

Notes on the systematics, morphology and biostratigraphy of holoplanktic Mollusca, 27¹.

Comments on a paper discussing Pteropoda (Gastropoda, Heterobranchia) systematics, recently (2019) published in *Bollettino Malacologico*

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Comments and critical notes are necessary concerning a paper on pteropod systematics, published by J. Rampal in 2019 (*Bollettino Malacologico* 55-2: 145-186). In that paper the author makes a number of statements on systematics and taxonomy that cannot be ignored or left undiscussed. The following issues are treated in this paper: (1) Notwithstanding earlier discussions, the author maintains an earlier published interpretation of *Cuvierina* species which in the present paper (again) is demonstrated to be erroneous. The unnecessary introduction of *Cuvierina major* Rampal, 2019, as a replacement name for *C. atlantica* Bé, McClintock & Currie, 1972, is rejected, and the name *Cuvierina atlantica* once more is accepted as valid; (2) The repeated argument to demonstrate the validity of the name *Creseis acicula* Rang, 1828, over *C. clava* Rang, 1828, is incorrect and superfluous: *Creseis clava* cannot be considered *nomen oblitum*, and the validity of the name *C. acicula* for the type species of *Creseis* Rang, 1828, was decided by the First Reviser, d'Orbigny (1836); (3) The genus *Altaspiratella* Korobkov, 1966, transferred to the Pseudothecosomata by Corse et al. (2013), repeated by Rampal (2019) is considered to be a true Euthecosomatous genus of the Limacinoidea. Species of *Altaspiratella* show a gradual despiralisation leading to the first recognised Creseidae; (4) The Eocene family Praecuvierinidae Janssen, 2005, is rejected by Rampal, who considers the two genera of that family to rep-

resent real *Cuvierina*, ancestral to modern Cuvierinidae. The earliest real *Cuvierina* species, however, developed from an ancestral *Ireneia* root during the late Oligocene/early Miocene (Janssen, 2005). Praecuvierinidae should be retained as an unsuccessful offshoot of (presumably) Creseidae; (5) The relationship of the genus *Vaginella* with the Cuvierinidae, as suggested by Rampal (2019 and earlier), is denied and *Vaginella* is retained in the Cavoliniidae family; (6) The revival of the classic genus *Hyalaea* Lamarck, 1799, is rejected. De Blainville (1821) is not its author and '*Hyalaea*' *cuspidata* Bosc, 1802, is not its type species. The name *Hyalaea* Lamarck, 1799, is a junior synonym of *Cavolinia* Abildgaard, 1791, with monotype *Cavolinia natans* Abildgaard, 1791 = *Anomia tridentata* Forsskål in Niebuhr, 1775; (7) Phylogenetic relationships given by Rampal (2019) are based on cladistical and molecular analyses that frequently are unclear or even contradictory. The molecular work was based on just two genes (COI and 28S). Divergence times of the various groups obtained from 'molecular clock' interpretations usually differ strongly from the fossil record evidence, mostly giving much older datings; (8) The introduction in Rampal (2019) of the taxa Heliconoididae and Thieleidae is accepted, be it with some doubt. The erection of Diacriinae and *Telodiacria* is considered useful. A new family **Hyalocylidae fam. nov.** is introduced herein.

Key words: *Altaspiratella*, *Heliconoides*, *Creseis*, Hyalocylidae, *Cuvierina*, *Praecuvierina*, *Vaginella*, *Hyalaea*, Diacriinae, Cavoliniinae, molecular analyses, molecular clock.

1 For nr 26 in this series see *Basteria* 83 (4-6): 102-108 (2019).

INTRODUCTION

Dr Jeannine Rampal, a biologist connected to the Aix-Marseille University (France), published numerous papers on systematics, morphology, biogeography and evolution of present-day planktic gastropods. She graduated with a voluminous thesis (485 pp) on Mediterranean present-day pteropods [Rampal, 1975]. More recently Dr Rampal cooperated with colleagues of the same university (Dr Emmanuel Corse and his team) on molecular research.

The author of this paper is a retired curator of Cenozoic Mollusca of the former 'Rijksmuseum van Geologie en Mineralogie' (currently incorporated in Naturalis Biodiversity Center, Leiden. The Netherlands), but he is still active as an associate of that institute, specialising since the early 1980s on predominantly fossil pelagic molluscs and producing multiple papers on systematics, morphology and biostratigraphy of that group of organisms.

Disagreements between Dr Rampal and this author have existed for a long time and have led to frequent email correspondence, but hardly ever to consensus. A recent paper (Rampal, 2019) in the *Bollettino Malacologico* requires a public rebuttal, as it gives rise to e.g. nomenclatural and systematic confusions in this important group of Mollusca. It is necessary to deal with it, since Pteropoda are currently used in world-wide studies as indicators of e.g. the status of marine ecosystem integrity.

SOME HISTORY

The paper recently published in *Bollettino* has a long preceding history. An early version (Rampal [2014]) was submitted to *ZooSystema*. The editor invited this author to review the manuscript, but as he never does a review anonymously, and supposed that Dr Rampal would not be very happy with him as reviewer, he replied to the editor only to be prepared to do so if Dr Rampal would accept him as reviewer. As expected, this was not the case, and therefore, the manuscript was reviewed by someone else. This apparently resulted in a rejection or withdrawal of the manuscript: it never appeared in *ZooSystema*.

A drastically changed version of that manuscript (Rampal, 2017) appeared in *BioRxiv*, which is an online internet archive accepting preprints of manuscripts without peer reviewing. Papers in *BioRxiv* are invalid for nomenclatural purposes and taxa described as new therein are unavailable. The 2017 version, therefore, was not indexed for MolluscaBase/WoRMS. A version with practically the same title has now formally been published in *Bollettino Malacologico*, but the various new taxa cited with the year 2017 are only validated in this paper and, therefore, should be dated 2019.

In the Rampal (2019) Acknowledgements no reviewers are

mentioned but two highly respected malacologists of the Muséum national d'Histoire naturelle, Paris, among others, are thanked for 'advice' or 'critically reading' of the manuscript. This was very surprising as it could not be believed that these malacologists would have accepted, or even agreed with some of Rampal's opinions and decisions. Both of them, however, did not read or approve the manuscript that was published in the *Bollettino Malacologico* (Ph. Bouchet, pers. comm., 3 February 2020). Such a strong but untrue claim of Rampal does not contribute to the author's credentials. Surprisingly, the manuscript passed the editorial procedures of *Bollettino*, and was accepted for publication.

RESULTS

Cladistics and molecular work

In her study the author at many places applies cladistic as well as molecular analyses to discuss interrelationships and phylogeny of species and higher taxa. Cladistics include 54 variables, 19 of which are based on shell characteristics and the other on soft part anatomy. The molecular work is almost exclusively based on Corse et al. (2013) and includes sequencing based on two of the three in this respect popular genes, *COI* and *28S*, the third gene that is frequently applied for molecular work, *18S*, is not discussed. Conclusions on relationships and phylogeny as presented in the 2019 Rampal paper are often unclear or even contradictory as e.g. (: 158) "Cladistic: *Styliola* is the sister group to *Hyalocylis* and to the Cavoliniidae, – 28S mol. data (0.83/): it is the sister group to *Hyalaea cuspidata* and to the Cavoliniidae, – 28S gene data set: it is the sister group to *Hyalaea cuspidata* and to *Cuvierina* and *Clio*". This probably is a result of the restricted number of analysed genes. A phylogenomic approach based on transcriptome sequencing of multiple genes to fully resolve the phylogeny of pteropods will yield far better and more reliable data (Peijnenburg et al., [2019] and in review). The 'molecular clock' is frequently used to estimate divergence times in geological history. Results of this method often differ strongly from what is known from the fossil record factual information and usually give much older dates than the fossil evidence does. Therefore, estimated divergence times based on the molecular clock should be treated with caution.

Columellar and umbilical morphology of gastropod shells

Rampal (2019, e.g.: 147) seems to misunderstand the morphology of a spiral gastropod shell, as is clear from the expression "spiral calcareous shells with an umbilicus (but no columella)". Generally speaking, a gastropod shell will consist of a number of whorls increasing in diameter from the apex downwards in a spiral around a central axis. If

the spiral is tight the most central portions of the whorls together will build a massive axis (or columella) and there will be no umbilicus at the base of the shell. If the spiral is less tight, the inner parts of the whorls will not touch, resulting in an open axis (or columella) and there will be a basal umbilicus (that can secondarily be covered again, as e.g. in *Neverita*). In shells in which the inner walls of the whorls have an even greater distance from the central axis these parts will form a wide open columella that allows a view into the interior from the base of the shell upwards, as is the case in the various despiralising *Altaspiratella* limacinid species and will appear as a twisted 3-dimensional spiral unit and not form an umbilicus as usual.

Systematic position of the genus *Altaspiratella*

Korobkov, 1966

The discussion on the systematic position of the genus *Altaspiratella* (Euthecosomata or Pseudothecosomata) was started in Corse et al. (2013, table 3) and is repeated in Rampal's (2019: 149) paper, with argumentation to reject *Altaspiratella* as belonging to the Limacinoidea and to demonstrate it as a Pseudothecosomata species related to the Peraclidae. Earlier authors, however, all considered *Altaspiratella* (or its synonym *Plotophysops* Curry, 1982) as a limacinid: Korobkov (1966); Curry (1982); Hodgkinson et al. (1992); Cahuzac & Janssen (2011), Janssen (1990, 2003); Janssen & Peijnenburg (2013, 2017), Garvie et al. (2020).

The type species of *Altaspiratella*, *Physa elongatoidea* Aldrich, 1887, for a long time was only known by its holotype, an incomplete specimen without apertural features preserved. Recently, however, well-developed specimens of that species were recovered, showing similar features as present in other *Altaspiratella* species: a three-dimensionally twisted columellar spiral; a thickened, reinforced apertural margin; and a notch at the base of the apertural margin (Garvie et al., 2020).

Based on Corse et al.'s (2013) opinion, Rampal (2019: 149) provided the following reasoning to demonstrate the *non*-limacinid character of the genus *Altaspiratella*: "One particular striking feature which distinguishes *Altaspiratella* from the Limacinidae is the absence of the umbilicus and the presence of a twisted columella ending in an abapical rostrum with a narrow columella membrane (Hodgkinson et al., 1992)" and "The columella itself is thickened and shows a distinct torsion in such a way that looking into the shell's interior is possible by a straight adapical view; the apertural margin is widened and internally reinforced with a rather solid ridge connected with the thickened columella" (Cahuzac & Janssen, 2010: 24)'.

Commenting on this statement we (Garvie et al., 2020) fail to find the expression "a twisted columella ending with an abapical rostrum" in Hodgkinson et al. (1992). Rampal (2019) has invented the phrase, not Hodgkinson et al.,

who only wrote (1992: 14) about *Altaspiratella bearnensis* (Curry, 1982): "... a twisted columella, an anterior sulcus, and a broad outer lip", agreeing with the original description of Curry (1982) and with actual specimens. The word 'rostrum' was nowhere used in the text of Hodgkinson et al. (1992). Indeed, in *Altaspiratella* an 'anterior rostrum' is not present, just a more or less strongly accentuated notch on the lower part of the thickened apertural margin, accentuating the sinus between that point of the margin and the base of the last whorl, not at all connected with the twisted columella proper. This feature is most clearly developed in *Altaspiratella multispira* (Curry, 1982) and is also present on the basal apertural margin of *Camptoceratops priscus* (Godwin-Austen, 1882) and *C. americanus* Garvie, 1992, the first Creseidae species developing from the despiralising limacinids. A similar notch on the apertural lip is now also known from another limacinid, *Heliconoides nikkiae* Janssen, 2017, from the Eo-Oligocene of Tanzania (Cotton et al., 2017). Though in some species of Peraclidae a twisted columella is present, this never is in a wide, three-dimensional torsion as in *Altaspiratella*. The Peraclidae columella is tight and forms no umbilicus, not even in species that are wider than high, and there is no possibility to observe the shell's interior, as in *Altaspiratella* species, in which the columellar torsion shows successive stages of despiralization. Furthermore, apertural reinforcements like thickening of the margin or a basal notch are absent in Peraclidae, in which, on the contrary, some of the species develop apertural spines, as well as a basal columellar rostrum, all of which are absent features in the various *Altaspiratella* species.

There also is the enormous difference in age: *Altaspiratella* ranged during Ypresian and Lutetian, whereas the oldest recognised Peraclidae species is known from the late Oligocene (Janssen, 2012b: 447), an age difference of about 20 million years. Where were they during that, for pteropods well-investigated interval?

Finally, the successive stages of despiralization in *Altaspiratella*, causing the presence of an open columellar spiral and leading to the first Creseidae *Camptoceratops* and *Euchilotheca*, can barely be denied and was basically already for a long time accepted by various authors among them also Rampal [1975] and Curry & Rampal (1979).

Accepting a transfer of *Altaspiratella* to the Pseudothecosomata would inevitably lead to the very unlikely conclusion that Creseidae have developed from pseudothecosomatous ancestors.

Distribution of *Heliconoides mercinensis* and *Limacina heatherae*

Rampal (2019: 147) states: "Among the earliest known spiral shelled Euthecosomata the fossil *Limacina mercinensis* Watelet & Lefèvre, 1885, emerged during the early Eocene

(Ypresian) (56.5 MY).” This species, however, was already present during the Thanetian: “The species is known from the latest Paleocene in Alabama, Tuscahoma Sand Formation, Bear Creek Marls (Naturalis collection)” (Garvie et al., 2020) and might even be considerably older. The one and only Cretaceous pteropod known (*Heliconoides* sp., see Janssen & Goedert, 2016) of Campanian age (~ 80 Ma) resembles *H. mercinensis* closely and is considered congeneric.

Also, on p. 147 it says: “The fossil *Limacina heatherae* Hodgkinson, 1992, is listed under Late Paleocene (Thanetian) (58.6 MY)?” Garvie et al. (2020), however, question this age, as the type material was collected from possibly downhole contaminated samples of the Baton Rouge borehole (Louisiana, U.S.A.). The type specimen of *L. heatherae* closely resembles a European Oligocene (Rupelian) species, *L. umbilicata* (Bornemann, 1855). As Rupelian sediments are, indeed, penetrated in the same borehole the age of *L. heatherae* might be early Oligocene instead.

Number of species in recent and fossil *Heliconoides*

The type species of the genus *Heliconoides* d’Orbigny, 1836, is a very common present-day pteropod species with a large geographical distribution. It is the only recent limacinid in which some shell reinforcement occurs, restricted to the last adult whorl and the aperture. These structures were already mentioned by d’Orbigny and later authors (e.g. van der Spoel, 1967: 51, figs 17-18), but were in more detail described by Janssen (2004), who distinguished two different morphologies in ‘*Heliconoides inflata*’ (the correct name should have been *H. inflatus*; ICZN Art. 30.1.4.4). These morphologies were indicated as forms A and B, with reference to different geographical distribution patterns of these morphs. Present-day specimens from the Mediterranean all belong to form A, whereas Caribbean material represents form B. Intermediate, or maybe just difficultly recognisable specimens, occur in the central Atlantic Ocean. Later (Janssen, 2012b) it was found that these two forms can already be clearly distinguished in lower Miocene rocks of Malta, in which they occur sympatrically. Such observations basically offer possibilities for a taxonomic separation, but so far this has not been sufficiently investigated. There are also indications that at least one further form might be distinguishable on shell characteristics in southern Atlantic, present-day material (Burridge et al., 2017).

On the basis of the various analyses, cladistics and molecular, Rampal (2019: 151) concludes: “The presence of two distinct lineages (1.00/100) in the Mediterranean and in the Caribbean Sea suggests the existence of different molecular geographically isolated species. Our present molecular analyses make out four several geographical species in the *inflata* group: Atlanto-Mediterranean, Indo-Pacific, South Eastern Atlantic and North Indian species entity; this last

is only a little different to the Atlantic entity (one base) but COI confirms his difference (unpublished data). They give evidence to a clade with several species.”

These conclusions confirm and extend Janssen’s (2004) observations and may justify the introduction of a family Heliconoididae Rampal, 2019. Since the year 2003 Janssen considered all other limacinids with any form of apertural reinforcement as belonging to the genus *Heliconoides*. This is, not for the first time, criticised in Rampal (2019), but the large variety of apertural structures in fossil limacinids does not (as yet) allow a more robust or useful subdivision, and it may be expected that ultimately a number of further genera will have to be introduced or validated next to *Heliconoides*, of which *Skaptotion* Curry, 1965, most likely will be allied. For the time being, and awaiting further subdivision, the fossil *Heliconoides* species may conveniently be considered Heliconoididae.

Type species of *Creseis* Rang, 1828, and the *Creseis clava*-*C. acicula* discussion

In Janssen’s (2007a) paper on Philippinian Pliocene fossils, it was stated that *Creseis clava* Rang, 1828, is the correct name for the *Creseis* type species, rather than the commonly applied name *Creseis acicula* Rang, 1828. I based my decision on the page priority of *C. clava* (which admittedly is not a valid reason) and on the fact that Rang’s wording in the descriptions was unclear, writing about *C. acicula*: “... c’est plutôt un variété” (“it is more likely to be a variety” [of *C. clava*]). Dr Rampal, during long e-mail discussions, insisted on *C. acicula* as the correct name. These two points of view ultimately led to consulting the opinions of three (ex-) commissioners of ICZN, who all three thought that *C. clava* could not be considered the valid name. Rampal also submitted a request to the Commission (ICZN 2018), asking for a formal decision (Case 3758). The Commission, however, returned the case as a decision of ICZN was not necessary, stating that the question could be solved by means of the First Reviser rulings in the Code. That ruling, indeed, was applied in Janssen’s (2018a) paper in which the validity of *C. acicula* over *C. clava* was accepted. His conclusion (2018a: 111) was: “It has to be accepted that formally the correct name for the *Creseis* type species is *Creseis acicula* and not *C. clava*, although I still feel that this is against the original meaning of Sander Rang. However, ICZN ruling is decisive here”.

Rampal (2019: 157), however, twisted the full extent of the argumentation by quoting only “ICZN ruling is decisive here”. Surprisingly, Rampal maintained her earlier reasoning to declare *C. clava* as invalid, referring to ICZN Case 3758 on which the Commission never took a decision. She declared *C. clava* a *nomen oblitum*, referring to ICZN Art. 23.9.1.2. But the argumentation is incorrect: to designate a taxon as *nomen oblitum* also Art. 23.9.1.1 has to be met, but

Creseis clava was used after 1899 as a valid taxon of the species group by Tesch (1913, 1948), Tokioka (1955), Chen & Bé (1964), van der Spoel (1967, 1976), and Janssen (2007), so it is according to the ICZN not a *nomen oblitum*. The validity of *C. acicula* over *C. clava*, therefore, was decided by the First Reviser, which was d’Orbigny (1836: 123).

Furthermore, Rampal (2019: 157) inexplicably cites the two names as: “Rang, 1828 described *Cleodora* (*Creseis*) *clava* var. *acicula*”. If this would have been true indeed, the whole long discussion about *acicula/clava* would have been superfluous and would make *C. clava*, by the difference in rank, automatically the valid name. But no, Rang (1828: 317, 318; the *C.* stands for *Creseis*, not *Cleodora* – see page 309) introduced both taxa at full specific rank: *Creseis clava* and *Creseis acicula*.

In Janssen (2012a), in a paper on East Mediterranean holoplanktic molluscs, he discussed the uncertainty about the type species of the genus *Creseis* Rang, 1828 and who had designated it. Zilch (1959: 49) considered *C. virgula* Rang to be the type species, which was accepted by van der Spoel (1967). Rampal (2002: 231), however, referred to *C. acicula* as the type and, indeed, it was found that Pelse-neer (1888: 45) had been the first to designate *C. acicula* as the type species of *Creseis*. Oddly enough, however, Rampal (2019: 155) without any comment again mentions *C. virgula* as the type.

Status of *Boasia* Dall, 1889

The monotypic taxon *Boasia*, introduced as a subgenus of *Creseis*, was based on the small present-day species *Cleodora chierchiai* Boas, 1886, originally described from the Pacific Ocean, off Panama. Its single species shows a few characteristics distinguishing it from other Creseidae, such as a regular annulation of the teleoconch, and a different shape of the protoconch. Even for specimens with lacking or reduced annulations the species can easily be recognised if a protoconch is present. Such smooth, or almost smooth morphs were described as ‘*Creseis virgula constricta*’ Chen & Bé, 1964, from the northern Atlantic Ocean and are known for example also from the Indian Ocean and Red Sea. Almogi-Labin, 1982 (a paper that Rampal (2019) twice erroneously refers to as ‘Almoggi-Labin, 1882’, also in the references) stated that most Red Sea specimens belong to the more or less smooth form, agreeing with my own observations (Janssen, 2007a: 152).

Interestingly, this species is present in lower-middle Miocene sediments of southern Australia (Janssen, 1990: 28) and it is also not rare in Pliocene deposits of Pangasinan (Philippines) (Janssen, 2007b: 66), both, however, represented exclusively the *constricta* form. This might indicate that the fully annulated form is a quite recent development in *C. chierchiai*. I do agree with a full generic status of *Boasia*, indeed.

The genus *Styliola* Gray, 1847

Rampal (2019: 157) stated: “This genus may have been present since the Late Oligocene”. The ‘may be’ is not necessary here, as *Styliola* has repeatedly been recorded from Cretaceous rocks, of the Mediterranean (Malta), France and the North Sea Basin.

More problematic is the phylogenetical relationship of *Styliola* with the other Cavolinioidea as expressed in several papers published during the last decade, including Corse et al. (2013), and repeated by Rampal (2019), demonstrating that *Styliola* is not monophyletic with the other Creseidae, but without giving a firm solution. Similar remarks can be made concerning the genus *Hyalocyclus*. Rampal concludes for both that they should no longer be included in the Creseidae family, where they have been placed traditionally and suggests to consider both as incertae sedis.

However, the general shell characteristics of especially ‘*Styliole*’ *recta* (de Blainville, 1827) = *Cleodora subula* Quoy & Gaimard, 1827, the type species of *Styliola*, are so close to *Creseis* that it cannot be separated from Creseidae, at least as long as no better solution is offered by the biologists.

The genus *Hyalocyclus*, the *Hyalocyclus* protoconch, and the genus *Praehyalocyclus*

The genus *Hyalocyclus* Fol, 1875 includes a single accepted present-day species, its type species is *Creseis striata* Rang, 1828. *Hyalocyclus striata* deviates more strongly from the Creseidae architecture than *Styliola* by its extremely fragile, slightly curved and annulated shell with an elliptical transverse section. Several related fossil taxa, such as *Tentaculites cretaceus* Blanckenhorn, 1889, *Praehyalocyclus haitensis* Collins, 1934 and *Hyalocyclus euphratensis* Avnimelech, 1945, were already synonymised (Janssen, 1999) with *H. striata*, but a Pliocene species from the Philippines, *Hyalocyclus marginata* Janssen (2007b: 71, pl. 3 figs 5-6; pl. 23 figs 9-11) differs basically by the possession of a clearly reinforced apertural margin.

The larval shell of *H. striata* remained unknown for a long time and several authors mentioned shedding of the protoconch and formation of a septum to close the apical opening. However, in the hundreds of specimens from sediment samples studied by the present author an apical septum could not be observed. Bandel & Hemleben (1995: 231, fig. 4E) explained this curious fact by describing an organic, uncalcified nature of the embryonic shell that will disappear rapidly after death of the animal. Still, calcification of this protoconch is also known, as Almogi-Labin (1982: 58) mentioned many juvenile specimens from the Red Sea, and from the Mediterranean Janssen (2012a) described specimens preserved as internal moulds. It was concluded that most probably calcification of the early shell parts depends on local circumstances.

The *Hyalocyclus* larval shell differs substantially from Cre-

seidae. There is an elliptical protoconch, about twice as high as wide, with a perfectly rounded tip. The transition to the teleoconch is a slight constriction, after which the annulation of the teleoconch starts right away (Janssen, 2012a, figs 43H-L).

The illustration of a *Hyalocyclus striata* protoconch given by Rampal (2019, fig. 12-O) has nothing to do with that species. Its pointed apex and stronger constriction rather make it *Styliola*.

The group of taxa included in the genus *Praehyalocyclus* Korobkov in Korobkov & Makarova, 1962 (not *Prehyalocyclus*, Rampal, 2019: 170) is known since the late Eocene Priabonian (not ‘Lower’ Oligocene, Rampal, 2019: 170). It differs from *Hyalocyclus* by its circular transverse section and less curved shell. A larval shell illustrated in Korobkov & Makarova (1962, fig. 9) resembles the protoconch of present-day *Hyalocyclus* closely. Therefore, it seems acceptable to consider *Praehyalocyclus* ancestral to *Hyalocyclus*. Considering the various fossil occurrences the transition between these two genera must have taken place during the early to middle Miocene. As genetical differences between *Hyalocyclus* and the Creseidae are also considerable, as demonstrated by Jennings et al. (2010: 7, fig. 3), Corse et al. (2013: 9, figs 3-4), BurrIDGE et al., (2017: 13, figs 2-3); Peijnenburg et al. ([2019] and in review) a family **Hyalocylidae fam. nov.** is here introduced to contain these two groups of species.

Cuvierinidae

Disagreements on Rampal’s and Janssen’s interpretations of the present-day *Cuvierina* species, *C. columnella* Rang, 1827, and *C. atlantica* Bé et al., 1972 also have initiated long discussions by e-mail that, as usual, did not lead to any form of agreement. The latter taxon was originally described by van der Spoel (1970) as *Cuvierina columnella* forma *atlantica*. Being introduced after 1964 at infrasubspecific rank that name was not available from its original publication. Rampal (2002), therefore, introduced the taxon *Cuvierina spoeli* instead, but that name was introduced at full species level, with a holo- and paratypes from the Indian Ocean, not from the Atlantic, where van der Spoel’s material came from. *Cuvierina spoeli*, therefore, cannot be considered a replacement name or *nomen novum*, but contrarily is an independent, available taxon of the species group. However, in Janssen’s (2005) paper on Cuvierinidae it was demonstrated that the type lot of *Cuvierina spoeli* did not represent the same species as the forma *atlantica* van der Spoel, 1970, but contrarily belongs to the Indian Ocean/Pacific species *C. columnella*. In that same paper one of the paratype specimens of *C. spoeli* was designated neotype of *C. columnella* and furthermore it was demonstrated that forma *atlantica* van der Spoel had been validated as a taxon of the species group as *C. columnella atlantica* by Bé et al., 1972. It was furthermore ascertained that *C. atlantica* was exclusively

distributed in the Atlantic Ocean and Caribbean, whereas *C. columnella* is restricted to the Indo-Pacific.

Cuvierina columnella differs from *C. atlantica* by a slightly larger shell height and the possession of micro-ornamentation that is absent in *C. atlantica*. Rampal (2019) still denies the larger size of *C. columnella* and insists that *C. atlantica* also occurs in the Indo-Pacific. However, the interpretation of sizes was erroneous: when measuring the shell height of the *Cuvierina columnella* specimen illustrated by Rang (1827: 323, pl. 45 figs 1-8) as 4.9 mm, Rampal did not realise that the bar accompanying Rang’s drawing represents actual shell height and not a 1 mm scale. The specimen illustrated by Rang contrarily was 11 mm high, not 4.9 mm. Ever since 2005 this discussion has continued and therefore Janssen explained the whole situation in his 2018b paper, to which the reader is referred for further details.

Rampal (2019), however, still maintains her points of view and now also, although initially accepted, denies the validity of Bé et al.’s name *Cuvierina atlantica*, saying: (2019: 161): “Bé et al., 1972 included the correct *Cuvierina columnella atlantica* in a calcareous shell study. They described *C. c. atlantica* but they illustrated *C. c. columnella*: there is a misidentification”. This statement, however, makes no sense in that specimens used by Bé et al. all were from the Atlantic, where *C. columnella* does not occur. It just demonstrates that Rampal still has a wrong idea of the two *Cuvierina* species. These two species, however, are perfectly defined by the *C. columnella* neotype and the *C. atlantica* lectotype. The decision to reject the name *C. atlantica* led Rampal (2019: 161) to the unnecessary introduction of the name *C. major* Rampal, 2019 as a replacement name for *C. atlantica*. The choice of the name *major* for the smaller of the two species under discussion once more demonstrates incorrect interpretation. The long discussion of ICZN ruling on p. 161 makes no sense. Rampal (2019: 161) increases the effort by stating: “Janssen (2005: 41, 45, 46, figs 8-11; 2019: 371) described *atlantica* but illustrated *columnella*”.

To avoid unjustified accusations of misidentifications in the Rampal (2019) paper it would have been useful if that author had taken a look at the relevant type specimens. By doing so, it would have been clear that the neotype of *Cuvierina columnella* also is a paratype of *C. spoeli*, and that the lectotype of *C. atlantica* is also the holotype of the unavailable *C. columnella* forma *atlantica*.

It was also pointed out (Janssen, 2018b: 372) that *Cuvierina* identifications in Corse et al. (2013, done by Rampal) were erroneous, as checked on their barcodes in GenBank by Alice BurrIDGE. Finally, Rampal, (2019: 160) lists several localities in the Indo-Pacific, with coordinates, for three *Cuvierina* species, which includes ‘*C. major*’ (= *C. atlantica*). All of these are places, where *Cuvierina atlantica* does not occur.

***Praecuvierina* and Eocene ‘Cuvierinidae’**

Hodgkinson et al. (1992: 31) considered several Paleogene genera from northern America to belong to the Cuvierininae: *Bucanoides* Hodgkinson, 1992, *Loxobidens* Hodgkinson, 1992, and *Tibiella* Meyer, 1884. Two of their new species were assigned to the genus *Cuvierina*, namely *Cuvierina gutta* Hodgkinson, 1992, and *C. lura* Hodgkinson, 1992. However, Janssen (2005) believes the first real *Cuvierina* species develops from an *Ireneia* ancestor not earlier than during the early Miocene. This first typical *Cuvierina* species, *C. torpedo* (Marshall, 1918), was described from the early Miocene (‘Late Otaian’ = Aquitanian) of New Zealand. In this species the shedding of the larval shell occurs close to the protoconch, the septum, therefore, is small and the shell retains an elongate spindle-shape with a slender basal part, strongly resembling species of *Ireneia*, inclusive of the presence of the longitudinal micro-ornament (Janssen, 2005: 29). For this reason and also for other reasons, like the strikingly small sizes and absence of micro-ornamentation, it was not possible to retain the two northern American Eocene species in *Cuvierina* and for them, in the same paper, two new genera were introduced: *Praecuvierina* and *Texacuvierina*, respectively, and a new family, Praecuvierinidae, was erected. It was suggested also that the Praecuvierinidae were not ancestral to the later Cuvierinidae, but represented an earlier, unsuccessful offshoot from (presumably) Creseidae.

The other genera considered by Hodgkinson et al. to belong to the Cuvierininae are now transferred to the Creseidae. The occurrence of a basally truncated shell (as a result of larval shell shedding) and the presence of a subsequent basal septum, that, however also is known from Creseidae, such as *Euchilotheca elegans* Harris, 1894 (Janssen et al., 2011), was why Hodgkinson et al. (1992) assigned these taxa to the Cuvierininae. However, the transverse striation as seen in species of *Bucanoides* or in *Tibiella* species, or the apertural structures as in *Loxobidens* and *Tibiella* species, are unknown in the Cuvierinidae but do occur in several Creseidae, thus supporting the transfer of *Bucanoides*, *Loxobidens* and *Tibiella* to the Creseidae (Garvie et al., 2020).

Rampal (2019: 161) concluded: “The bottle shaped fossil *C. lura* that appeared early in the Middle Eocene may constitute the original phenotype characteristic of the Indo-Pacific Ocean”. Rampal also stated (2019: 163) concerning the two species of ‘Praecuvierinidae’ (*sic*), that their assignment in a separate family “is not very convincing for several reasons, e.g.: these fossils appeared at the same time as the other Cuvierininae fossils”. However, these Eocene ‘Cuvierininae fossils’, are all considered to belong to the Creseidae now. The origin of the genus *Cuvierina*, as a linear descendant of *Ireneia* during the Late Oligocene/Early Miocene is not contradicted by evidence provided by Rampal (2019, or earlier).

The genus *Hyalaea*

One of the most curious and incomprehensible acts in the Rampal (2019: 154, 163) paper is the ‘revival’ of the long-forgotten genus *Hyalaea* for which de Blainville, 1821, is considered the author and ‘*Hyalaea cuspidata* Bosc, 1802’ the type species.

It is unclear to which ‘de Blainville 1821, p. 9’ paper Rampal is referring. In the two papers mentioned in the list of references, one is a well-known paper in Dictionnaire des Sciences Naturelles, vol. 22, p. 65 with the title ‘HYALE, *Hyalaea*. (Malacoz.)’ with in the first line of text: “M. de Lamarck est le premier qui ait établi, sous cette dénomination, un genre bien distinct”, which is a clear reference to Lamarck (1799: 89), where the genus is introduced with the monotype ‘*Anomia tridentata* Forsk.’. The genus *Hyalaea* therefore is a junior synonym of *Cavolinia* Abildgaard, 1791 (Abildgaard, 1791: 172), with monotype *C. natans* Abildgaard, 1791 = *Anomia tridentata* Forskåll in Niebuhr, 1775. This makes clear that neither de Blainville, nor ‘*Hyalaea cuspidata*’ have anything to do with this genus. In the same paper de Blainville (1821: 93) stated about ‘*Hyalaea cuspidata*’: “... que l’on peut presque assurer positivement que ce n’est pas à cette famille qu’elle appartient”.

A ‘re-establishing’ of a genus *Hyalaea* to include *Clio cuspidata* makes no sense at all and Rampal’s act only leads to unnecessary confusion. The genus group name *Bellardiclio* Janssen, 2004, was introduced to contain *Clio cuspidata* (type species!) and some related species.

Systematic position of the genus *Vaginella* Daudin, 1800

As the genus *Vaginella* is exclusively known from the fossil record there are no possibilities for molecular work and phylogenetical interpretations therefore can only be based on shell characteristics. Just as in earlier papers Rampal (2019: 162) insists on ‘close phenotypical affinities between *Vaginella* and *Cuvierina*’: ‘In *Vaginella* several phenotypical features are strongly reminiscent of *Cuvierina*: a bottle-shaped teloconch with a central bulge, a dorso-ventrally depressed peristome (with an ellipsoid to semi-circular shape) with a slightly concave ventral edge, a blunt apex ending in a septum, and a circular to sub-oval transverse section depending on the species.

Although some of the argumentations seem to justify Rampal’s point of view, a number of similar facts can be used to demonstrate a closer relationship between *Vaginella* and the Cavoliniidae: dorso-ventral compression, presence of lateral carinae, dorsal apertural margin higher than the ventral one, shedding of larval shell is only present in two of the many *Vaginella* species, the lack of lateral slits occurs also in several Cavoliniidae (e.g. in *Gamopleura*), etc. But the most important and quite convincing characteristic demonstrating affinity with Cavoliniidae; the ‘ontogenetic criterion’ as Rampal indicated it after Cahuzac & Janssen

(2010), but further left it out of consideration. This character was extensively described (although at the time not fully understood) in Janssen (1985), demonstrating a drastic shell metamorphosis during the transition from larval to adult specimen, very similar as what is known from *Cavolinia* and *Diacria*, but absent in Cuvierinidae.

In the case of the late Oligocene species *Ireneia striatocarinata* Piehl, 2007, Cahuzac & Janssen (2010: 75) admitted that the presence of lateral carinae might suggest a common ancestor of *Vaginella* and the Cuvierinidae. This feature occurs occasionally, e.g. it was also present in the late Oligocene/early Miocene genus *Spoelia*, also included in the Cuvierinidae. But neither the earliest species of *Vaginella* from the Rupelian, nor any other *Vaginella* species, demonstrate similarities to *Ireneia* or any other cuvierinid.

Clio pyramidata

Rampal (2019: 163, fig. 21) maintains the two subspecies of *Clio pyramidata*, traditionally naming them '*C. pyramidata pyramidata* Linnaeus, 1767, and *C. p. lanceolata* (Lesueur, 1813)'. However, these two names are demonstrated to be synonyms (Janssen et al., 2018). For the nominal subspecies a neotype was designated, whereas for the morph usually indicated as *C. pyramidata pyramidata*, restricted to the North Atlantic, the name *C. pyramidata angusta* Boas, 1886, was activated.

Corse et al.'s (2013) estimate of the Cliidae age (37.8 Ma) seems correct. The earliest *Clio* species is known from the Bartonian (41.3–38 Ma), not from the 'Lower' Oligocene, as Rampal states.

Cavoliniidae

In Janssen (2012a), a paper on East Mediterranean holoplanktic molluscs, comments were included on the taxonomy of *Cavolinia* species, as proposed in Rampal's (2002) publication, as he could not agree with some of Rampal's opinions and statements. Dr Rampal soon reacted with a new paper in the Bollettino (Rampal, 2014) in such an offensive way that Janssen did not find it worth a reaction, considering that all relevant facts had been given and thinking that every researcher interested in the topic could easily evaluate the correctness of these statements.

As far as Rampal's (2019) new Cavoliniidae systematics are concerned, the present author agrees with the erection of a Diacriinae subfamily, as more than sufficient distinguishing features are present between that group and Cavoliniidae proper. Also the new genus *Telodiacria* Rampal, 2019 (not 2017) seems useful, but it is a pity that as type species *Telodiacria quadridentata* (de Blainville, 1821) was designated, without making clear what exactly has to be understood under that name: no type material of that taxon is available and it is not clear if van Leyen & van der Spoel's (1982) interpretation covers the original description.

They record the species from the Indian and tropical Pacific Ocean, but de Blainville (1821: 81) mentioned as type locality 'l'Océan Atlantique, assez près des Barbades: lat. 23°, 36', longit. 27°, 22'. This will need further research to find out what exactly is *Diacria quadridentata*, and thus, what exactly is *Telodiacria*.

Rampal's 2019 'new classification'

Ever since the classification of Bouchet et al. (2017: 357), based on the work of Klussmann-Kolb & Dinapoli (2006) and Burridge et al. (2017), the classic Order Thecosomata, with two suborders (Euthecosomata and Pseudothecosomata) was abandoned, and the Order Pteropoda, with three suborders (Euthecosomata, Pseudothecosomata, Gymnosomata) was applied instead. Rampal (2019: 168) does not follow this and maintains Thecosomata, but without comment.

Rampal's (2019) new families, Heliconoididae and Thieleidae, are accepted here, although both taxa contain just a single genus, each of them with a single present-day described species. The reference in Rampal (2019: 153) 'Thieleidae (Rampal, 1975)' is of course incorrect as the taxon is introduced as new in the 2019 paper.

In the Cavolinioida group the present author prefers to retain Cuvierinidae and Cliidae at full family rank and not as subfamilies of Cavoliniidae, as species in each of these groups offer so much mutual similarity in shell-morphology, whereas each separate group displays massive differences in comparison with Cavoliniidae s.str. A subdivision of Cavoliniidae into Cavoliniinae and Diacriinae is considered useful.

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