 1813 description of *Hyalea lanceolata* and recognised it as his 'variété A' he did not use Lesueur's name for it, agreeing with his habit to indicate a 'variété' with a single character only.

D'Orbigny (in de la Sagra, 1841: 83) again described *Cleodora pyramidata*, mentioning it specifically also from the Caribbean ('Antilles'). In a footnote on p. 83 the specimen illustrated by La Martinière (1797) is introduced as a new species: '*L'espèce figurée par Lapeyrouse pl. 20, f. 1-3, que nous avons rencontrée dans le grand Océan , nous paraît distincte de celle de l'océan Atlantique, et nous la nommons* Cleodora Lamartinieri'. This name is repeated on one of the last pages of '*Voyage dans l'Amérique*' (1846: 688), as the caption of plate 8 figs 30-31, which, however, represent a specimen with strongly concave carinae, very much different from La Martinière's illustrations (see Figure 6 above). This discrepancy led van der Spoel (1967) to citing 'd'Orbigny (1841, non 1846)' for *Clio pyramidata* f. *pyramidata*, but 'd'Orbigny (1846, non 1841)' for *C. pyramidata* f. *lanceolata*.

Two fossil pteropod species were introduced by Calandrelli (1844) from the Pliocene of Monte Vaticano, Roma, Italy, namely *Cleodora vaticana* and *C. riccioli*. The former, however, illustrated in Calandrelli's upper figures A-B, is a subjective junior synonym of *Clio pyramidata*, and represents the form with concave carinae, as explained in Janssen (1995: 90 fig. 1). In Calandrelli's illustration not only the two new species were drawn, but also (his fig. C) a specimen of '*Cleodora caudata* with reference to Rang (1829, pl. 49 fig. 1)'. The reference is erroneous, it is not a copy of Rang's illustration, but it is based on Péron & Lesueur (1810, pl. 2 fig. 14, as 'Cléodore pyramidale'), and redrawn by Calandrelli. That drawing indeed resembles several earlier illustrations of *C. pyramidata*, as interpreted in those times. Calandrelli's figures are copied herein as Fig. 12.

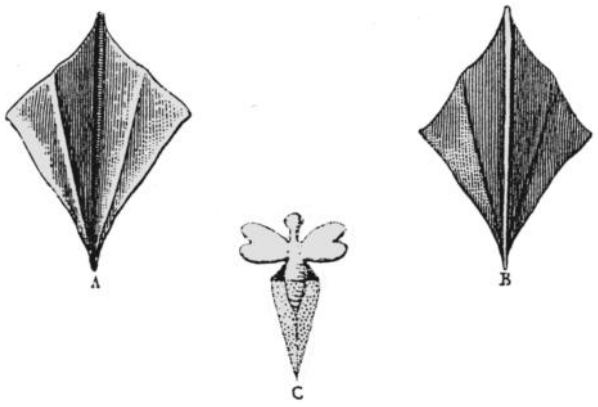

Fig. 12. *Cleodora vaticana* Calandrelli, 1844 (A, B) and '*Cleodora caudata*'(C), from Calandrelli (1844). Fig. A represents the external mould, Fig. B the internal one, both of the same specimen. Fig. C according to the author after Rang (1829), but in reality is redrawn after Péron & Lesueur (1810, pl. 3 fig. 14, as 'Cleodore pyramidale').

Gould (1852: 488; 1856, pl. 51 fig. 605, 605a-b) introduced *Cleodora exacuta* from the Pacific Ocean (44°N, 154°W). We agree with van der Spoel (1967: 69) that his large figure, here reproduced in Fig. 13, represents the form of *Clio pyramidata* with concave carinae. However, his fig. 605a, showing the transverse shape of the shell, does not really agree with *C. pyramidata*, the transverse shape of which is much more triangular. Hence, in our list of synonyms in the systematic chapter below we accept this name with a query.

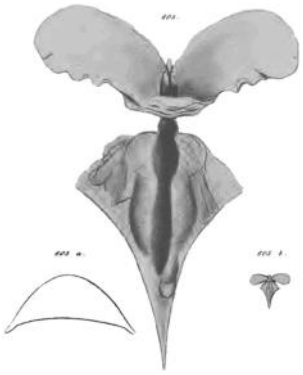

Fig. 13. *Clio exacuta* Gould, 1851 from the North Pacific Ocean. Size indicated as 'length about half an inch, breadth equal to about two thirds the length'.

Souleyet, in Rang & Souleyet (1852: 50, pl. 5 figs 7-9), described *Cleodora pyramidata*, but considered Péron & Lesueur (1810) to be the authors of this combination although referring to Browne's (1756) and Linné's (1767) descriptions in the synonyms. He also considered *Cleodora lanceolata* Lesueur to be a synonym, as in his opinion (obviously based on d'Orbigny, 1834: 114) it is just a more adult form of *C. pyramidata*. The illustrations (copied herein as Fig. 14) represent a well-developed specimen of the shell form with concave carinae and, contrary to their text, indicated in the plate caption as *Cleodora lanceolata*. The genus *Clio* was discussed on p. 77ff, but included only the gymnosome species.

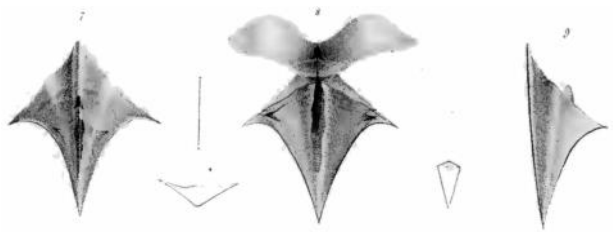

Fig. 14. *Cleodora lanceolata* Lesueur, after Souleyet, in Rang & Souleyet, 1852.

According to its short description, *Cleodora occidentalis* Dall (1871: 140), not illustrated by the author, is a form of *Clio pyramidata* with concave carinae. It was collected in the Pacific Ocean, off the California coast, at coordinates 33°N, 130°W.

In Reeve's *Conchologia Iconica*, G.B. Sowerby (1878, Pteropoda pl. 4 fig. 24) described *Cleodora lobata* (Fig. 15 herein) and compared it to d'Orbigny's (1834-1836) *Hyalæa pyramidata* var. A, while considering it a separate species. The rather poor illustration represents a *Clio pyramidata* with concave carinae. In the same work (fig. 25) also *Cleodora pyramidata* is illustrated, equally showing a specimen with concave carinae. His fig. 22 is named *Cleodora australis*, with reference to d'Orbigny (1834, pl. 8 figs 12-14 ([incorrect, meant were figs 9-11]). According to van der Spoel (1967: 71), however, Sowerby's specimen belongs to *C. pyramidata* forma *sulcata* (Pfeffer, 1879), whereas the reference in d'Orbigny, again according to van der Spoel (1967: 72), represents *C. pyramidata* forma *antarctica* Dall, 1908.

Fig. 15. *Cleodora lobata* G.B. Sowerby, 1878, from the Atlantic Ocean, dimensions not indicated.

Boas (1886: 69, 203), discussing '*Cleodora pyramidata*', introduced three named varieties: var. *angusta* (agreeing with d'Orbigny's var. B), var. *lata* (d'Orbigny's var. A) and var. *convexa*. He also gave differing geographical areas for these forms. The 'variety *convexa*' for a long time was indeed considered to be a form of *Clio pyramidata* (see van der Spoel, 1967, 1969), but is currently accepted as an independent species (Bé & Gilmer, 1977; Richter, 1979; Rampal, 2002; Janssen, 2007a, b) not occurring in the Atlantic Ocean.
In his list of synonyms Boas referred to '*Hyalæa lanceolata* Lesueur', but curiously did not use it as an older name for his variety *lata*. On plate 6 figs 96a-g a series of seven specimens is represented in outline (Figure 16 herein), showing an increasing degree of concavity of the carinae. Although there is not an obvious boundary between them Boas considered numbers 96a-f to belong to his variety *angusta* and only 96g as variety *lata.*

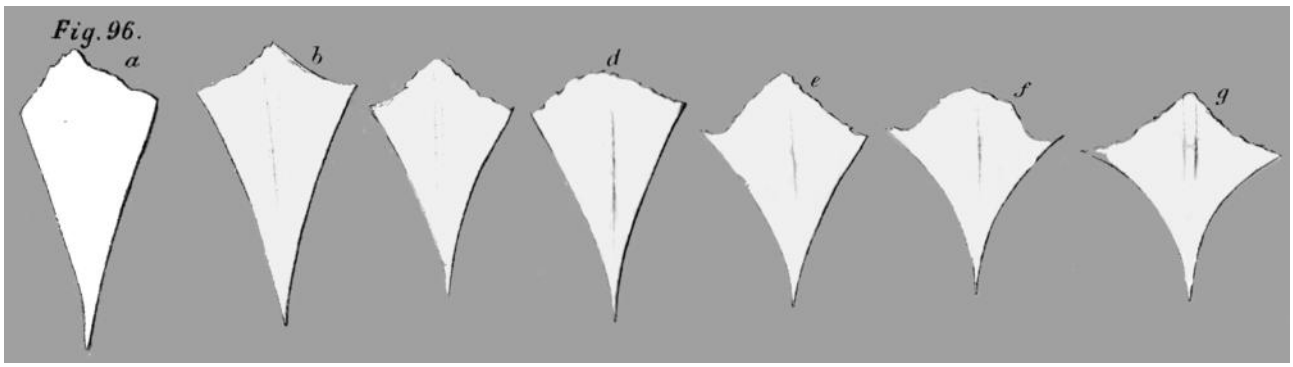

Fig. 16. *Cleodora pyramidata* after Boas (1886, pl. 6 fig 96) figs a-f = var. *angusta,* and fig. g = var. *lata*.

From the late Miocene Navidad Formation of Chili *Clio promaucana* Philippi (1887: 112, pl. 13 fig. 18) was described. Judging from the poor illustration (herein copied as Fig. 17) we interpret it as a probable junior synonym of *Clio pyramidata*. According to Nielsen (2003: 198) the type specimen is lost.

Fig. 17. *Clio promaucana* Philippi, 1887, holotype, shell height 6.5 mm (after Philippi, 1887).

Twentieth century and present-day concept

Tesch (1913) distinguished *Clio pyramidata* with three subspecies. For *Clio pyramidata pyramidata*, a long and rather uncritical list of synonyms is given, among which Browne (1756), Linné (1767, with *C. caudata* and '? *C. retusa*' included), and finally also Boas' var. *angusta*. The latter form is illustrated in Tesch's fig. 31A-C, of which fig. 31A is a reproduction of Boas' fig. 96a. The author repeated Boas' distribution data saying that this form is restricted to the North Atlantic between 40°N and 60°N and eastern parts of the South Pacific, and adding 'occasionally to Davis Strait and Spitzbergen'.

Tesch's second subspecies is *Clio pyramidata lanceolata*, for which also several synonyms are given, starting with Lesueur (1813) and concluded with Boas' (1886) var. *lata*. As distribution is given the warmer parts of oceans between 40°N and 30°S, also in the Mediterranean and the West Pacific Ocean.

Tesch's diagnosis of subspecies *Clio pyramidata convexa* is erroneous. The clearly distinguishing characteristic of the double-lined carinae is not mentioned and also his distributional data do not agree with the real area of occurrence of *Clio convexa.* Based on an unpublished opinion of McGowan (1960), *C. convexa* was raised to full species level by Bé & Gilmer (1977: 773).

A fossil species from the Pliocene Bowden Beds of Jamaica was introduced as *Cleodora bowdenensis* Collins (1934: 201, pl. 12 figs 3-7). It was synonymised with *Clio pyramidata* by Robba (1977: 600) and with *C. pyramidata* f. *lanceolata* by Janssen (1999: 21, pl. 3 figs 13-17). The holotype is re-illustrated herein as Fig. 18.

Two drawings of the form with concave carinae were published by Korobkov (1955: 430 fig. 195) represening an Italian Pliocene specimen (a) and a recent one (b), indicated with the name *Clio pyramidata* (Fig. 19).

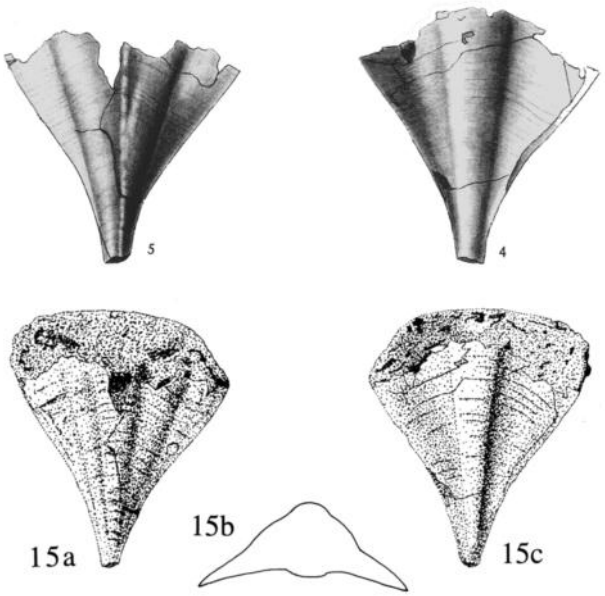

Fig. 18. Holotype of *Clio bowdenensis* (Collins, 1934). Upper row: after Collins (1934), lower row: after Janssen (1999).

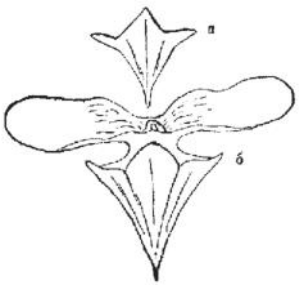

Fig. 19. *Clio pyramidata* L., according to Korobkov (1955).

The nomenclature as maintained by Tesch (1913) is not followed by van der Spoel (1967: 67) who interpreted Tesch's three subspecies of *Clio pyramidata* as formae, together with several further, earlier described taxa. For the North Atlantic, van der Spoel followed the interpretation of Tesch as far as shell characteristics and distribution are concerned. According to van der Spoel's fig. 348 *Clio pyramidata* f. *pyramidata* is distributed in the North Atlantic between 45° and 65°N, whereas *Clio pyramidata* f. *lanceolata* occurs between 50°N and 45°S worldwide, inclusive of the the Mediterranean, but excluding the larger part of the Caribbean. Van der Spoel's (1967) interpretation of *Clio pyramidata* f. *convexa* follows Tesch's morphological data.

The interpretation of two subspecies in the Atlantic Ocean, a northern one with virtually straight (forma '*pyramidata*') and a southern one with strongly concave carinae (forma '*lanceolata*'), is maintained in most of the recent literature (Rampal, 1975, 2002, 2017; Janssen, 2007b, 2012). Several further taxa are distinguished in the subantarctic region (Fig. 20).

Discussion

Following the historical overview of *Clio pyramidata*,it is clear that the current concept of 'typical' *C. pyramidata* being the form with straight shell sides finds its origin in the older literature and illustrations therein, but is here considered to be erroneous. In this respect especially the illustration in Browne (1756), here copied in Fig. 2, is noteworthy, as it is exactly that figure on which the taxon *Clio pyramidata* was based by Linné, 1767 (as it was the only reference given). Browne's illustration indeed seems to represent a specimen with straight shell sides. D'Orbigny's (1834: 113) remark that Browne's drawing represents a juvenile specimen is incorrect, as Browne himself, in his text on p. 386 mentioned the size of the species as 'seldom exceeds half an inch', which certainly does not pertain to very juvenile specimens.

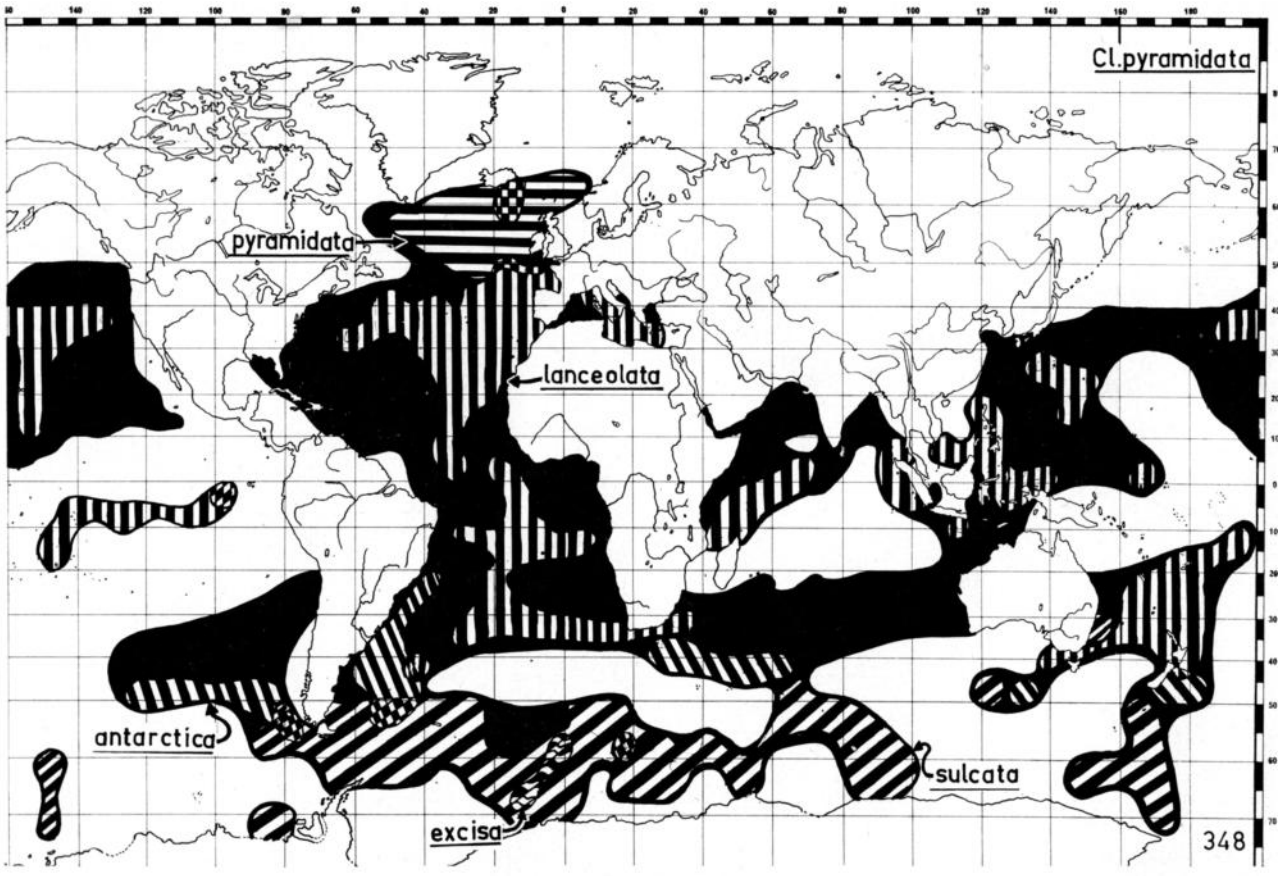

Fig. 20. Van der Spoel's (1967 fig. 348) distribution map of *Clio pyramidata* formae.

In our opinion Browne's illustration is incorrect and too much schematised. A form of *Clio pyramidata* with such straight carinae does not occur in the area from where Browne's illustrated specimen was collected, which is the Caribbean Sea near the island of Jamaica. The typical form of *C. pyramidata* occurring in that area has shells with distinctly concave sides, described in 1813 by Lesueur as *Hyalea lanceolata*, that we consider a subjective junior synonym of *C. pyramidata.* In the systematic chapter below we illustrate 11 specimens from Jamaica that invariably demonstrate these clearly concave carinae of their shell (Figs 24 & 25). We examined the relationship of the two shell forms of *C. pyramidata* and conclude that the form with concave sides (occurring in the warm waters of the Atlantic, Caribbean and Mediterranean) should be considered typical '*C. pyramidat*a' and the form with straight sides could be indicated as '*angusta*' Boas, 1886, but at subspecies rank only.

Molecular methods

To test whether forms '*pyramidata*' and '*angusta*' are genetically different, genomic DNA was extracted from soft tissue of nine *Clio pyramidata* specimens using the DNA barcoding pipeline at Naturalis Biodiversity Center (described in detail in Wall-Palmer et al., 2018). A fragment of ~600 basepairs (bp) of the mitochondrial Cytochrome Oxydase I (COI) gene was amplified using the primers from Geller et al. (2013) according to methods described in Wall-Palmer et al. (2018). Nucleotide sequences of COI were examined and aligned using the MUSCLE algoritm in MEGA 6 (Tamura et al., 2013). A Maximum Likelihood (ML) analysis was used to estimate evolutionary relationships among taxa (Felsenstein, 1981) in RaxmlGUI 1.3 (Stamatakis, 2006; Silvestro and Michalak, 2012). For this the GTR (General Time Reversible) model was selected, using codon-specific evolutionary rates.

Five specimens morphologically resembled '*pyramidata*' with concave shell sides and four specimens resembled '*angusta*' with more straight shell sides, and were numbered according to the degree of concavity of shell sides (Fig. 21). Specimens from the Caribbean Sea were collected during the GU1101 expedition in 2011 (*N*=2 '*pyramidata*' from 2 stations). Specimens from the North Atlantic Ocean were collected from three locations during the MAR-ECO cruise in 2004 (*N*=4 '*angusta*' and *N*=2 '*pyramidata*'), and from one location further south during the Atlantic Meridional Transect 24 (AMT24) in 2014 (*N*=1 '*pyramidata*'; Table 1, Fig. 21. Outgroup taxa for phylogenetic analyses were *Clio cuspidata* (Bosc, 1801) (N=1) and *Clio recurva* (Children, 1823) (*N*=1; Table 1; Burridge et al., 2015, 2017). All locality data are specified in Table 1.

Taxonomy & Species	Reference	Collection date	Latitude	Longitude	Cruise	Station	Long code	Shortcode	CO1	Pictures *N*
Thecosomata, Euthecosomata, Cavolinioidea										
Clio pyramidata pyramidata	This study	2011-04-18	16°10'N	86°45'W	GU1101	71	Cl_pyr_GU1101_71_01	CLpyGU7101	MH101647	1
Clio pyramidata pyramidata	This study	2011-04-23	19°30'N	85°27'W	GU1101	100	Cl_pyr_GU1101_100_02	CLpyGU1002	MH101648	1
Clio pyramidata angusta	This study	2004-06-12	57°10'N	31°07'W	MAR-ECO	6	Cl_ang_MAR_06_01	CLagMA0601	MH101649	2
Clio pyramidata angusta	This study	2004-06-25	48°04'N	29°20'W	MAR-ECO	26	Cl_ang_MAR_26_01	CLagMA2601	MH101650	1
Clio pyramidata angusta	This study	2004-06-25	48°04'N	29°20'W	MAR-ECO	26	Cl_ang_MAR_26_02	CLagMA2602	MH101651	1
Clio pyramidata pyramidata	This study	2004-06-27	42°35'N	27°29'W	MAR-ECO	28	Cl_pyr_MAR_28_01	CLpyMA2801	MH101652	1
Clio pyramidata angusta	This study	2004-06-27	42°35'N	27°29'W	MAR-ECO	28	Cl_ang_MAR_28_02	CLagMA2802	MH101653	1
Clio pyramidata pyramidata	This study	2004-06-27	42°35'N	27°29'W	MAR-ECO	28	Cl_pyr_MAR_28_03	CLpyMA2803	MH101654	1
Clio pyramidata pyramidata	This study	2014-10-08	17°49'N	28°42'W	AMT24	10	Cl_pyr_AMT24_10_02	CLpyA41002	MH101655	5
Clio cuspidata	Burridge et al., 2015	2008-10-27	12°50'S	25°00'W	AMT18	66	Cl_cus_AMT18_66_02	CLcuAM6602	KP292789	2*
Clio recurva	Burridge et al., 2017	2004-06-19	51°34'N	33°17'W	MAR-ECO	16	Cl_rec_MAR_16_01	CLreMA1601	MF048923	1*

Table 1. Overview of *Clio* sequences used in a phylogenetic analysis based on Cytochrome Oxidase I. Picture numbers indicated with an asterisk are available in the Dryad digital repository at DOI: 10.5061/dryad.bp106.

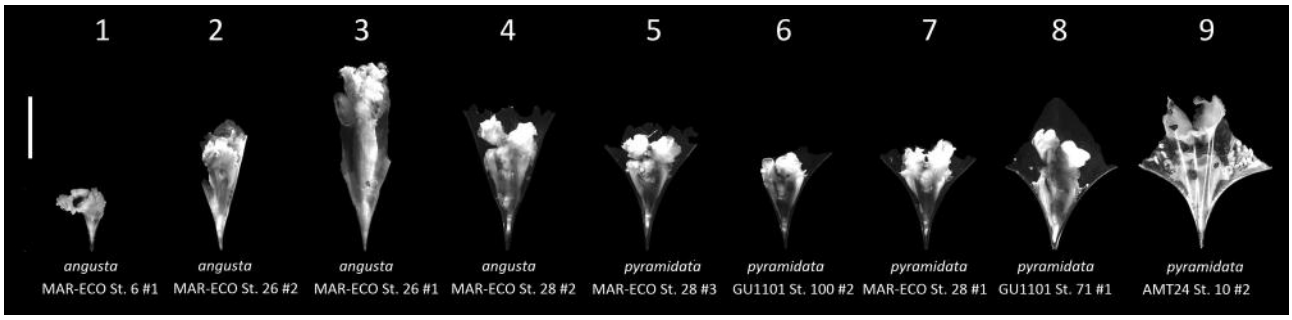

Fig. 21. Overview of the nine *Clio pyramidata* specimens used for molecular phylogenetic analysis. Specimens are arranged based on degree of concavity of shell sides. Bar size is 5 mm.

Molecular results

Based on the phylogenetic analysis of CO1 gene sequences, support was found for monophyly of all nine *C. pyramidata* specimens (Fig. 23). The shell forms '*pyramidata*' and '*angusta*' could not be distinguished, nor was there any support for a distinction between specimens from the Caribbean Sea and specimens from the open North Atlantic Ocean. It is noteworthy that our sampling included intermediate shell forms (Fig. 21) and that both shell forms were found in the same zooplankton sample (station 28 from the MARECO expedition, Fig. 22). Hence, notwithstanding our limited sampling of specimens and molecular markers, we suggest that different shell forms do not represent distinct species

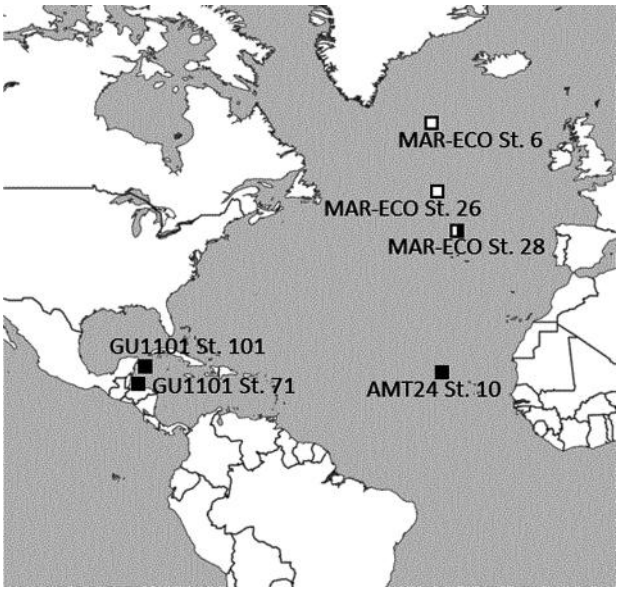

Fig. 22. Overview of sampling locations of *Clio pyramidata* specimens (N=9) used for molecular phylogenetic analysis. White square = '*angusta*'; Black square = '*pyramidata*'; Half-white square = '*angusta*' and '*pyramidata*' at the same location.

Conclusions

We conclude that the interpretation of 'typical' *Clio pyramidata* has been erroneous throughout history, and that the taxon *Hyalea lanceolata*, introduced from the Mediterranean by Lesueur (1813), is a subjective junior synonym of *Clio pyramidata* Linné, 1767. We stabilise nomenclature by the designation of a neotype for *Clio pyramidata* on the basis of a specimen from the type locality, the sea around Jamaica (see sytematic part below), 'with the express purpose of clarifying its taxonomic status'(ICZN art. 75.3.1).

It is evident that the form occurring in the northern Atlantic Ocean can no longer be indicated as *Clio pyramidata* (f.) *pyramidata* as it distinctly differs from neotypical *C. pyramidata* by its straight rather than concave sides of the shell. For this morphotype the name *angusta* Boas,1886, is available and to avoid any future misunderstanding we designate a lectotype from Boas' syntypical material housed at the Natural History Museum of Denmark, Copenhagen (see systematic part, below).

The even older name *Clio lamartinieri* d'Orbigny, 1841, based on La Martinière's 1797 illustration, represents a species from the NE Pacific Ocean, where a form of *Clio pyramidata* with straight carinae does not occur. Therefore, and also because of d'Orbigny's 1841 and 1846 differing interpretations, we consider the name *C. lamartinieri* a *nomen dubium*. Also we cannot exclude the possibility that it, in fact, represents *Clio convexa* (Boas, 1886).

Our molecular results demonstrate that the shell forms '*pyramidata*' and '*angusta*' are unlikely to represent distinct species, meaning that the latter name can only be applied at subspecific rank.

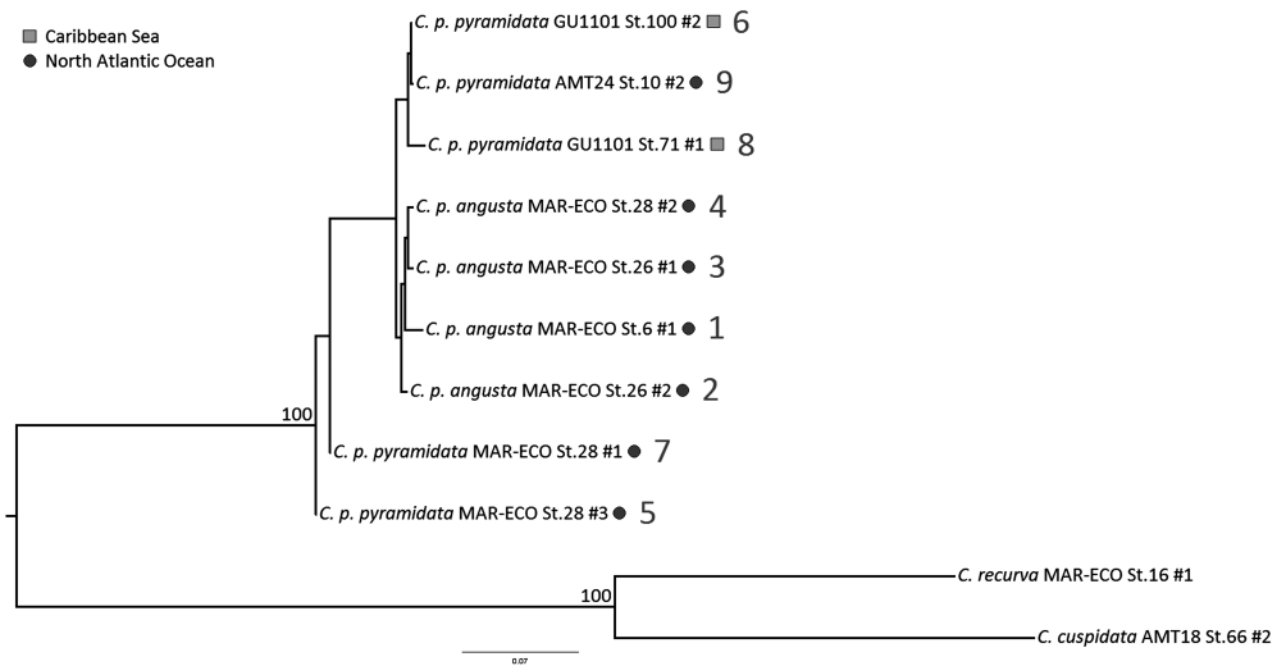

Fig. 23. Phylogeny based on mitochondrial Cytochrome Oxidase I sequences of *Clio pyramidata* (N=9) and outgroup taxa *C. cuspidata* (N=1) and *C. recurva* (N=1). Numbers 1-9 follow numbers in Figure 22.

Systematics

Order Pteropoda Cuvier, 1804
Suborder Euthecosomata Meisenheimer, 1905
Family Cliidae Jeffreys, 1869

Cleodoridae Gray, 1840: 148, 155 (designated *nomen oblitum* by Bouchet & Rocroi, 2005: 51).
Cliidae Jeffreys, 1869: 118; ICZN, 2006, Opinion 2133.
Clionae van der Spoel, 1967: 31, 57 (*partim*).
Clioidae Bouchet & Rocroi, 2005: 51.
Cavoliniidae Bouchet et al. 2017: 357 (*partim*).
Non Clioidae Menke, 1828: 5 (as Cliodinae), currently Clionidae (Gymnosomata).

Note – Cliidae was synonymised with Cavoliniidae by Bouchet et al. (2017: 357), based on molecular work of Burridge et al. (2017). The general morphology of species earlier included in Cliidae, however, is so analogous and different from other Cavolinioidea that we suppose that further detailed and integrative taxonomic research eventually will result in a more robust subdivision validating this family.

Clio Linné, 1767

Clio Browne, 1756: 386 (unavailable, pre-Linnean).
Clio Linné, 1767: 1094. Type species *Clio pyramidata* Linné, 1767 by subsequent designation of Gray (1847: 203).
Cleodora Péron & Lesueur, 1810: 66. Monotype 'le Cléodore pyramidale'(=*Clio pyramidata* Linné, 1767).
? *Balantium* Children, 1823: 220. Monotype *Balantium recurvum* Children, 1823.
? *Balantium (Flabellulum)* Bellardi, 1873: 32. Type species *Balantium braidense* Bellardi, 1873 (here designated).
? *Balantium (Poculina)* Bellardi, 1873: 33. Homonym of *Poculina* Gray, 1868: 742 (Gastropoda, Calyptraeidae).
Euclio Bonnevie, 1913: 20. Objective junior synonym of *Clio.*
? *Proclio* Hubendick, 1951: 3. Monotype *Proclio subteres* Hubendick (1951: 6 fig. on p. 7, pl. 1 figs 1, 2) = *Clio antarctica* (Dall, 1908).
? *Bellardiclio* Janssen, 2004: 114. Type species by original designation *Hyalæa cuspidata* Bosc, 1801.

Clio pyramidata Linné, 1767 *s. str.* (Figs 24, 25)

Below we list the various names and name combinations used for the typical form of this species during time. For more extensive synonymy see van der Spoel (1967) and Janssen (2012).

Clio vagina triquetrâ pyramidata, ore oblique truncato. The smaller *Clio*, with a trilateral sheath – Browne, 1756: 386, pl. 43 fig. 1. [non binom.]
Clio pyramidata Linné, 1767: 1094.
? *Clio caudata* Linné, 1767: 1094.
? *Clio retusa* Linné, 1767: 1094.
'Insecte' – La Martinière, 1787a: 207, pl. 11 figs 1-3.
Hyalæa pyramidata – Bosc, 1801: 241, pl. 9 figs 1-3; Lamarck,

1819: 290.

'Cléodore Pyramidale' – Péron & Lesueur, 1810: pl. 2 fig.. 14.

Hyalea lanceolata Lesueur, 1813: 284, pl. 5 fig. 3.

Cleodora pyramidalis [*sic*] – Bowdich, 1822: 23, 56, pl. 5 fig. 2.

? *Cleodora Brownii* de Blainville, 1824: 272; 1825: 481; 1827, pl. 46bis figs 1, 1a-b).

Hyalæa (Cleodora) pyramidata Linn. Var. A – d'Orbigny, 1834: 113; 1836, pl. 7 figs 25-32.

? *Cleodora Lamartinieri* d'Orbigny, 1841: 83 (footnote).

Cleodora Vaticana Calandrelli, 1844: 13 figs A, B.

? *Cleodora exacuta* Gould, 1852: 488; pl. 51 fig, 605, 605a-b (1856).

Clio occidentalis Dall, 1871: 140.

Cleodora pyramidata (L.) var. *lata* Boas, 1886: 72, 203, pl. 9 figs 96g.

? *Clio promaucana* Philippi, 1887: 112, pl. 13 fig. 18.

Clio (Clio) pyramidata Linné – Pelseneer, 1888: 63.

Clio (Euclio) pyramidata Linné var. *lata* – Bonnevie, 1913: 23 fig. 22B.

Clio pyramidata lanceolata (Lesueur) – Tesch, 1913: 36 fig. 32A-C.

Cleodora bowdenensis Collins, 1934: 201, pl. 12 figs 3-7.

Euclio pyramidata (Linné) form *lata* – Tesch, 1946: 14, pl. 2 figs 11a-f.

Euclio pyramidata lanceolata (Lesueur), 1813 – Tokioka, 1955: 62, pl. 8 figs 11-13.

Clio pyramidata Linnaeus, 1767 forma *lanceolata* (Lesueur, 1813) – van der Spoel, 1967: 68 figs 50-54, 60 (with extensive synonymy).

Clio (Clio) pyramidata Linnaeus, 1767 forma *lanceolata* (Lesueur, 1813) – Janssen, 2012: 44 figs 16A-D, 17A-F, 49J-L (with additional synonymy).

Neotype – RGM 777 444 figure 24a-d, here designated.

Neotype locality – Jamaica, East Channel, bottom sample no. Est 875F, leg. Ivan Goodbody, R/V Eastward, 17 February 1972; don. M.K. Webber, November 2016.

Description (after van der Spoel, 1967: 69-70, as *Clio pyramidata* forma *lanceolata*). — "Shell nearly straight, pyramidally shaped, thin and transparent. The lateral ribs are thickened, and very strongly diverging. The dorsal rib is straight and protrudes distinctly above the shell aperture. The lateral ribs are very long too, but never end in free processes. The cross-section through the shell is rounded near the posterior top, triangular in the middle and the anterior half of the shell. Anteriorly the ventral surface is hollow so the cross-section assumes a lunar shape.' This hollow shape of the ventral side is effected by the lateral ribs bent ventrally in the upper part. At both latero-dorsal sides of the shell three longitudinal ribs are present and one rib is found on the ventral side. The transverse striation and growth lines are distinct but usually not as pronounced as in the forma *pyramidata* [= *angusta* herein]. The greatest width of the shell is found near the middle of the shell. The lateral ribs are rounded near the posterior shell top. The oval embryonic shell is more elongated than in the forma *pyramidata* [= *angusta* herein]. The radula (formula 1-1-1) shows about 6 transversal rows. The shell length is about 20 mm; the maximal width about 15 mm."

Material examined. — Apart from the neotype specimen, 10 additional specimens from the neotype locality, RGM 777 445 (Fig. 25) (see caption of Fig. 24 for details).

Discussion. — The lot of 11 specimens of *Clio pyramidata* Linné, 1767 from the neotype locality Jamaica (Figures 24-25) demonstrates convincingly that specimens of *C. pyramidata* from that area have strongly concave shell sides. Therefore the form of this species with straight or almost straight sides, occurring in the northern Atlantic Ocean, indicated as *C. pyramidata* (f.) *pyramidata* by several authors (e.g., Tesch, 1913; van der Spoel, 1967; Janssen, 2012) cannot be considered to be typical *C. pyramidata*. The form with strongly concave carinae currently is usually indicated in literature with the name *C. pyramiata* (f.) *lanceolata* (Lesueur, 1813) which is herewith demonstrated to be a subjective junior synonym of *C. pyramidata* Linné, 1767. As this is one of the most common and widely distributed pteropod species, a correct naming of the species is of importance.

Clio pyramidata angusta (Boas, 1886) (Fig. 26)

Cleodora pyramidata (L.) var. *angusta* Boas, 1886: 72, 203, pl. 6 fig. 96a-f.

Clio (Euclio) pyramidata Linné (var.) *angusta* – Bonnevie, 1913: 23 fig. 22A.

Clio pyramidata pyramidata L. – Tesch, 1913: 35 fig. 31A (*non* Linné).

Clio pyramidata Linnaeus, 1767 forma *pyramidata* Linnaeus, 1767 – van der Spoel, 1967: 67 figs 48a-b, 49 (*non* Linnaeus).

Clio pyramidata angusta – Bé & Gilmer, 1977: 766.

Description (after van der Spoel, 1967: 68, as *Clio pyramidata* forma *pyramidata*). — "Shell, hyaline sometimes with a reddish shine and thin, straight pyramidally shaped. The two lateral ribs are thickened and only slightly diverging and bent. Transverse striation and growth lines are distinct. Cross-section triangular in all parts except the most posterior part. The dorsal rib protrudes slightly above the shell aperture. The laterodorsal sides are both provided with three swellings of the shell, and one longitudinal rib runs over the ventral shell surface. The greatest width of the shell, the aperture width, is found above the middle of the shell. The lateral ribs of the shell are rounded, especially near the embryonic shell. The embryonic shell is droplet-shaped and provided with a small cusp. The radula (formula 1-1-1) is composed of about 7 rows.

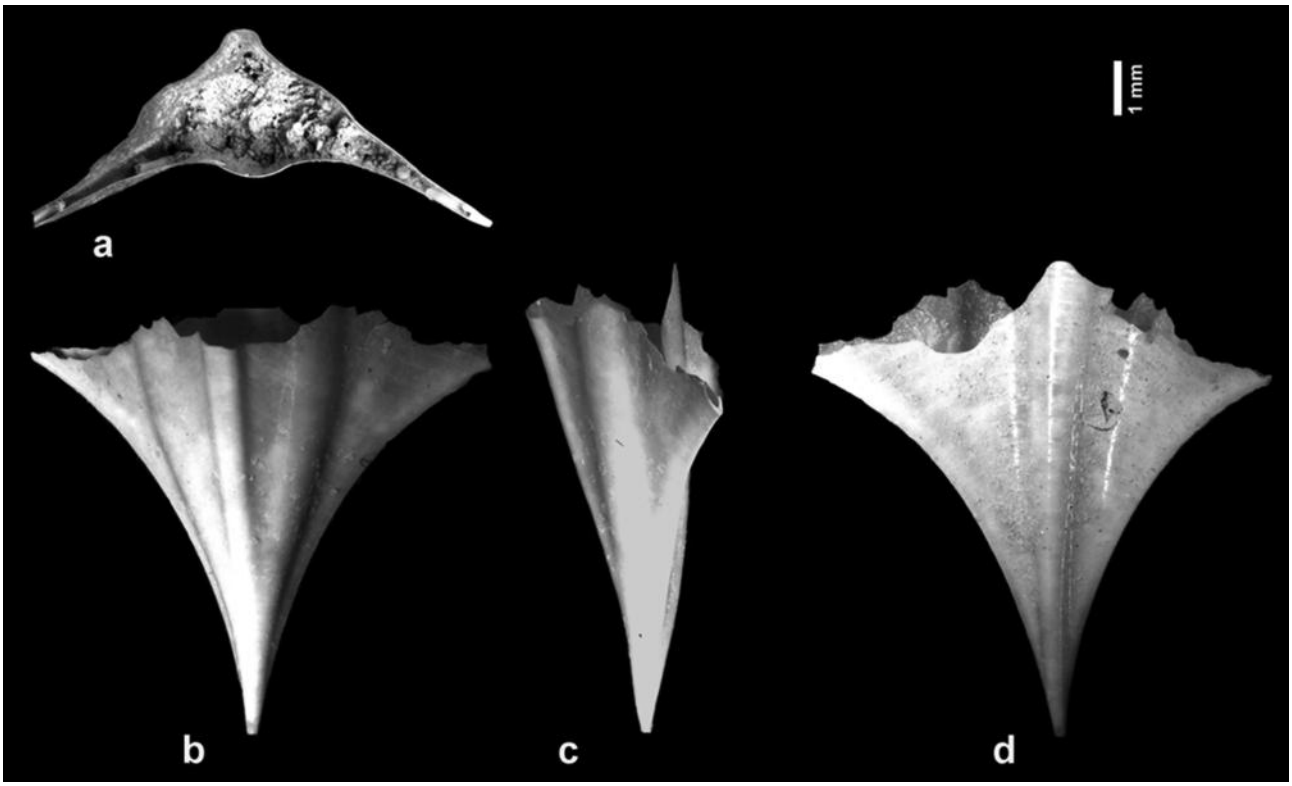

Fig. 24. *Clio pyramidata* Linné, 1767. Neotype, RGM 777 444. Jamaica, East Channel, bottom sample nr Est 875F, leg. Ivan Goodbody, R/V Eastward, 17 February 1972; don. M.K. Webber, November 2016; a: apertural, b: dorsal, c: right lateral, and d: ventral views.

The shell length is about 20 mm; its width about 10 mm."

Lectotype (here designated). — NHMD 199348, North Atlantic Ocean, 58°N 28°W (Figure 26a).

The following syntypical lots, now paralectotypes, are available:

NHMD 199251 - 58°27'N 26°43'W (2 specimens, one of which illustrated in Fig, 26b).

NHMD 199261 - 59°3'N 13°32'W; 14 specimens.

NHMD 199331 - 58°27'N 26°43'W; 18 specimens, one of which illustrated in Fig. 26c.

NHMD 199348 - 58°N 28°W (lectotype locality); 17 specimens, two of which illustrated in Figs 26a and 26d).

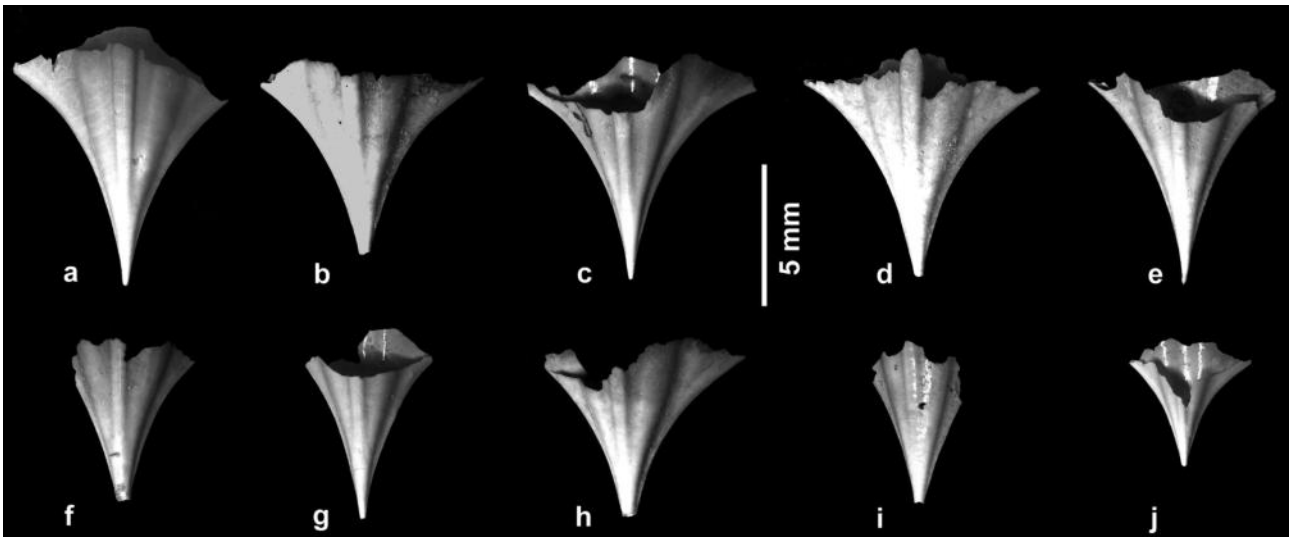

Fig. 25. *Clio pyramidata* Linné, 1767 s. str., additional specimens (all dorsal views) from the neotype locality (see caption of Fig. 24 for details), RGM 777 445. The protoconch is only preserved in specimen e.

NHMD 199365 - 58°26'N 19°WE; 23 specimens, includes many juveniles.
NHMD 1993375 - 59°17'N 8°W; 6 specimens .
NHMD 199380 - 59°N 18°W; 28 specimens.
NHMD 199399 - 60°18'N 16°48'W; 2 specimens.

Discussion. — *Clio pyramidata angusta*, as far as currently known, is restricted to the northern Atlantic Ocean, north of c. 45°N and may have developed from *C. pyramidata* s. str. under the influence of lower seawater temperatures. Locally these two shell forms may occur sympatrically and intermediate shell forms occur. Furthermore, so far no genetic differences are found between the two shell forms and thus they are unlikely to be reproductively isolated.

Several authors (e.g., d'Orbigny, Boas, Tesch) mentioned similar occurrences with more or less straight carinae also from the Pacific Ocean and illustrations of similar specimens can be found in various websites. However, it cannot be excluded that such specimens from the Pacific or Indian Ocean are in fact *Clio convexa* (Boas, 1886), a species at first glance very similar in shape, but easily distinguished by the double-lined carinae with a square transverse section and a different shape of its larval shell.

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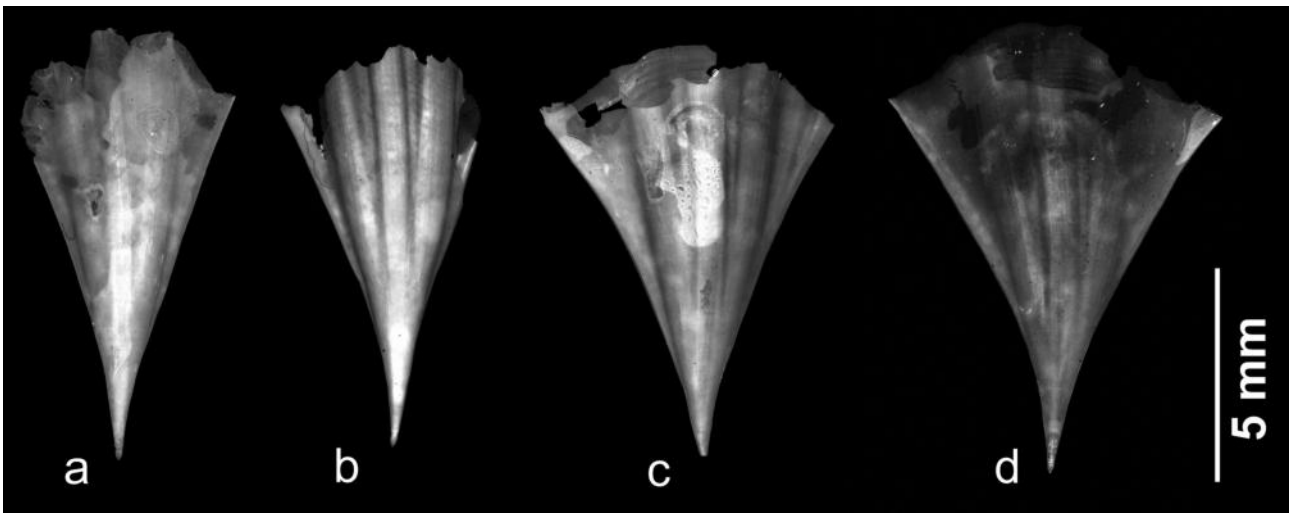

Fig. 26. *Clio pyramidata angusta* (Boas, 1886); a: lectotype; b-d: paralectotypes; c-d: transitional forms to *Clio pyramidata* s. str. Northern Atlantic Ocean, a and d from NHMD 199348, 58°N 28°W, b from NHMD 199251, 58°27'N 26°43'W, c from NHMD 199331, 58°27'N 26°43'W.

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