



Taxonomic revision of the fossil genera *Bulimactaeon*, *Hemiauricula* (= *Liocarenus*)
and *Nucleopsis*, with description of a new Recent genus and species
(Gastropoda: Heterobranchia: Acteonidae)

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ABSTRACT

The genus *Liocarenus* (Acteonidae) was originally described from Eocene fossil material and has subsequently come to include three subgenera (*Liocarenus s. s.*, *Bulimactaeon* and *Nucleopsis*) and nine species, including a Recent one (*L. globulinus*). Together, these have been accorded status as a subfamily, Liocareninae. We here present a taxonomic revision of all the species and subgenera historically ascribed to *Liocarenus*. We show that the genus name *Liocarenus* is an objective synonym of *Hemiauricula*. All three taxa (*Bulimactaeon*, *Hemiauricula* and *Nucleopsis*) are accepted at genus level and a new genus, *Rapturella*, is erected for the Recent species. *Rapturella* is diagnosed by a thick shell with rounded whorls, slightly stepped spire, two closely spaced subsutural spiral grooves, a weak columellar fold and a tooth-like palatal thickening. Three of the formerly included species of *Liocarenus* are here excluded from the Acteonidae. The revised classification is as follows: *B. bernayi* (Cossmann, 1892), *H. edentula* (Férussac, 1821), *H. hilarionis* (Bayan, 1870) n. comb., *N. subvaricatus* (Conrad, 1860), *R. globulina* (Forbes, 1844) n. comb. and *R. ryani* n. sp. (Acteonidae); *Hamlinia eliai* (Shalem, 1928) n. comb. and *Globiconcha formosa* (Cragin, 1893) n. comb. (Cylindrobullinidae); *Ringicula lata* (Conrad, 1865) n. comb. (Ringiculidae). *Acteon costellatus* Conrad, 1833 is considered a *species inquirenda*.

INTRODUCTION

The superfamily Acteonoidea consists of seven families (Gofas, 2015); three of them (Acteonidae, Aplustridae and Bullinidae) have Recent representatives, while the others (Acteonellidae, Cylindrobullinidae, Tubiferidae and Zardinellidae) are known only as fossils. The higher classification of Acteonoidea is not resolved; in phylogenetic analyses the superfamily has variously been recovered as nested within 'lower heterobranchs', as sister to Rissoelloidea or as the sister taxon of either Nudipleura or Tectipleura (Bouchet *et al.*, 2005; Malaquias *et al.*, 2009; Göbbeler & Klussmann-Kolb, 2010; Jörger *et al.*, 2010; Gründel & Nützel, 2012; Zapata *et al.*, 2014).

The Acteonidae probably has the largest number of extant species, with about 110 described to date, distributed among 16 genera (Göbbeler & Klussmann-Kolb, 2010; Bouchet, Rosenberg & Gofas, 2015). Members of the family are characterized by the absence of the rachidian tooth (except *Crenilabium* Cossmann, 1889) and the presence of five to more than 200 lateral teeth on each side of the radula (Rudman, 1971; Yonow, 1989). Besides the radula, the soft anatomy of most acteonid species has not been studied, making it harder to establish clear generic boundaries (Valdés, 2008). The genera therefore remain poorly characterized

and even readily-observable conchological characters are not consistently used in diagnoses. Some of these could be plesiomorphic within the Cephalaspeida, like the series of punctate spiral grooves on the teleoconch (also present in Philinidae, Ringiculidae, Haminoeidae and Bullinidae; e.g. Valdés, 2008; Helwerda, 2015). According to Kollmann & Yochelson (1976), the spiral grooves on many Recent and fossil cephalaspeids have not received due attention, as this ornamentation might be of functional significance in relation to distribution of mucus and/or shell stability during burrowing. Another conchological character, largely ignored (but see Valdés, 2008), is the subsutural spiral groove(s), which may differ from the remaining spiral grooves of the teleoconch. Characters such as these might prove useful for generic diagnoses when properly studied from a phylogenetic perspective. Shell sculpture and other conchological characters, such as varices, determinate growth and apertural ornament, are discussed below.

The current knowledge on the ecology and life histories of acteonoids is also far from complete. Studies on feeding behaviour and gut content of a few species indicate that they are vermivorous, feeding on polychaete worms (Yonow, 1989; Wägele *et al.*, 2008). The animals are considered to be infaunal, burrowing through soft sediments and occurring from the lower intertidal to depths exceeding 3,000 m (Burn & Thompson, 1998; Helwerda,

2015). Recently, a large number of new acteonoid species from the tropical southwestern Pacific have been described, showing a previously unrecognized high diversity of this group in deep-water environments (Valdés, 2008; provisionally designated as ‘*Acteon*’ due to lack of information on radular characters).

The Acteonidae also contain six fossil genera (Bouchet *et al.*, 2015). The family’s fossil record dates back to the Lower Jurassic (Pliensbachian or even Sinemurian) of France, but it only diversified later, in the Upper Jurassic and Cretaceous (Cossmann, 1895; Tracey, Todd & Erwin, 1993; Gründel & Nützel, 2012).

Liocarenus Harris & Burrows, 1891 was originally proposed for fossil species and has commonly been considered to include three subgenera (e.g. Cossmann, 1895): *Liocarenus s. s.*, *Bulimactaeon* Cossmann, 1892 and *Nucleopsis* Conrad, 1865b. These were considered distinct genera by Zilch (1959), who erected the subfamily Liocareninae for them. *Tornatella globulina* Forbes, 1844 was tentatively included in the genus *Liocarenus* by Nordsieck (1972) and this has since been accepted in the literature (see synonymy below). However, as discussed below, *Liocarenus* is an unnecessary replacement name and *Hemiauricula* Deshayes, 1853 has priority.

As this genus complex (and putative subfamily) is poorly discussed and figured in the literature, we present here a taxonomic revision of all fossil and Recent species that have been included within it. Based on conchological differences, we describe a new genus to accommodate the Recent snails previously assigned to *Liocarenus*, as well as a new Recent species. Finally, we consider whether this putative subfamily is a natural grouping within the Acteonidae.

MATERIAL AND METHODS

Study material, including type specimens, was obtained from 10 museums, university collections and private collections worldwide (of more than 60 contacted). Material examined is listed in Supplementary Material. For those species where specimens could not be studied, original literature and illustrations were used to assess their validity and status. For detailed examination, samples were mounted on stubs and observed uncoated in an environmental scanning electron microscope at the SMNS and at the Department of Malacology of the ANSP (Phenon). Measurements were made with the software ImageJ (Rasband, 2012).

Abbreviations used in the text are as follows: ANSP, Academy of Natural Sciences of Drexel University (Philadelphia, USA); BEG, Bureau of Economic Geology, University of Texas (Austin, USA); FS, Frank Swinnen, private collection (Belgium); MNHM, Muséum National d’Histoire Naturelle (Paris, France); NHMW, Naturhistorisches Museum Wien (Vienna, Austria); PRI, Paleontological Research Institution (Ithaca, USA); RMNH, Naturalis Biodiversity Centre (former Rijksmuseum van Natuurlijke Historie; Leiden, The Netherlands); SMNS, Staatliches Museum für Naturkunde Stuttgart (Stuttgart, Germany); SSS-IFSM, Stichting Schepel Schelp, International Fossil Shell Museum (Utrecht, The Netherlands); UCMP, University of California Museum of Paleontology (Berkeley, USA). Shell measurements: *H*, shell height parallel to coiling axis; *D*, greatest shell width perpendicular to *H*; *h*, aperture height (maximum length parallel to coiling axis); *d*, greatest width of aperture (maximum width perpendicular to coiling axis). The ratios *D/H*, *h/H* and *d/h* are used as measures of shell shape; spire height is defined as (*H-h*).

SYSTEMATIC DESCRIPTIONS

Family ACTEONIDAE d’Orbigny, 1843

Bulimactaeon Cossmann, 1892

Actaeon (*Bulimactaeon*) Cossmann, 1892: 72 (type species: *Actaeon bernayi* Cossmann, 1892, by original designation).

Liocarenus (*Bulimactaeon*)—Cossmann, 1895: 57.

Bulimactaeon?—Zilch, 1959: 12.

Bulimactaeon—Millard, 2011: 633.

Diagnosis: Shell ovate-conical (‘bulimoid’); spire profile slightly convex; sculptured by fine, widely-spaced spiral grooves. Aperture ovate, peristome slightly thickened.

Description: Shell ovate-conical (‘bulimoid’); imperforate; *D/H* 0.48. Teleoconch sculptured by fine, widely-spaced, spiral grooves (*c.* 13); each groove composed of small punctae. Spire profile slightly convex; spire whorls convex; suture distinct. Aperture ovate, relatively small; *h/H* 0.53. Peristome slightly thickened, especially on columellar and lower parietal regions.

Remarks: As material of this genus could not be found, the diagnosis and description are based on the descriptions and figures of the type species by Cossmann (1892, 1895) and Zilch (1959). *Bulimactaeon* differs from *Hemiauricula*, *Nucleopsis* and other acteonids by its higher spire and smaller aperture, displaying, as its name implies, an overall shell profile reminiscent of the land snail genus *Bulimulus* (Bulimulidae). As such, the shell of *B. bernayi* closely resembles those of species of the acteonid genus *Crenilabium*, but its shape is more broadly ovate, the spire less elongated, more convex and less turreted.

The teleoconch sculpture of the single included species, *B. bernayi*, consists of widely spaced fine spiral grooves (Cossmann, 1895; Zilch, 1959), with each groove appearing to be composed of small punctae (Cossmann, 1892: pl. 3, fig. 10; reproduced in Fig. 1A). This is a common (and likely plesiomorphic, see above) pattern among Recent acteonids, but not shown by either *Hemiauricula* or *Nucleopsis* (see below). Based on these differences, we consider *Bulimactaeon* to be a distinct genus from both *Hemiauricula* and *Nucleopsis*.

Bulimactaeon bernayi (Cossmann, 1892)

(Fig. 1A)

Actaeon (*Bulimactaeon*) *bernayi* Cossmann, 1892: 73; pl. 3, fig. 10 (Valmondois, Val-d’Oise, France; Eocene [Bartonian]; whereabouts of types unknown).

Liocarenus (*Bulimactaeon*) *bernayi*—Cossmann, 1895: 57. Cossmann & Pissarro, 1910–1913: fig. 235-2.

Bulimactaeon bernayi—Zilch, 1959: 12; fig. 28.

Hemiauricula (*Bulimactaeon*) *bernayi*—Le Renard & Pacaud, 1995: 127. Pacaud & Le Renard, 1995: 172.

Diagnosis and description: As for genus (see above). *H* = 7.5 mm, *D* = 3.5 mm (Cossmann, 1893).

Remarks: This species was originally described from a single specimen in Bernay’s private collection. The whereabouts of this collection is unknown and we could not trace the specimen.

Hemiauricula Deshayes, 1853

Orthostoma Deshayes, 1842: 611 (type species: *Auricula conovuliformis* Deshayes, 1824 [= *H. edentula* (Férussac, 1821)], by subsequent designation (Cossmann, 1895); in part; not Lacordaire, 1830: Coleoptera).

Hemiauricula Deshayes, 1853: 51. Millard, 2011: 633.

Acteon—d’Orbigny, 1850: 343 (in part).

Fortisia Bayan, 1870: 460 (not Rondani, 1861: Diptera). Bayan, 1870: 476.

Liocarenus Harris & Burrows, 1891: 113 (n. syn.). Cossmann, 1892: 73. Zilch, 1959: 11. Akers & Akers, 1997: 257.

Liocarenus (*Liocarenus*)—Cossmann, 1895: 55.

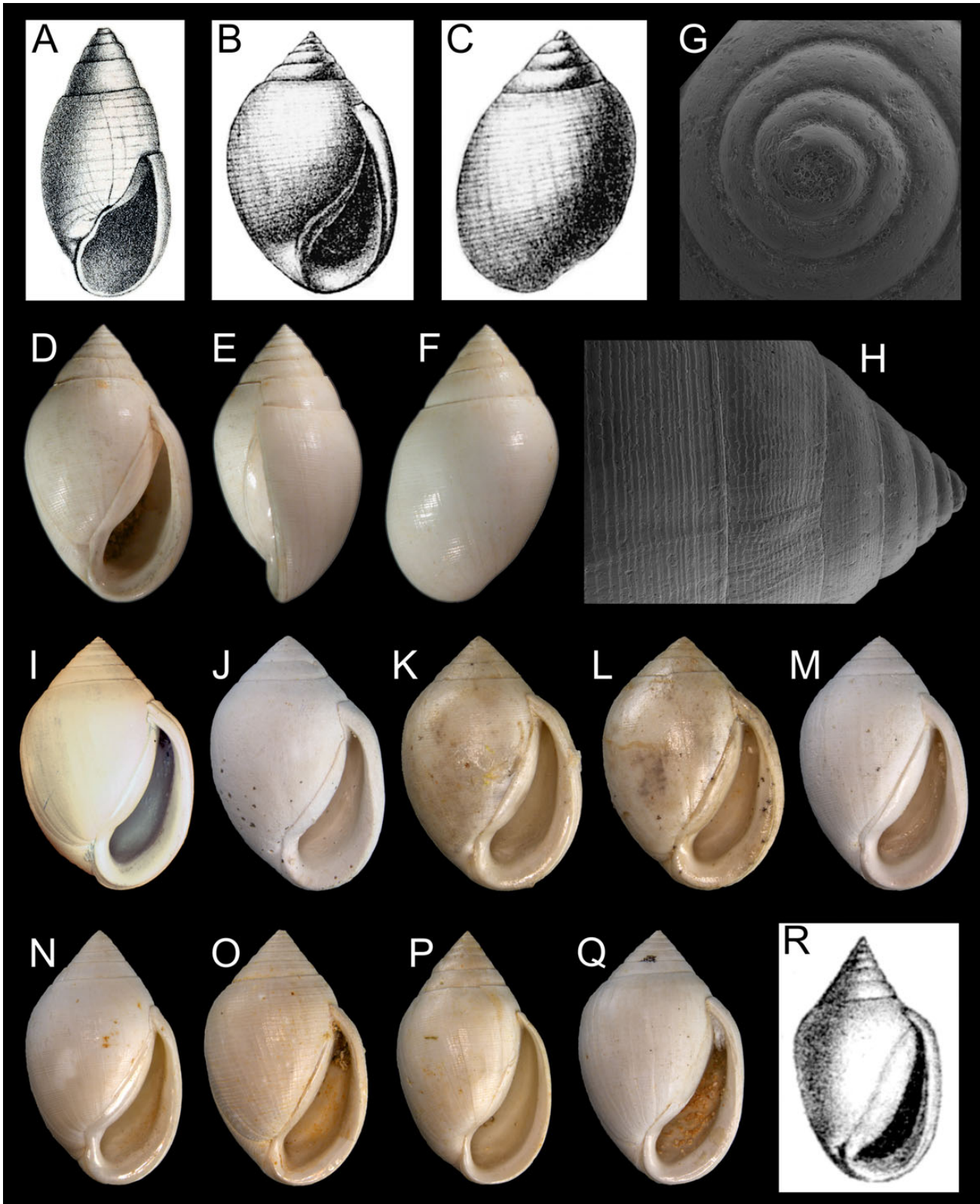


Figure 1. **A.** *Bulimactaon bernayi*, original illustration by [Cossmann \(1892: pl. 3, fig. 10\)](#) ($H = 7.5$ mm, according to [Cossmann, 1893](#)). **B.** **C.** *Hemiauricula conovuliformis*, original illustrations by [Deshayes \(1824: pl. 6, figs 9, 10, respectively\)](#) (H not reported). **D–H.** *Hemiauricula edentula*, syntype MNHN.F.A 52951 ($H = 14.8$ mm), Valognes? (see text). **D.** Apertural view. **E.** Lateral view. **F.** Dorsal view. **G.** Protoconch detail. **H.** Teleoconch sculpture detail. **I–Q.** *Hemiauricula edentula* in apertural view, showing variation in shell shape. **I.** MNHN.F.A 52494 ($H = 14.3$ mm), Cauvigny [Lutetian]. **J.** MNHN.F.A 52496 ($H = 18.0$ mm), Chaumont-en-Vexin [Lutetian]. **K.** MNHN.F.A 52499 specimen 1 ($H = 18.1$ mm), les Groux [Lutetian]. **L.** MNHN.F.A 52499 specimen 2 ($H = 16.8$ mm), les Groux [Lutetian]. **M.** MNHN.F.A 52492 specimen 1 ($H = 15.6$ mm), Cauvigny [Lutetian]. **N.** MNHN.F.A 52495 specimen 1 ($H = 19.0$ mm), Villiers-Saint-Frédéric [Lutetian]. **O.** MNHN.F.A 52498 ($H = 13.9$ mm), Thiverval-Grignon [Lutetian]. **P.** MNHN.F.A 52495 specimen 2 ($H = 16.4$ mm), Villiers-Saint-Frédéric [Lutetian]. **Q.** MNHN.F.A 52492 specimen 2 ($H = 15.2$ mm), Cauvigny [Lutetian]. **R.** *Hemiauricula hilarionis*, original illustration by [De Gregorio \(1880: pl. 1, fig. 10\)](#) ($H = 17$ mm, according to [De Gregorio, 1880](#)).

Diagnosis: Spire low conical; spire profile almost straight; spire whorls almost flat. Teleoconch sculptured by numerous fine spiral striae. Aperture tear-drop shaped, elongated; peristome greatly thickened; parietal callus strongly thickened and delimited.

Description: Shell ovate-conical, imperforate. Protoconch rounded, smooth. Teleoconch sculptured by numerous fine spiral striae; subsutural thread well developed. Spire low conical, profile almost straight; spire whorls almost flat-sided; suture distinct. Last whorl rounded, sometimes with slight shoulder. Aperture narrowly tear-drop shaped; peristome strongly thickened; parietal callus strongly thickened and delimited. Up to 3 well-marked axial clefts on spire and last whorl, interpreted as varices (corresponding to thickening of peristome and subsequent growth).

Remarks: In the original description of *H. conovuliformis*, Deshayes (1824) placed this species in *Auricula* Lamarck, 1799 (= *Ellobium* Röding, 1798; Ellobiidae) due to a fold on the columella. Later Deshayes concluded that this fold was caused by an accident in the handling of the fossil (Deshayes, 1864) and, therefore, transferred it to the new genus *Orthostoma*, which was a name preoccupied by a coleopteran insect genus. Deshayes (1853) finally introduced the generic name *Hemiauricula* in the caption of a plate (as *H. conovuliformis*), but nevertheless the name is considered valid (ICZN, 1999: Arts 12.2.5, 12.2.7). Unaware of Deshayes's work, Bayan (1870) erected the genus *Fortisia* for *H. conovuliformis* and also included a new fossil species, *H. hilarionis*. However, *Fortisia* was also preoccupied, which led Harris & Burrows (1891) to coin *Liocarenus* as its replacement. *Liocarenus* is therefore an unnecessary replacement for *Fortisia* and an objective synonym of *Hemiauricula*. Some recent authors have used the name *Hemiauricula* in this sense, but without discussing the rationale for this usage (e.g. Le Renard & Pacaud, 1995; Pacaud & Le Renard, 1995; Pacaud, 2008).

Later, additional fossil species were added to *Liocarenus* (e.g. Cossmann, 1892; Zilch, 1959; Akers & Akers, 1997) from North America (*Cylindrites formosus* Cragin, 1893, *Acteonina subvaricata* Conrad, 1860, *Acteon costellatus* Conrad, 1833 and *Acteon latus* Conrad, 1865a), from Europe (*B. bernayi*) and from the Near East (*Akera eliai* Shalem, 1928).

Not all of these species actually belong to the genus, as we discuss below. In addition, Cossmann (1895) alluded to a ‘*Liocarenus* sp.’ that could represent another species (see Supplementary Material). According to Nordsieck (1972), *Tornatella globulina* Forbes, 1844 was the sole Recent species deemed to belong to *Liocarenus*. However, it actually represents a distinct genus (see below). Finally, a single fossil species from France, *H. edentula*, remained largely ignored, but also belongs to *Hemiauricula*, as discussed below.

The genera *Bulimactaeon* and *Nucleopsis* were initially considered subgenera of *Liocarenus* (e.g. Cossmann, 1895) and raised to full genus rank by Zilch (1959); the latter position is adopted here.

The strong thickening of the peristome and apertural callus, together with the presence of varices, are noteworthy and suggest an episodic and determinate growth pattern (see Discussion, below).

***Hemiauricula edentula* (Férussac, 1821)**

(Fig. 1B–Q)

Auricula edentula Férussac, 1821: 104 (Valognes(?), Normandy, France; syntype MNHN.F.A52951 [old no. MNHN IM-2000-50690; Valognes; Férussac Coll.], Fig. 1D–H, $H = 14.8$ mm, $D = 8.7$ mm).

Hemiauricula edentula—Pacaud, 2008: 72.

Auricula conovuliformis Deshayes, 1824: 67; pl. 6, figs 9–11, 16 (Fig. 1B–C, herein) (Parnes, Oise, France; Eocene (Lutetian); whereabouts of types unknown).

Acteon conovuliformis?—d'Orbigny, 1850: 343.

Hemiauricula conovuliformis—Deshayes, 1853: 51; pl. 81, figs 15–16. Le Renard & Pacaud, 1995: 127.

Orthostoma conovuliformis—Deshayes, 1864: 615.

Fortisia conovuliformis—Bayan, 1870: 476.

Liocarenus (*Liocarenus*) *conovuliformis*—Cossmann, 1895: 55.

Liocarenus conovuliformis—Cossmann & Pissarro, 1910–1913: fig. 235-1 (as *conovuliformis*). Zilch, 1959: 11; fig. 26.

Hemiauricula (*Hemiauricula*) *conovuliformis*—Pacaud & Le Renard, 1995: 172.

Diagnosis: Spire low (h/H 0.7–0.8); spire profile straight to slightly convex. Aperture elongate tear-drop shaped.

Description: $H = 14.0$ – 19.5 mm; $D = 8.0$ – 12.5 mm; D/H 0.55–0.70. Shell ovate-conical, 8 whorls, imperforate. Protoconch rounded, smooth; about 1 mm diameter and 3 whorls, but transition to teleoconch unclear. Teleoconch sculptured by numerous fine spiral striae (interspaces 2–3 times width of grooves). Suture distinct; subsutural thread well-marked. Spire low conical, spire profile straight to slightly convex; spire whorls flattened. Last whorl rounded, sometimes with slight shoulder. Aperture elongate tear-drop shaped; h/H 0.7–0.8; peristome strongly thickened; parietal callus strongly thickened and delimited. Up to 3 well-marked axial clefts on spire and last whorl (Fig. 1D, E, I, P), interpreted as varices.

Distribution: France: Aisne (Saint-Gobain), Oise (Cauvigny, Chaumont-en-Vexin, Liancourt, Mouchy-le-Châtel, Parnes, Uilly-St-Georges, Vaudancourt), Normandy (Valognes?), Yvelines (Thiverval-Grignon; Villiers-Saint-Frédéric). Age: Eocene (Ypresian? [Cuisian], Lutetian).

Remarks: The name *A. edentula* remained largely forgotten since its description, while *H. conovuliformis*, the type species of the genus, was well described and documented; however, Pacaud (2008) gave *H. conovuliformis* as a synonym of *H. edentula*, although in a species list and without explanation. The type locality (‘Valognes’) and stratum of *H. edentula* are problematic. All the marls in the region of Valognes are of Early Jurassic (Hettangian) or Holocene age (BRGM, 2015; Clement Poirier, personal communication). If the type material really originates from the Hettangian layers, this would be the earliest record of the family Acteonidae and would give the species an uncommonly large time span (Jurassic–Eocene). As such, this age seems doubtful, since the syntype (and *Hemiauricula* as a whole) has a much more modified shape than the simpler forms known from the Early Jurassic (Gründel & Nützel, 2012) and also seems too well preserved to be of Jurassic age. It is more likely that the locality ‘Valognes’ is incorrect and that the syntype originated from Eocene layers of neighbouring regions of northern France.

The syntype of *H. edentula* (Fig. 1D–H) has a narrower shell with taller spire than Deshayes' (1824) figures of *H. conovuliformis* (Fig. 1B, C) and also a more narrowly elongated aperture. Nevertheless, with a large series of specimens available, it can be seen that these forms represent extremes in a spectrum of shell shape (Fig. 1I–Q). The family Acteonidae is well known for such intraspecific variability (Smriglio & Mariottini, 1996; Stilwell & Zinsmeister, 2002; Valdés, 2008). Therefore, *H. conovuliformis* is treated here as a synonym of *H. edentula*.

***Hemiauricula hilarionis* (Bayan, 1870) new combination**

(Fig. 1R)

Fortisia hilarionis Bayan, 1870: 476 (Croce Grande, Lombardy, Italy; whereabouts of types unknown). De Gregorio, 1880: 7; pl. 1, fig. 10 (Fig. 1R, herein).

Liocarenus (*Liocarenus*) *hilarionis*—Cossmann, 1895: 56.

Measurements: $H = 17$ mm, $D = 11$ mm (De Gregorio, 1880).

Distribution: Italy: Lombardy (Croce Grande), Veneto (San Giovanni Ilarione). Age: Eocene.

Remarks: Unfortunately, no material of this species was found. According to Bayan (1870), *H. hilarionis* can be distinguished from *H. edentula* by a more elongated shell, lack of sculpture and a narrower and more elongated aperture. This is consistent with the only figure of the species (De Gregorio, 1880; Fig. 1R). The lack of sculpture reported by Bayan (1870) is likely due to poor preservation. Although De Gregorio (1880) apparently had access to better preserved material, he did not comment on the presence or absence of sculpture.

Judging by the figure given by De Gregorio (1880), *H. hilarionis* has a more cylindrical and shouldered outline, a taller and slightly concave spire, and a narrower and more crescentic aperture than *H. edentula*. The sharply curved anterior part of the aperture of *H. hilarionis* is probably its main diagnostic feature. Nevertheless, all these features can be observed, but to a lesser degree, in specimens of *H. edentula* (cf. Fig. 1P). Furthermore, the same kind of morphological variation is seen in *N. subvaricatus* (see below). Therefore, it is possible that *H. hilarionis* is a synonym of *H. edentula*, but this can only be addressed when more material becomes available.

Nucleopsis Conrad, 1865

Acteonina—Conrad, 1860: 294 (in part).

Acteon (*Nucleopsis*) Conrad, 1865b: 34 (type species: *A. subvaricata* Conrad, 1860, by subsequent designation, Cossmann, 1895).

Tornatella (*Nucleopsis*)—Tryon, 1883: 356.

Liocarenus (*Nucleopsis*)—Cossmann, 1895: 56.

Nucleopsis—Gardner, 1945: 259. Zilch, 1959: 11.

Diagnosis: Shell ovate-conical. Teleoconch sculptured by coarse spiral threads. Spire profile slightly concave. Peristome slightly thickened. Varices present.

Description: Shell ovate-conical, *c.* 7 whorls, imperforate; D/H 0.62–0.64. Protoconch rounded, smooth, of about 3 whorls and 1 mm diameter; transition to teleoconch clear. Teleoconch sculptured by numerous (30–35) coarse spiral threads; distance between threads about 0.5–1.0 width of thread, but greater near suture; weak spiral striae present between threads; spiral threads with slight granules where they intersect with axial growth lines. Suture distinct. Spire with slightly concave profile; spire whorls almost flat-sided. Last whorl rounded or slightly shouldered. Aperture elongate tear-drop shaped; h/H 0.60–0.63. Peristome slightly thickened, with a swollen rib-like thickening externally. Parietal callus slightly thickened, narrow, well delimited. Up to 3 weak axial thickenings on spire and last whorl (Fig. 2C, H), interpreted as varices (corresponding to rib terminating final whorl).

Remarks: Conrad (1865b) did not provide a description for *Nucleopsis*, merely listing it as a subgenus of *Acteon*. The other two species included in *Nucleopsis* by Conrad (1865b) also originate from the Eocene of Alabama, USA: *A. costellatus* Conrad, 1833 and *A. latus* Conrad, 1865a. They were poorly described, not figured and never reported again, thus being considered doubtful by later researchers (Cossmann, 1895; Palmer, 1937; Gardner, 1945).

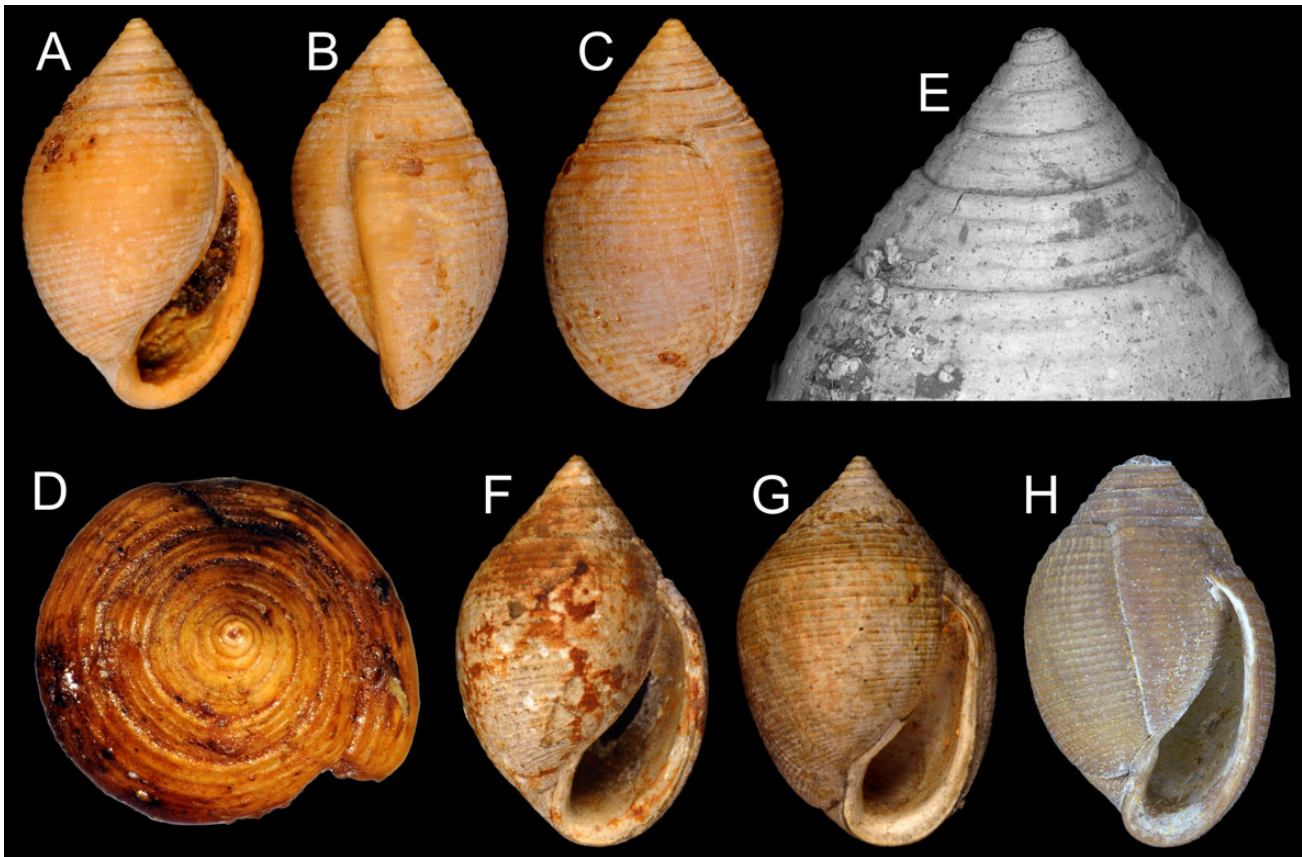


Figure 2. *Nucleopsis subvaricatus*. **A–D.** Lectotype ANSP 30692 ($H = 10.8$ mm). **A.** Apertural view. **B.** Lateral view. **C.** Dorsal view. **D.** Apical view. **E.** Teleoconch sculpture detail. **F.** Paralectotype 1 ANSP 30693 ($H = 11.6$ mm), apertural view. **G.** Paralectotype 2 ANSP 30693 ($H = 10.3$ mm), apertural view. **H.** PRI 3374 ($H = 9.1$ mm), apertural view.

Conrad's types are housed at the ANSP, but the type of *A. costellatus* could not be located (it was considered lost by Palmer, 1937); it is considered here as a *species inquirenda*. The species *A. latus* actually belongs to *Ringicula* (see Supplementary Material).

Gardner (1945) provided a good description of *Nucleopsis*, distinguishing it from other acteonids mainly by its well-marked spiral sculpture. Later, Zilch (1959) made the distinction between *Nucleopsis*, *Hemiauricula* and the remaining acteonids on the same grounds. In addition, *Nucleopsis* can be distinguished from *Hemiauricula* by the smaller size of the shell and a slightly concave spire profile. However, both show varices and apertural thickening, indicating episodic and determinate growth (see Discussion, below).

***Nucleopsis subvaricatus* (Conrad, 1860)**

(Fig. 2A–H)

Acteonina subvaricata Conrad, 1860: 294; pl. 47, fig. 22 (Claiborne, Alabama, USA; lectotype ANSP 30692 [designated by Palmer, 1937], Fig. 2A–E, $H = 10.8$ mm, $D = 6.7$ mm; 2 paralectotypes ANSP 30693, Fig. 2F–G).

Acteon (*Nucleopsis*) *subvaricatus*—Conrad, 1865b: 34.

Acteon subvaricatus—Conrad, 1866: 9.

Tomatella (*Nucleopsis*) *subvaricatus*—Tryon, 1883: 356; pl. 88, fig. 49 (as *subdivaricatus*).

Acteon (*Nucleopsis*) *subvaricatus*—De Gregorio, 1890: 166; pl. 16, fig. 37 (reproduction of Conrad, 1860: pl. 47, fig. 22).

Nucleopsis subvaricatus—Conrad, 1893: 48; pl. 1, fig. 6. Zilch, 1959: 11; fig. 27. Palmer, 1937: 502; pl. 74, figs 23, 24, 26; pl. 90, fig. 18. Brann & Kent, 1960: 602.

Liocarenus (*Nucleopsis*) *subvaricatus*—Cossmann, 1895: 56.

Nucleopsis sp.—Gardner, 1945: 260; pl. 16, figs 9, 10.

Nucleopsis subvaricatus—Palmer & Brann, 1965: 801 (as *subvaricata*).

Diagnosis and description: As for genus (see above). Measurements: $H = 9.0$ – 11.0 mm; $D = 6.0$ – 8.0 mm.

Distribution: USA: Alabama (Monroe County), Mississippi (Clarke County, Wautubbee). Mexico: Nuevo León (El Zacate). Age: Eocene (Bartonian–Priabonian).

Remarks: Some specimens show a broader and less rounded shell with a more angled shoulder, which accentuates the conical aspect of the spire, and with the palatal region of the peristome nearly parallel to the coiling axis (including paralectotype 2; Fig. 2G). This is considered to fall within normal intraspecific morphological variation in this family (Smriglio & Mariottini, 1996; Stilwell & Zinsmeister, 2002; Valdés, 2008).

Gardner (1945) reported a specimen of *Nucleopsis* sp. from the Priabonian (Upper Jackson Formation) of Mexico. We have examined this specimen, a juvenile (10 mm, without apertural thickening), and consider it consistent with *N. subvaricatus*.

***Rapturella* new genus**

Tomatella—Forbes, 1844: 191 (in part).

Acteon—Galindo, 1977: 4 (in part).

Liocarenus—Nordsieck, 1972: 9. Fasulo, Izzillo & Perna, 1982: 9. Sabelli, Giannuzzi-Savelli & Bedulli, 1990: 52. Sabelli, Giannuzzi-Savelli & Bedulli, 1992: 422. Segers, Swinnen & Prins, 2009: 248. Hernández, Rolán & Swinnen, 2011: 270. Millard, 2011: 632. (All in part.)

Type species: *Tomatella globulina* Forbes, 1844.

ZooBank registration: lsid:zoobank.org:act:12E3F740-4650-4765-8B3B-835310B32FC1

Etymology: Named after the deep-sea city Rapture, from the science-fiction video game series BioShock. Gender: feminine.

Diagnosis: Spire low, spire whorls rounded, slightly stepped profile. Shell thick. Teleoconch sculptured by spiral grooves, each composed of rounded punctae; the two subsutural grooves more closely spaced, composed of punctae of different shape from those of remaining spiral grooves. Aperture rounded-trapezoid. Columellar region thickened, bearing a weak fold. Anal canal narrow, shallow; siphonal canal region rounded. Slight tooth-like axial thickening on palatal region of aperture.

Description: Shell oval, small ($H = 3.0$ – 3.5 mm), imperforate or with narrow umbilicus. Protoconch coaxial (*sensu* Schröder, 1995), rounded, smooth, 1 whorl; transition to teleoconch distinct. Teleoconch sculptured by mostly widely and regularly spaced spiral grooves, each consisting of a row of rounded to slightly oval punctae; distance between grooves up to 10 times width of groove, decreasing towards aperture. Two closely spaced subsutural spiral grooves, composed of punctae of different shape from those of remaining spiral grooves (Fig. 4B–C, E–F); shape of punctae species-specific. Spire whorls well rounded, spire profile slightly stepped. Aperture rounded-trapezoid; h/H 0.35–0.55; columellar region thickened, bearing weak fold (Fig. 4D). Anal canal narrow, shallow; siphonal canal region rounded. Weak tooth-like axial thickening on the palatal region of aperture (Fig. 4A). Parietal callus thin, well delimited.

Remarks: *Rapturella* is characterized by a slightly stepped spire, a much smaller size and fewer whorls in comparison with *Bulimactaeon*, *Hemiauricula* and *Nucleopsis*. *Rapturella* also differs from *Hemiauricula* and *Nucleopsis* in teleoconch sculpture. *Rapturella* resembles all Recent acteonid genera (except *Ovulactaeon* Dall, 1889) in having punctate spiral grooves, but it is diagnosable by its combination of thick shell, trapezoid aperture, thickened peristome, only a weak fold on the columellar region and by the unique weak tooth-like thickening on the palatal region (Fig. 4A, D).

Rapturella resembles *Bathyaeteon* Valdés, 2008 in its minute size (<5 mm), well-spaced spiral grooves, well delimited parietal callus and its columellar region, but differs by its stepped spire, having spiral grooves covering the entire teleoconch (the posterior quarter of each whorl lacks spiral grooves in *Bathyaeteon*), rounded shape of the punctae forming the spiral grooves (*Bathyaeteon* has oval ones) and presence of a columellar fold and palatal tooth-like thickening.

Included in this new genus are *R. globulina* from the Eastern Atlantic and Mediterranean, and *R. ryani* n. sp. from Florida Keys.

***Rapturella globulina* (Forbes, 1844) new combination**

(Figs 3A–E, 4A–C)

Tomatella globulina Forbes, 1844: 191 (Serpho [Scriphos, Cyclades], Greece; type material unknown).

Acteon globulinus—Parenzan, 1970: 216 (as *Actaeon*). Galindo, 1977: 4.

Liocarenus (?) *globulinus*—Nordsieck, 1972: 10; pl. 1, fig. 10.

Liocarenus globulinus—Fasulo *et al.*, 1982: 9; figs 9, 10. Cecalupo & Giusti, 1986: 295; fig. 5. Sabelli *et al.*, 1990: 228. Ardovini & Cossignani, 1999: 80; textfig. Koutsoubas & Koukouras, 1993: 193. Smriglio & Mariottini, 1996: 187; fig. 12a, b. Bouchet, Le Renard & Gofas, 2001: 198. Beck, Metzger & Freiwald, 2006: 25. Segers *et al.*, 2009: 249 [not pl. 54, fig. 8]. Coll *et al.*, 2010: 219. Cossignani & Ardovini, 2011: 368; textfig. Hernández *et al.*, 2011: 270; fig. 92K, L. Manousis, 2012: 202; textfig.

Acteon pusillus—Jeffreys, 1870: 84 (in part; not Forbes, 1844).

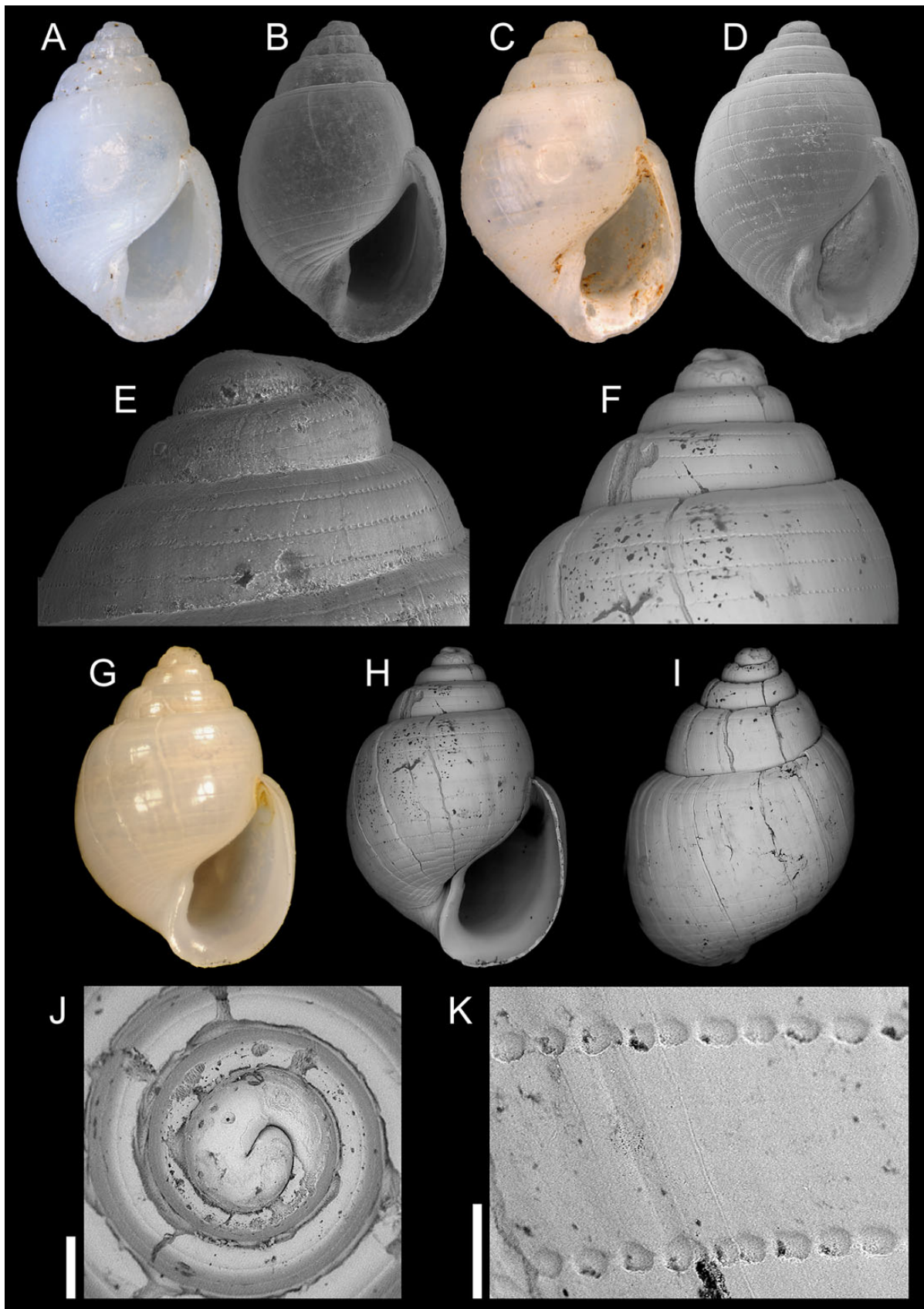


Figure 3. **A, B.** *Rapturella globulina*, Cape Verde, RMNH.MOL.30520 ($H = 3.4$ mm), apertural view. **C–E.** *R. globulina*, Madeira (FS unnumbered; $H = 2.8$ mm). **C, D.** Apertural view. **E.** Protoconch and teleoconch sculpture detail. **F–K.** *Rapturella ryani* n. sp., holotype, ANSP 312562 ($H = 3.4$ mm), Lower Florida Keys, USA. **F.** Teleoconch sculpture detail. **G, H.** Apertural view. **I.** Dorsal view. **J.** Protoconch detail, apical view. **K.** Detail of teleoconch sculpture, showing rounded punctae. Scale bars: **J** = 200 μ m; **K** = 50 μ m.

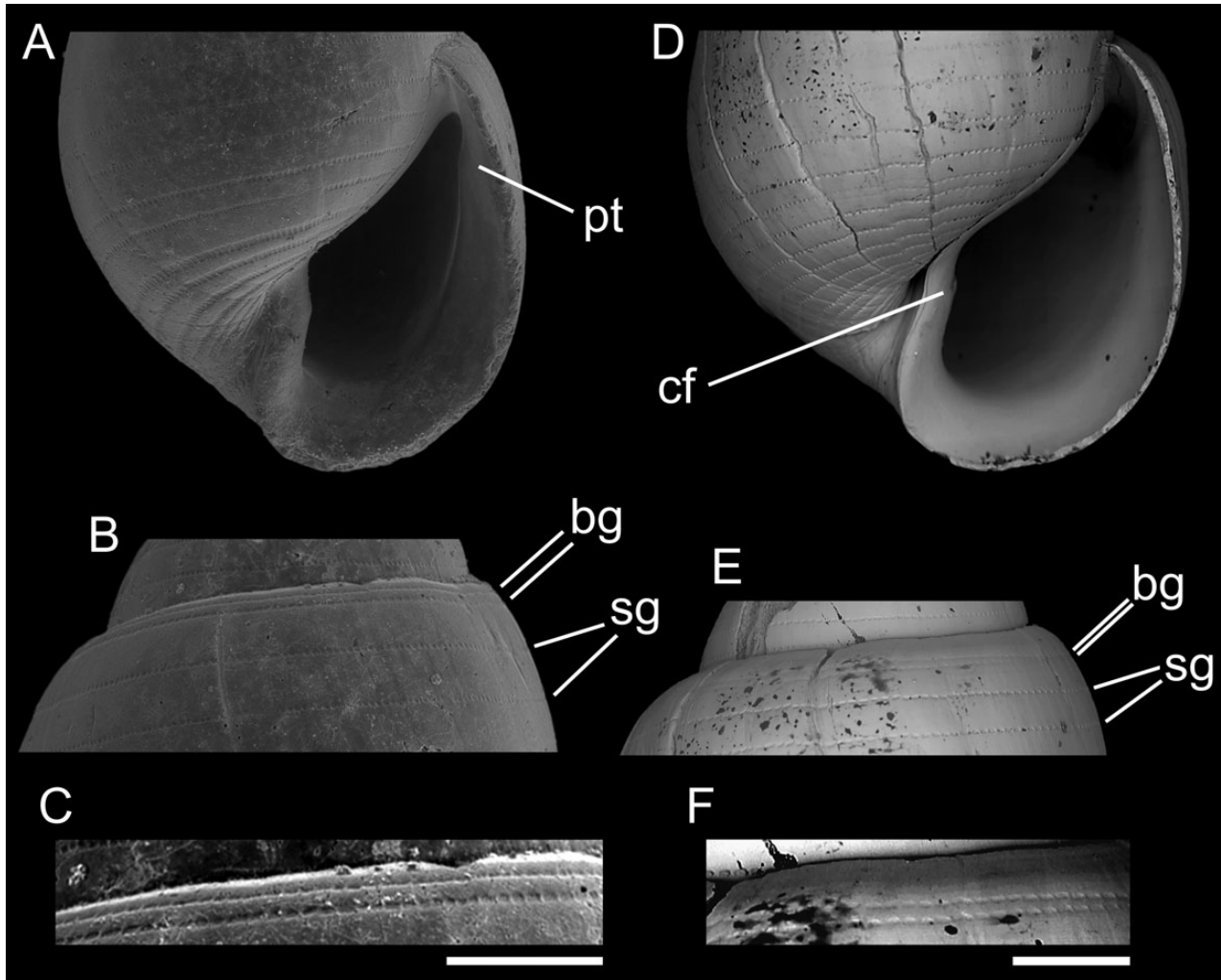


Figure 4. **A–C.** *Rapturella globulina*, Cape Verde (RMNH.MOL.30520). **A.** Detail of tooth-like axial thickening (pt) on palatal region of aperture, delimiting anal canal. **B.** Detail of penultimate whorl showing pair of subsutural spiral grooves (bg) and adjacent ‘normal’ spiral grooves (sg). **C.** Greater magnification of quadrangular-rounded punctae of subsutural grooves. **D–F.** *Rapturella ryani* n. sp., holotype (ANSP 312562). **D.** Detail of weak columellar fold (cf). **E.** Detail of penultimate whorl showing pair of subsutural spiral grooves (bg) and the ‘normal’ spiral grooves (sg). **F.** Greater magnification of elongated oval shape of punctae of subsutural grooves. Scale bars = 200 µm.

Diagnosis: D/H 0.60–0.65. Last whorl with 16 spiral grooves. Pair of subsutural spiral grooves composed of rounded-quadrangular, closely spaced punctae. Aperture relatively narrow; $d/h < 0.6$; h/H 0.55–0.6. Shell imperforate.

Description: H 2.8–3.5 mm; D 1.9–2.2 mm. Shell oval, thick, last whorl with rounded profile, imperforate; D/H 0.60–0.65; spire short, spire whorls rounded, suture distinct, profile slightly step-like. Colour white, glossy. Protoconch of 1 whorl, 0.45 mm diameter, smooth, clearly separated from teleoconch. Teleoconch sculptured by regularly spaced, narrow spiral grooves (16 on last whorl; Fig. 3B, D), separated by up to 10 times groove width (0.12–0.18 mm), becoming closer towards umbilicus. Grooves composed of small (0.02 mm) round punctae, spaced about half their diameter apart. The two more closely spaced subsutural grooves are different from the rest, composed of rounded-quadrangular punctae, closer together (Fig. 4B, C). Aperture anteriorly rounded, narrowed posteriorly, h/H 0.55–0.60; anal canal narrow, shallow, $1/6 h$; parietal region $3/5 h$, with thin, well delimited callus; columellar region broad, slightly expanded, with sharp edge, bearing a weak fold; palatal region with weak tooth-like axial thickening (Fig. 4A); outer lip sharp, thickened externally.

Distribution: Eastern Atlantic (Portugal, Azores, Madeira, Canary Islands, Cape Verde) and Mediterranean (France to Aegean Sea) (Nordsieck, 1972; Fasulo *et al.*, 1982; Smriglio & Mariottini, 1996; Segers *et al.*, 2009). The records of the species from the coast of Israel (Avnimelech & Boskovitz, 1955; Barash & Danin, 1971; Barash & Danin, 1992) seem to belong to *Japonactaeon pusillus* (Forbes, 1844) (H. K. Mienis, personal communication).

Habitat: From 150–1850 m deep (Fasulo *et al.*, 1982), but all records are of empty shells.

Remarks: Despite lacking type material and original figure, the description of Forbes (1844) has been sufficient to identify this species, mainly by the shell size, colour, number of whorls, short spire, aperture shape and thick columellar region. These characters are adequate, especially in the context of the other acteonids described by Forbes. Further descriptions by Jeffreys (1870) and Fasulo *et al.* (1982) have helped to establish the species identity.

Jeffreys (1870) stated that *R. globulina* was a juvenile of *Japonactaeon pusillus*, but then considered it valid since it is easily

diagnosed by its more compact and less turreted shell, aperture shape and teleoconch sculpture (Fasulo *et al.*, 1982).

The shell of this species is remarkably constant throughout its distribution, although we could not examine material from the Mediterranean (data on specimens from this region comes from literature). Unfortunately, previous works did not report the number of spiral grooves or the shape of the subsutural punctae, which might be of taxonomic value.

***Rapturella ryani* new species**

(Figs 3F–K, 4D–F)

Type material: Holotype ANSP 312562 ($H = 3.4$ mm, $D = 2.3$ mm, $h = 2.0$ mm, $d = 1.1$ mm); off Alligator Reef Light, 183 m depth; Lower Florida Keys, Florida, USA.

ZooBank registration: lsid:zoobank.org:act:DE5AF848-821C-444A-B2C8-7D4059A85EED

Etymology: In honour of Andrew Ryan, the founder of the deep-sea city Rapture, from the science-fiction video game series BioShock.

Diagnosis: D/H 0.68. Last whorl with 20 spiral grooves. Pair of subsutural spiral grooves composed of elongated oval punctae. Aperture relatively broad. Umbilicus narrow, slit-like.

Description: Shell oval, thick, last whorl with rounded profile; D/H 0.68; spire short, spire whorls rounded, suture distinct, profile slightly step-like. Colour white, glossy. Protoconch of 1 whorl, 0.48 mm diameter, smooth, clearly separated from teleoconch. Teleoconch sculptured by regularly spaced, narrow spiral grooves (20 on last whorl; Fig. 3H), separated by up to 10 times groove width (0.12–0.18 mm), becoming closer towards umbilicus. Grooves composed of small (0.02 mm) round to slightly oval punctae, spaced about half their diameter apart. The two more closely spaced subsutural grooves are different from the rest, composed of elongated oval punctae, closer together (Fig. 4E, F). Aperture anteriorly rounded, narrowed posteriorly, h/H 0.59; anal canal narrow, shallow, $1/6 h$; parietal region $3/5 h$, with thin, well delimited callus; columellar region broad, slightly expanded, with sharp edge, bearing a weak fold; palatal region with weak tooth-like axial thickening (Fig. 4A); outer lip sharp, thickened externally. Umbilicus narrow, slit-like.

Distribution: Known only from type locality.

Remarks: *Rapturella ryani* n. sp. differs from *R. globulina* in having a slightly rounder shell, a narrow slit-like umbilicus and a larger number of spiral grooves (20) on the last whorl. It also differs in the morphology of the punctae of the pair of subsutural spiral grooves: elongated oval in *R. ryani* (Fig. 4E, F) and rounded-quadrangular in *R. globulina* (Fig. 4B, C). Despite being known only from the holotype, the description of this new species is justified not only by its distinct conchological characters, but also by its locality, which falls well outside the known distribution of its Eastern Atlantic and Mediterranean congener. It should also be taken into account that cephalaspids previously considered of ampho-Atlantic distribution are now generally not regarded as conspecific (e.g. Malaquias & Reid, 2008).

About 30 species of Acteonidae have been recorded in the Western Atlantic (Marcus, 1974, 1977; Rosenberg, 2009; Cunha, 2011; Zelaya, Schejter, & Ituarte, 2011), 17 of which occur in the North Atlantic. *Rapturella ryani* is clearly diagnosable from nearly all of them by its greatly thickened columellar region, bearing a weak fold and the tooth-like axial thickening on the palatal region. It most resembles *A. melampoides*, mainly by its trapezoid aperture and weak columellar fold, but differs by having a higher

spire (h/H 0.59 in *R. ryani* and 0.65 in *A. melampoides*), a thicker shell and a more conspicuous columellar fold. Despite this close resemblance, examination of the holotype of *A. melampoides* (USNM 358205) has shown that it lacks the diagnostic features of *Rapturella*: the distinct subsutural grooves and the palatal tooth-like axial thickening.

Rapturella ryani differs from the following species by having a shorter spire and by the tooth-like axial thickening on the palatal region of the aperture: *A. danaida* Dall, 1881, *A. incisus* Dall, 1881, *A. perforatus* Dall, 1881, *A. delicatus* Dall, 1889, *A. juvenis* Dall, 1927, *A. lacunatus* Dall, 1927, *A. parallelus* Dall, 1927, *A. finlayi* McGinty, 1955, *Crenilabium exile* (Jeffreys, 1870) and *Mysouffa turrata* (Watson, 1883). Finally, *R. ryani* differs from the following species by having spiral lines distributed over the entire teleoconch: *A. splendidulus* Mörch, 1875, *A. exiguus* Mörch, 1875, *A. particolor* Dall, 1927, *A. semicingulatus* Dall, 1927, *A. candens* Rehder, 1939 and *J. punctostriatus* (C. B. Adams, 1840).

DOUBTFUL AND EXCLUDED SPECIES

The following species have all historically been classified in *Liocarenus* (= *Hemiauricula*) or *Nucleopsis*, but are here excluded from Acteonidae. *Akera eliai* Shalem, 1928, from the Cretaceous (Cenomanian) of Jerusalem, is transferred to the genus *Hamlinia* (Cylindrobullinidae). *Cylindrites formosus* Cragin, 1893, from the Cretaceous (Aptian–Albian) of Texas, USA, is reassigned to *Globiconcha* (Cylindrobullinidae). *Nucleopsis latus* Conrad, 1865, from the early Eocene of Alabama, USA, is transferred to *Ringicula* (Ringiculidae). A more thorough taxonomic treatment of these taxa can be found in the Supplementary Material.

DISCUSSION

The subfamily Liocareninae was established by Zilch (1959) to house the three genera *Hemiauricula* (then *Liocarenus*), *Nucleopsis* and *Bulimactaeon*. As shown above, these genera (especially *Bulimactaeon*) are quite different from each other regarding shell morphology and teleoconch sculpture: species of *Hemiauricula* present numerous spiral striae, *N. subvaricatus* has coarse spiral threads and *B. bernayi* has finely punctuated spiral grooves. As such, their classification in a single subfamily does not appear to be well supported, since there is no possible synapomorphic conchological feature to unite this group.

Bulimactaeon and *Rapturella* share the punctate sculptural pattern of the majority of Recent acteonid genera, but the interpretation of this resemblance is equivocal. According to Gosliner (1994), the shell of acteonids is the plesiomorphic type within ‘opisthobranchs’: thickly calcified, with an elevated spire and a punctate spiral teleoconch sculpture. The punctate teleoconch sculpture excludes Opisthobranchia in the narrow sense, but is found in nearly all Recent acteonids (with the exception of *Ovulactaeon*) and in a handful of other cephalaspidean genera, from different families (e.g. *Scaphander*, *Philine*, *Cylichna*, *Berthella*). Although both *Bulimactaeon* and *Rapturella* display this typical acteonid sculpture, *Hemiauricula* and *Nucleopsis* do not (instead they display similarly simple spiral grooves, coarser in *Nucleopsis*). If punctate sculpture is plesiomorphic in Acteonidae, its absence in *Hemiauricula* and *Nucleopsis* could be interpreted as a synapomorphy of these genera (though this is not unique in the Cephalaspidea; punctate sculpture is absent in several genera of Ringiculidae and the Jurassic bullinid *Sulcoacteon*, e.g. Kaim & Beisel, 2005). It should also be noted that the subfamily and family-level distinctions of cephalaspidean taxa (especially acteonids and ringiculoids) become more blurred as one goes back through the fossil record (Gründel & Nützel, 2012).

A phylogenetic relationship between *Hemiauricula* and *Nucleopsis* could also be indicated by another conchological character: the

presence of varices, not found elsewhere in Acteonoidea. Varices are evidence of periodic halts during growth, when a thickened lip develops (Leal, 2002), i.e. growth is episodic (and often determinate). Varices are well known in Caenogastropoda (e.g. Beu, 1980; Houart, 1994; Andrade, Costa & Pimenta, 2011) and so could be considered a plesiomorphic character within Heterobranchia (and hence, Acteonoidea). Nevertheless, varices are not unknown elsewhere in Heterobranchia, being present in some Ellobiidae (e.g. *Ellobium*, Glibert, 1962; *Pythia*, Martins, 1995). Varices could alternatively be a derived character in Acteonidae and thus interpreted as a synapomorphy of *Hemiauricula* and *Nucleopsis*.

Taken together, the absence of punctate sculpture and presence of varices (both possible synapomorphies) in *Hemiauricula* and *Nucleopsis* lead us to propose the restriction of the subfamily Liocareninae to these two genera. More rigorous testing of this hypothesis must await further resolution of the phylogeny of Recent acteonoids and its integration with the fossil record of the group.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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REFERENCES

- AKERS, R.E. & AKERS, T.J. 1997. *Texas Cretaceous gastropods*. Texas Paleontology Series Publication 6. Houston Gem and Mineral Society, Houston.
- ANDRADE, B.G., COSTA, P.M.S. & PIMENTA, A.D. 2011. Taxonomic review of the genus *Opaliopsis* (Gastropoda: Nystiellidae) from Brazil, with description of a new species. *Journal of the Marine Biological Association of the United Kingdom*, **91**: 1561–1566.
- ARDOVINI, R. & COSSIGNANI, T. 1999. *Atlante delle conchiglie di profondità del Mediterraneo*. L'Informatore Piceno, Ancona.
- AVNIMELECH, M. & BOSKOVITZ, V. 1955. Some problems of the present distribution of molluscan shells on the Mediterranean coast of Israel. *Bulletin of the Research Council of Israel*, **5B**: 178–188.
- BARASH, A. & DANIN, Z. 1971. Opisthobranchia (Mollusca) from the Mediterranean waters of Israel. *Israel Journal of Zoology*, **20**: 151–200.
- BARASH, A. & DANIN, Z. 1992. *Fauna Palaestina. Mollusca I—annotated list of Mediterranean molluscs of Israel and Sinai*. Israel Academy of Sciences and Humanities, Jerusalem.
- BAYAN, M.F. 1870. Sur les terrains tertiaires de la Vénétie. *Bulletin de la Société Géologique de France, Série 2*, **27**: 444–487.
- BECK, T., METZGER, T. & FREIWALD, A. 2006. *Biodiversity inventorial atlas (BIAS) of macrofaunal associations from OASIS seamount study sites*. Friedrich-Alexander-University of Erlangen-Nuremberg, Nuremberg.
- BEU, A.G. 1980. Taxonomy of gastropods of the families Ranellidae (= Cymatiidae) and Bursidae. Part 2. Descriptions of 14 new modern Indo-West Pacific species and subspecies, with revisions of related taxa. *New Zealand Journal of Zoology*, **13**: 273–355.
- BOUCHET, P., LE RENARD, J. & GOFAS, S. 2001. Mollusca. In: *European register of marine species* (M.J. Costello, C.S. Embrow & R. White, eds), pp. 180–213. Muséum National d'Histoire Naturelle, Paris.
- BOUCHET, P., ROCROI, J.-P., FRYDA, J., HAUSDORF, B., PONDER, W., VALDES, A. & WARREN, A. 2005. Classification and nomenclator of gastropod families. *Malacologia*, **47**: 1–397.
- BOUCHET, P., ROSENBERG, G. & GOFAS, S. 2015. *Acteon* Montfort, 1810. World Register of Marine Species. Available at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=137618> [accessed 19 March 2015].
- BRANN, D.C. & KENT, L.S. 1960. Catalogue of the type and figured specimens in the Paleontological Research Institution. *Bulletins of American Paleontology*, **40**: 1–995.
- BRGM (BUREAU DE RECHERCHES GÉOLOGIQUES ET MINIÈRES). 2015. InfoTerre. Available at <http://infoterre.brgm.fr/> [accessed 11 March 2015].
- BURN, R. & THOMPSON, T.E. 1998. Order Cephalaspidea. In: *Mollusca: the southern synthesis. Part B, Fauna of Australia*. Vol. 5 (P.L. Beesley, G.J.B. Ross & A. Wells, eds), pp. 943–959. CSIRO Publishing, Melbourne.
- CECALUPO, A. & GIUSTI, F. 1986. Rinvenimenti malacologici a sud ovest dell'isola de Capria. *Bollettino Malacologico*, **22**: 293–298.
- COLL, M., PIRODDI, C., STEENBEEK, J., KASCHNER, K., LASRAM, F.B.R., AGUZZI, J., BALLESTEROS, E., BIANCHI, C.N., CORBERA, J., DAILIANIS, T., DANOVARO, R., ESTRADA, M., FROGLIA, C., GALIL, B.S., GASOL, J.M., GERTWAGEN, R., GIL, J., GUILHAUMON, F., KESNER-REYES, K., KITSOS, M.S., KOUKOURAS, A., LAMPADARIOU, N., LAXAMANA, E., CUADRA, C.M.L., LOTZE, H.K., MARTIN, D., MOUILLOT, D., ORO, D., RAICEVICH, S., RIUS-BARILE, J., SAIZ-SALINAS, J.I., SAN VICENTE, C., SOMOT, S., TEMPLADO, J., TURON, X., VAFIDIS, D., VILLANUEVA, R. & VOULTSIADOU, E. 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS ONE*, **5**: e11842.
- CONRAD, T.A. 1833. *Fossil shells of the Tertiary formations of North America*. Vol. 1, No. 4. W.P. Gibbons, Philadelphia.
- CONRAD, T.A. 1860. Description of new species of Cretaceous and Eocene fossils of Mississippi and Alabama. *Journal of the Academy of Natural Sciences of Philadelphia, Ser. 2*, **4**: 275–298.
- CONRAD, T.A. 1865a. Descriptions of new Eocene shells of the United States. *American Journal of Conchology*, **1**: 142–149.
- CONRAD, T.A. 1865b. Catalogue of the Eocene and Oligocene Testacea of the United States. *American Journal of Conchology*, **1**: 1–35.
- CONRAD, T.A. 1866. Checklist of the invertebrate fossils of North America. Eocene and Oligocene. *Smithsonian Miscellaneous Collections*, **200**: 1–41.
- COSSIGNANI, T. & ARDOVINI, R. 2011. *Malacologia mediterranea. Atlante delle conchiglie del Mediterraneo*. L'Informatore Piceno, Ancona.
- COSSMANN, M. 1892. Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. *Annales de la Société Royale Zoologique de Belgique*, **26**: 7–167.
- COSSMANN, M. 1893. Notes complémentaires sur la faune éocénique de l'Alabama. *Annales de Géologie et de Paléontologie*, **12**: 1–51 + 2 pl.

- COSSMANN, M. 1895. *Essais de paléoconchologie comparée*. Vol. 1. Comptoir Géologique, Paris.
- COSSMANN, M. & PISSARRO, G. 1910–1913. *Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris*. Vol. 2. Scaphopodes, gastropodes, brachiopodes, céphalopodes & supplément, Paris.
- CRAGIN, F.W. 1893. A contribution to the invertebrate paleontology of the Texas Cretaceous. *Fourth Annual Report of the Geological Survey of Texas*, **9**: 139–294.
- CUNHA, C.M. 2011. A new species of *Acteon* (Opisthobranchia, Acteonidae) from off northeast Brazil. *Zoologia*, **28**: 229–232.
- DE GREGORIO, A. 1880. *Fauna di S. Giovanni Ilarione (Parisiense) monografia. Parte I: cefalopodi e gasteropodi*. Montaina, Palermo.
- DE GREGORIO, A. 1890. *Monographie de la faune Éocénique de l'Alabama et surtout de celle de Claiborne de l'étage Parisien (horizon à Venericardia planicosta Lamk.)*. Librairie Internationale L. Pedone Lauriel de Charles Clausen, Palermo.
- DESHAYES, G.P. 1824. *Description des coquilles fossiles des environs de Paris*. Vol. 2. Mollusques. J. Tastu, Paris.
- DESHAYES, G.P. 1853. *Traité élémentaire de conchytiologie: avec les applications de cette science à la géologie. Explication des planches*. Victor Masson, Paris.
- DESHAYES, G.P. 1864. *Description des animaux sans vertèbres découverts dans le bassin de Paris*. Vol. 2. Baillière, Paris.
- FASULO, G., IZZILLO, F. & PERNA, E. 1982. Malacofauna vivente nel Golfo di Napoli, parte 3. Famiglia Acteonidae. *La Conchiglia*, **14**: 6–11.
- FÉRUSSAC, A.E.A. 1821. *Animaux mollusques classés en familles naturelles*. A. Bertrand, Paris.
- FORBES, E. 1844. Report on the Mollusca and Radiata of the Aegean Sea and on their distribution, considered as bearing on Geology. *Report of the Annual Meeting of the British Association for the Advancement of Science*, **13**: 130–193.
- GALINDO, E.S. 1977. *Index and register of seashells (with cross references)*. Librería de Porrúa Hermanos & Cia., Mexico City.
- GARDNER, J. 1945. Mollusca of the tertiary formations of northeastern Mexico. *Geological Society of America Memoirs*, **11**: 1–306.
- GLIBERT, M. 1962. Euthyneura et Pulmonata fossiles du Cénozoïque étranger des collections de l'Institut Royal des sciences naturelles de Belgique. *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique*, **70**: 1–140.
- GÖBBELER, K. & KLUSSMANN-KOLB, A. 2010. The phylogeny of the Acteonoidea (Gastropoda): molecular systematics and first detailed morphological study of *Rictaxis punctocaelatus* (Carpenter, 1864). *Journal of Molluscan Studies*, **76**: 303–316.
- GOFAS, S. 2015. Acteonoidea d'Orbigny, 1843. World Register of Marine Species. Available at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=382223> [accessed 19 March 2015].
- GOSLINER, T.M. 1994. Gastropoda: Opisthobranchia. In: *Microscopic anatomy of invertebrates*. Vol. 5 (F.W. Harrison & A.J. Kohn, eds), *Mollusca I*, pp. 253–355. Wiley-Liss, New York.
- GRÜNDEL, J. & NÜTZEL, A. 2012. On the early evolution (Late Triassic to Late Jurassic) of the Architectibranchia (Gastropoda: Heterobranchia), with a provisional classification. *Neues Jahrbuch für Geologie und Paläontologie*, **264**: 31–59.
- HARRIS, G.F. & BURROWS, H.W. 1891. *The Eocene and Oligocene beds of the Paris Basin*. Geologists' Association, London.
- HELWERDA, R.A. 2015. Acteonidae, Bullinidae and Ringiculidae (Gastropoda: Heterobranchia) from the Plio-Pleistocene of the Philippines. *Zootaxa*, **3990**: 197–220.
- HERNÁNDEZ, J.M., ROLÁN, E. & SWINNEN, F. 2011. Gastropoda: Opisthobranchia. In: *Muliscos y conchas marinas de Canarias* (E. Rolán, ed.), pp. 270–295. ConchBooks, Hackenheim.
- HOUART, R. 1994. *Illustrated catalogue of Recent species of Muricidae named since 1971*. Christa Hemmen, Wiesbaden.
- ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE). 1999. *International code of zoological nomenclature*. Edn 4. International Trust for Zoological Nomenclature, London.
- JEFFREYS, J.G. 1870. V. Mediterranean Mollusca. *Annals and Magazine of Natural History, Ser. 4*, **6**: 65–86.
- JÖRGER, K.M., STÖGER, I., KANO, Y., FUKUDA, H., KNEBELSBERGER, T. & SCHRÖDL, M. 2010. On the origin of Acochlidia and other enigmatic euthyneuran gastropods, with implications for the systematics of Heterobranchia. *BMC Evolutionary Biology*, **10**: 323.
- KAIM, A. & BEISEL, A.L. 2005. Mesozoic gastropods from Siberia and Timan (Russia). Part 2: Neogastropoda and Heterobranchia. *Polish Polar Research*, **26**: 41–64.
- KOLLMANN, H.A. & YOCHELSON, E.L. 1976. Survey of Paleozoic gastropods possibly belonging to the subclass Opisthobranchia. *Annalen des Naturhistorischen Museums in Wien*, **80**: 207–220.
- KOUTSOUBAS, D. & KOUKOURAS, A. 1993. An account of our knowledge on the opisthobranch mollusc fauna of the Aegean Sea. *Bollettino Malacologico*, **29**: 191–200.
- LEAL, J.H. 2002. Gastropods. In: *The living marine resources of the Western Central Atlantic*. Vol. 1: *Introduction, molluscs, crustaceans, hagsfishes, sharks, batoid fishes, and chimaeras* (K.E. Carpenter, ed.), pp. 99–147. FAO Species Identification Guide for Fishery Purposes. FAO.
- LE RENARD, J. & PACAUD, J.M. 1995. Révision des mollusques paléogènes du Bassin de Paris II—liste des références primaires des espèces. *Cossmanniana*, **3**: 65–132.
- MALAQUIAS, M.A.E., MACKENZIE-DODDS, J., BOUCHET, P., GOSLINER, T. & REID, D.G. 2009. A molecular phylogeny of the Cephalaspidea *sensu lato* (Gastropoda: Euthyneura): Architectibranchia redefined and Runcinacea reinstated. *Zoologica Scripta*, **38**: 23–41.
- MALAQUIAS, M.A.E. & REID, D.G. 2008. Systematic revision of the living species of Bullidae (Mollusca: Gastropoda: Cephalaspidea), with a molecular phylogenetic analysis. *Zoological Journal of the Linnean Society*, **153**: 453–543.
- MANOUSIS, T. 2012. *The seashells of Greece*. Kyriakidis Brothers, Thessaloniki.
- MARCUS, E. 1974. On some Cephalaspidea (Gastropoda: Opisthobranchia) from the Western and middle Atlantic warm waters. *Bulletin of Marine Science*, **24**: 300–371.
- MARCUS, E. 1977. An annotated checklist of the western Atlantic warm water opisthobranch Molluscs. *Journal of Molluscan Studies, Supplement*, **4**: 1–23.
- MARTINS, A.M.F. 1995. A new species of *Pythia* Roding, 1798 (Pulmonata, Ellobiidae), from New Ireland, Papua New Guinea. *Molluscan Research*, **16**: 59–67.
- MILLARD, V. 2011. *Classification of Mollusca: a classification of world wide Mollusca*. Edn 5. Victor Millard, Cape Town.
- NORDSIECK, F. 1972. *Die europäischen Meeresschnecken: (Opisthobranchia mit Pyramidellidae, Rissoacea); vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer*. Fischer, Stuttgart.
- ORBIGNY, A.D'. 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnées faisant suite au cours élémentaire de paléontologie*. Vol. 1. Victor Masson, Paris.
- PACAUD, J.-M. 2008. Mollusca. In: *Le contenu paléontologique du Lutétien du bassin de Paris* (D. Merle, ed.), pp. 40–94. Muséum National d'Histoire Naturelle, Paris.
- PACAUD, J.-M. & LE RENARD, J. 1995. Révision des mollusques paléogènes du Bassin de Paris IV—liste systématique actualisée. *Cossmanniana*, **3**: 151–187.
- PALMER, K.V.W. 1937. The Claibornian Scaphopoda, Gastropoda, and dibranchiate Cephalopoda of the southern United States. *Bulletins of American Paleontology*, **7**: 1–548.
- PALMER, K.V. & BRANN, D.C. 1965. Catalogue of the Paleocene and Eocene Mollusca of the southern and eastern United States. Part 1. Pelecypoda, Amphineura, Peteropoda, Scaphopoda and Cephalopoda. *Bulletins of American Paleontology*, **48**: 1–471.
- PARENZAN, P. 1970. *Carta d'identità delle conchiglie del Mediterraneo*. Vol. 1. *Gasteropodi*. Bios Taras, Taranto.
- RASBAND, W.S. 2012. *ImageJ*. U. S. National Institutes of Health, Bethesda.
- ROSENBERG, G. 2009. *Malacolog 4.1.1: A database of Western Atlantic marine Mollusca*. URL <http://www.malacolog.org/>.

- RUDMAN, W.B. 1971. The family Acteonidae (Opisthobranchia, Gastropoda) in New Zealand. *Journal of the Malacological Society of Australia*, **2**: 205–214.
- SABELLI, B., GIANNUZZI-SAVELLI, R. & BEDULLI, D. 1990. *Catalogo annotato dei molluschi marini del Mediterraneo*. Vol 1. Libreria Naturalistica Bolognese, Bologna.
- SABELLI, B., GIANNUZZI-SAVELLI, R. & BEDULLI, D. 1992. *Catalogo annotato dei molluschi marini del Mediterraneo*. Vol 2. Libreria Naturalistica Bolognese, Bologna.
- SCHRÖDER, M. 1995. Frühontogenetische Schalen jurassicher und unterkretazischer Gastropoden aus Norddeutschland und Polen. *Palaontographica, Abteilung A*, **238**: 1–95.
- SEGBERS, W., SWINNEN, F. & PRINS, R. 2009. *Marine molluscs from the Portuguese province of Madeira: Madeira and Selvagens Archipelago; Monoplacophora, Polyplacophora, Gastropoda, Bivalvia & Scaphopoda*. Snoeck, Heule.
- SHALEM, N. 1928. Fauna nuova cenomaniana della argille verdi di Gerusalemme. *Bollettino della Società Geologica Italiana*, **47**: 69–108.
- SMRIGLIO, C. & MARIOTTINI, P. 1996. Central Tyrrhenian Sea Mollusca: XI. Description of *Callostracon tyrrhenicum* sp. nov. (Gastropoda, Acteonidae) and remarks on other Mediterranean species of the family. *Basteria*, **60**: 183–193.
- STILWELL, J.D. & ZINSMEISTER, W.J. 2002. A new, large acteonid gastropod (Mollusca) from the latest Cretaceous of Antarctica. *Journal of Paleontology*, **76**: 1102–1105.
- TRACEY, S., TODD, J.A. & ERWIN, D.H. 1993. Mollusca: Gastropoda. In: *The fossil record 2* (M.J. Benton, ed.), pp. 131–167. Chapman & Hall, London.
- TRYON, G.W. 1883. *Structural and systematic conchology: an introduction to the study of the Mollusca*. Vol. 2. G. W. Tryon, Philadelphia.
- VALDÉS, Á. 2008. Deep-sea “cephalaspidean” heterobranchs (Gastropoda) from the tropical southwest Pacific. *Mémoires du Muséum National d'Histoire Naturelle*, **196**: 587–792.
- WÄGELE, H., KLUSSMANN-KOLB, A., VONNEMANN, V. & MEDINA, M. 2008. Heterobranchia I: the Opisthobranchia. In: *Phylogeny and evolution of the Mollusca* (W.F. Ponder & D. Lindberg, eds), pp. 385–408. University of California Press, Berkeley.
- YONOW, N. 1989. Feeding observations on *Acteon tornatilis* (Linnaeus) (Opisthobranchia: Acteonidae). *Journal of Molluscan Studies*, **55**: 97–102.
- ZAPATA, F., WILSON, N.G., HOWISON, M., ANDRADE, S.C.S., JÖRGER, K.M., SCHRÖDL, M., GOETZ, F.E., GIRIBET, G. & DUNN, C.W. 2014. Phylogenomic analyses of deep gastropod relationships reject Orthogastropoda. *Proceedings of the Royal Society B*, **281**: 1–26.
- ZELAYA, D.G., SCHEJTER, L. & ITUARTE, C. 2011. *Neactaeonina argentina*, new species, and family placement of the genus *Neactaeonina* Thiele, 1912 (Mollusca: Gastropoda). *Malacologia*, **53**: 251–263.
- ZILCH, A. 1959–1960. Euthyneura. In: *Handbuch der Paläozoologie*. Vol. 6, Part 2 (W. Wenz, ed.), pp. 1–834. Gebrüder Borntraeger, Berlin.