



Paraclavatula (Gastropoda: Conoidea: Clavatulidae), a new genus with a distinctive radula type from West Africa

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(Received 4 December 2017; editorial decision 9 March 2018)

ABSTRACT

A unique radular configuration for Conoidea, consisting of five teeth in a transverse row (acuspate plate-like central and laterals, and duplex marginal teeth), was found in three species previously described in the genus *Clavatula*: *C. delphinae*, *C. pseudomystica* and *C. christiana*. Analysis of the COI gene demonstrated that they belong to the family Clavatulidae. *Paraclavatula* n. gen. is described. No similar radulae have been found previously among Conoidea and their morphology suggests that the presence of well-defined lateral teeth is more broadly distributed within Conoidea than previously anticipated. Based on radular morphology alone, it would not be possible to attribute the genus to any presently recognized family of Conoidea.

INTRODUCTION

Clavatulidae Gray, 1853, as now understood, is a relatively small family of Conoidea, which presently encompasses 13 Recent genera, two of them included tentatively (Bouchet *et al.*, 2011). The representatives of the family are distributed in the Atlantic, Indian and Pacific Oceans from intertidal to bathyal depths, and are particularly diverse in West, South and southeast Africa. Overall, the shell and radular characters display much disparity within the family.

The radulae and soft body morphology of Clavatulidae remain rather poorly studied. Line drawings of radulae of several species from South Africa and Mozambique were provided by Kilburn (1985) and scanning electron micrographs of a few additional species were published by Bouchet *et al.* (2011).

The genus *Clavatula* Lamarck, 1801 (type species *Clavatula coronata* Lamarck, 1801 by monotypy) is particularly diverse in West Africa and includes over 40 species, several having been described recently (e.g. Nolf, 2006, 2008, 2011), using shell characters alone.

In the course of a systematic revision of the genus *Clavatula* from West Africa (J. Horro, E. Rolán and P. Ryall, unpublished), an extremely unusual radula was found in two species. This unique radular morphology called into question the systematic position of the species. We were able to obtain one specimen with a similar radula, collected in the Republic of the Congo, and adequately preserved for DNA sequencing. A molecular phylogenetic analysis confirmed its position within the family Clavatulidae. Based on morphological and molecular evidence, we provide a detailed description of the radula and describe the new genus *Paraclavatula* for three species from West Africa, previously attributed to *Clavatula*.

MATERIAL AND METHODS

Specimens examined in this study were mostly collected by Xico Fernandes in Angola during the 1990s. The shells were preserved in ethanol and stored in the collections of the second and third authors. One specimen (MNHN-IM-2009-26535) was obtained during fieldwork in the Republic of the Congo and is stored in the Muséum National d'Histoire Naturelle in Paris (MNHN). For the latter specimen a tissue clip of the foot was preserved on the spot in 95% ethanol. To test the taxonomic affinities of MNHN-IM-2009-26535, several specimens belonging to various genera of Clavatulidae, as well as samples belonging to other families of Conoidea, were included in the dataset (Table 1). These samples were collected during several expeditions conducted by the MNHN and from other sources (see Table 1 for details). All of them are stored in the collections of the MNHN. Details of localities and photos of the specimens are available on the website of the MNHN at <https://science.mnhn.fr/institution/mnhn/collection/im/item/> by adding the registration number of the specimen (without prefix IM-) after the last backslash.

DNA was extracted using the Epmotion 5075 robot (Eppendorf), following the manufacturers' recommendations. A fragment of the cytochrome oxidase subunit I (COI) gene was amplified using universal primers LCO1490/HCO2198 (Folmer *et al.*, 1994). The protocol for the PCR reactions followed Puillandre *et al.* (2017). PCR products were purified and sequenced by the Eurofins sequencing facility. Sequences were deposited in BOLD (Barcode of Life Datasystem) and GenBank (Table 1). The phylogenetic tree was reconstructed using MrBayes (Huelsenbeck & Ronquist, 2001), as implemented on the Cipres

Table 1. List of studied material.

MNHN reg. no.	Family	Genus	Species	Expedition	Country	BOLD ID	GenBank acc. no.
IM-2009-19153	Clavatulidae	<i>Clavatula</i>	<i>caerulea</i> (Weinkauff, 1875)		Gabon	CONO2124-18	MH034143
IM-2009-24979	Clavatulidae	<i>Clavatula</i>	<i>muricata</i> (Lamarck, 1822)	Port ZANAGA	Republic of the Congo	CONO2128-18	MH034145
IM-2009-24982	Clavatulidae	<i>Clavatula</i>	<i>pyramidata</i> (Kiener, 1840)	Port ZANAGA	Republic of the Congo	CONO2130-18	MH034155
IM-2009-24970	Clavatulidae	<i>Clavatula</i>	<i>regia</i> (Röding, 1798)		Principe Island	CONO2126-18	MH034146
IM-2009-14901	Clavatulidae	<i>Clavatula</i>	<i>taxea</i> (Röding, 1798)	ATIMO VATAE	Madagascar	CONO2122-18	MH034148
IM-2009-14968	Clavatulidae	<i>Clavatula</i>	<i>tripartita</i> (Weinkauff, 1876)	ATIMO VATAE	Madagascar	CONO2123-18	MH034149
IM-2009-17233	Clavatulidae	<i>Clionella</i>	<i>krausii</i> (E. A. Smith, 1877)	ATIMO VATAE	Madagascar	CONO2121-18	MH034144
IM-2009-24980	Clavatulidae	<i>Fusiturris</i>	<i>pluteata</i> (Reeve, 1843)	Port ZANAGA	Republic of the Congo	CONO2129-18	MH034151
IM-2007-17745	Clavatulidae	<i>Makiyamaia</i>	<i>mammillata</i> Kuroda, 1961	TAIWAN 2004	Taiwan	CONO530-08	MH034153
IM-2013-44508	Clavatulidae	<i>Makiyamaia</i>	sp.	NANHAI 2014	Taiwan	CONO2131-18	MH034152
IM-2009-26535	Clavatulidae	<i>Paraclavatula</i>	<i>delphinae</i> (Nolf, 2008)		Republic of the Congo	CONO2125-18	MH034147
IM-2007-17833	Clavatulidae	<i>Perrona</i>	<i>subspirata</i> Martens, 1902		Angola	CONO005-08	EU015641
IM-2007-17829	Clavatulidae	<i>Perrona</i>	<i>xanteni</i> (Nolf & Verstraeten, 2006)		Angola	CONO001-08	EU015637
IM-2007-17830	Clavatulidae	<i>Pusionella</i>	<i>compacta</i> Strebelt, 1914		Angola	CONO002-08	EU015638
IM-2007-17832	Clavatulidae	<i>Pusionella</i>	<i>nifat</i> (Bruguière, 1789)		Cameroon	CONO004-08	EU015640
IM-2007-17834	Clavatulidae	<i>Pusionella</i>	<i>vulpina</i> (Born, 1780)		Angola	CONO006-08	EU015642
IM-2009-24977	Clavatulidae	<i>Scaevatula</i>	<i>pellisserpentis</i> Gofas, 1990		Principe I.	CONO2127-18	MH034154
IM-2007-42294	Clavatulidae	<i>Tomellana</i>	<i>lineata</i> (Lamarck, 1816)		Angola	CONO532-08	MH034150
IM-2013-57344	Clavatulidae	<i>Turricula</i>	<i>javana</i> (Lamarck, 1816)		Vietnam	CONO2132-18	MH034156
IM-2007-17849	Clavatulidae?	<i>Gemmuloborsonia</i>	<i>colorata</i> (Sysoev & Bouchet, 2001)	EBISCO	Chesterfield Is	CONO192-08	EU015658
IM-2007-17920	Cochlespiridae	<i>Cochlespira</i>	<i>pulchella</i> (Schepman, 1913)	PANGLAO 2005	Philippines	CONO295-08	EU015720
IM-2007-17914	Conidae	<i>Conasprella</i>	<i>pagoda</i> (Kiener, 1847)	PANGLAO 2005	Philippines	CONO313-08	EU015729
IM-2007-17840	Horaiclavidae	<i>Horaiclavus</i>	<i>splendidus</i> (A. Adams, 1847)	EBISCO	Chesterfield Is	CONO183-08	EU015649
IM-2007-17754	Turridae	<i>Turris</i>	<i>babylonia</i> (Linnaeus, 1758)	PANGLAO 2004	Philippines	CONO226-08	EU015677
IM-2007-42448	Turridae	<i>Lucerapex</i>	<i>casearia</i> (Hedley & Petterd, 1906)	PANGLAO 2005	Philippines	CONO719-08	HQ401581

Science Gateway (MrBayes v. 3.2.2 on XSEDE; <http://www.phylo.org/portal2>). The three codon positions of the COI gene were treated as independent partitions and the substitution model was set to GTR + I + G; the parameters of the substitution model were evaluated independently for each partition during the analyses. Each of the two runs consisted of eight Markov chains and 10,000,000 generations, with five swaps at each generation, a sampling frequency of one tree each 1,000 generations and a chain temperature set at 0.02. Convergence of each analysis was evaluated using TRACER v. 1.4.1 (Rambaut & Drummond, 2014) to check that all effective sample size values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. Nodal support was assessed with posterior probability (PP) of each node.

Radulae were prepared using standard methods (Kantor & Puillandre, 2012) and investigated with a JEOL JSM 840A scanning electron microscope at the MNHN.

Institutional abbreviations

- MNHN Muséum National d'Histoire Naturelle, Paris
- NHMUK Natural History Museum, London
- RBINS Royal Belgian Institute of Natural Sciences, Brussels

RESULTS

The tree based on COI sequences is characterized by relatively low support of the nodes (Fig. 1). The family Clavatulidae, albeit monophyletic, is not statistically supported (PP = 0.86). Two species of the genus *Makiyamaia* Kuroda, 1961 are sister to a highly supported clade (PP = 1) that contains all other clavatulid species (except *Gemmuloborsonia*, the inclusion of which in the family is doubtful; Bouchet *et al.*, 2011). Most nodes within this clade are

unsupported. The genus *Clavatula* itself does not constitute a monophyletic group as the species attributed to it are scattered in three clades, two with high support (PP = 1; *C. taxea* + *C. tripartita*; *C. caerulea* + *C. pyramidata*) and one with low support (PP = 0.90; *C. regia* + *C. muricata*). Since the tree based on the single gene obviously cannot resolve relationships within the family, we refrain from any taxonomic decisions at the current stage. However the position of the new genus *Paraclavatula* within the Clavatulidae is supported.

SYSTEMATIC DESCRIPTIONS

Superfamily CONOIDEA Fleming, 1822

Family CLAVATULIDAE Gray, 1853

Paraclavatula n. gen.

Type species: Clavatula delphinae Nolf, 2008; here designated

Zoobank registration: urn:lsid:zoobank.org:act:C851F468-8B91-4C14-82ED-BD0190EC5CCB

Description: Shells of small to moderate size, between 10 and 30 mm, general shape rhomboid to oval. Protoconch smooth, of 2.5–3 whorls. Teleoconch of 6–8 whorls. Body whorl occupies from 1/2 to 2/3 of shell length (SL). Sculpture of usually oblique, flexuous axial ribs, 14–25 on last whorl, and numerous spirals cords, from 15 to 20, some more distinct, and strong subsutural cord nodulose at intersections with axials. Siphonal canal short, open; sinus U-shaped, on subsutural ramp; parietal callus usually lacking or very weakly developed. Colour from brownish to bluish or greyish, with variable darker brown and yellowish to white dots, blotches and/or flammules. Periostracum brown when fresh.

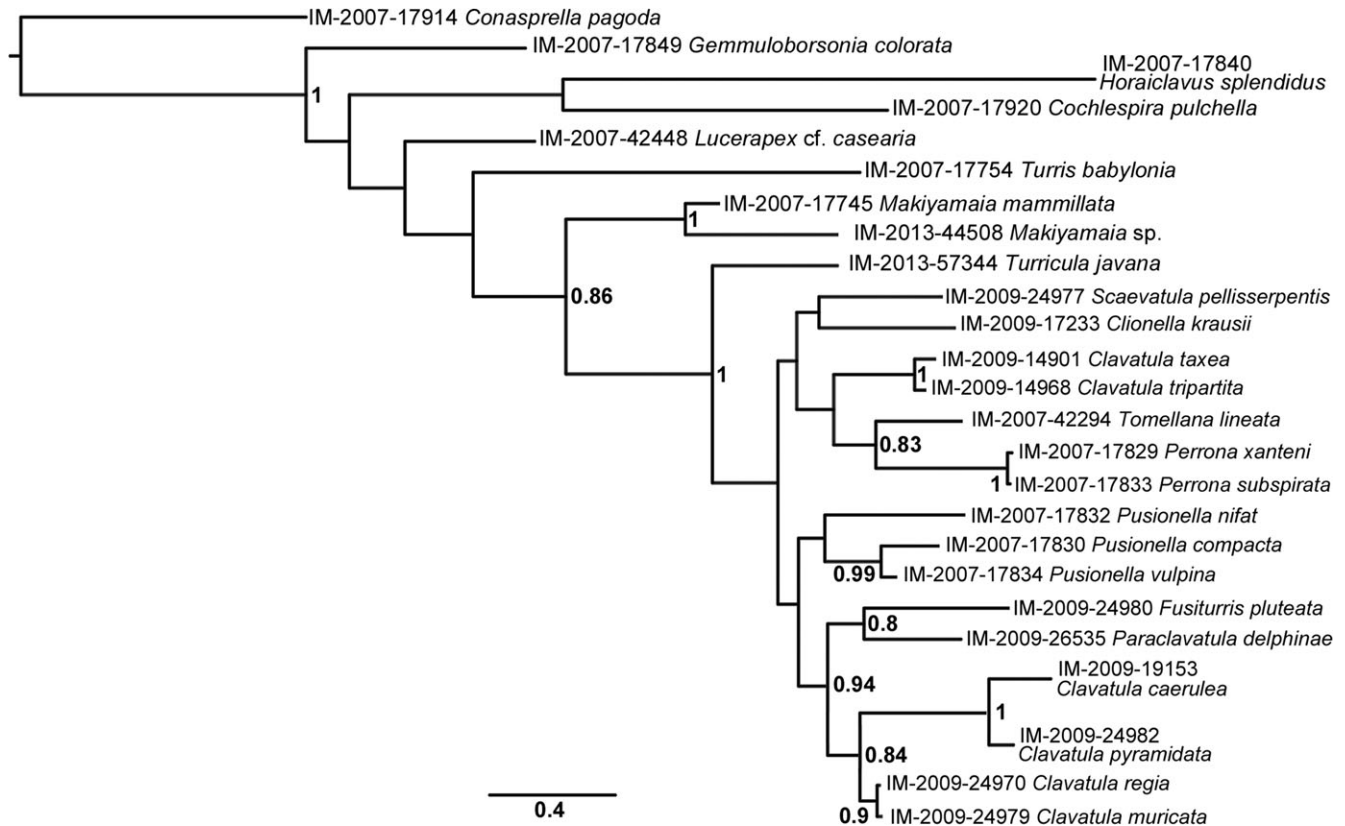


Figure 1. Bayesian phylogenetic tree obtained with partial COI sequences. Only posterior probabilities ≥ 0.80 are shown.

Radula with five teeth in transverse row; marginal teeth duplex with sharp-edged major limb and more or less pronounced socket where accessory limb is inserted. Accessory limb from large, about 2/3 of major limb length, to very small, vestigial, about 1/3 of major limb length (*P. delphinae*). Lateral teeth irregularly shaped, plate-like, with elevated posterior outer corner forming obtuse large cusp. Central teeth with strongly to moderately arcuate anterior margin, forming two or three elevated transverse ridges.

Included species: Three species, all originally described in *Clavatula*, are assigned to the new genus based on their similar radular type: *P. delphinae* (Nolf, 2008), the type species, *P. christiana* (Nolf, 2011) and *P. pseudomystica* (Nolf, 2008).

Besides the three species which we attribute to this genus, some others have recently been described as *Clavatula* that may belong to *Paraclavatula*, having similar shell characters and habitat, among them *C. congoensis* Nolf & Verstraeten, 2008 and *C. hattenbergeri* Nolf & Verstraeten, 2008. However, in the absence of data on radular morphology, we abstain from attributing those species to *Paraclavatula*.

Habitat and range: The species of the genus extend along the West African coast, from Ghana (and probably Senegal) to southern Angola. No records are known from islands in the Gulf of Guinea. They live in shallow water, from low tide to 10 m, usually in sandy mud, or under rocks and rock crevices.

Remarks: *Paraclavatula* differs from all other clavatulid genera in the presence of well-developed, plate-like and acusate lateral teeth, as well as in the acusate central teeth with elevated transverse ridges.

***Paraclavatula delphinae* (Nolf, 2008) n. comb.**
(Figs 2, 3, 6A)

Clavatula delphinae Nolf, 2008: 6–7, pl. I, figs 1–8, pl. II, figs 9, 10, 16 (holotype RBINS; Plage Koraf, Pointe-Noire, mouth of the Songolo River, Republic of the Congo, 4 m).

Material examined: Pointe-Noire, Republic of the Congo, stn CP505, 4°42.250' S, 11°47.000' E, 16–17 m, MNHN-IM-2009-26535, coll. A.Fedosov, 1 specimen (Fig. 2A–D)

The figured shell (of the sequenced specimen and from which a radula was extracted) came from the type locality. It is a somewhat atypical specimen, compared to the specimens illustrated by Nolf (2008), due to the presence of the dark blotches; it is not fully adult (the species reaches SL 16.3 mm), however it agrees in most features. F. Nolf kindly confirmed the identification.

Description: Protoconch: multispiral, first 2.75 whorls smooth, strongly convex, then 9 narrow but distinct arcuate axial ribs, occupying approximately half a whorl. Border with teleoconch indistinct, detected by slight changes in character of axial ribs, which become broader and less arcuate.

Anterior foregut: proboscis medium-long, conical. Proboscis retractors numerous, attached to rhynchodaeum in its posterior-most part. Buccal mass large, occupying posterior half of inverted proboscis, strongly protruding backwards. Oesophagus leaving buccal mass forming a short loop before passing through massive nerve ring. Salivary glands paired, acinous, small. Venom gland large, strongly convoluted, passing through nerve ring towards its opening posterior to radular sac. Radular sac relatively very large, situated at right side of buccal mass.

Radula (Figs 2E–H, 6A): duplex marginal teeth with sharp-edged major limb with flattened dorsolateral area, where vestigial minor limb (Fig. 2H) inserts; length of minor limb about 1/3 of

major limb. Lateral teeth irregularly shaped, narrowing towards rounded posterior margin. Posterior margin elevated in side view (Fig. 2G), producing blunt cusp. Central teeth in dorsal view heart-shaped, with notched anterior margin. Central part of tooth elevated in side view (Fig. 2G), producing blunt but broad triangular cusp.

***Paraclavatula pseudomystica* (Nolf, 2008) n. comb.**
(Fig. 4)

Clavatula pseudomystica Nolf, 2008: 7–8, pl. III, figs 17–21, pl. IV, figs 22–25 (holotype RBINS; Saco Mar, Namibe, southern Angola, in rock crevices, 3 m).

Material examined: Cacuaco Bay, Angola, 3 m, coll. J. Horro, 2 specimens.

The figured shell (Fig. 4A–C), from which a radula was extracted, has SL 18.3 mm. We believe it agrees with specific characters stated in the description of this species, particularly in that the, “...lower part of columella has a typical white blotch changing into dark brown on the parietal wall” (Nolf, 2008: 7).

Description: Protoconch (Fig. 4D): partially eroded, multispiral, of about 3 whorls, upper ones smooth and strongly convex, posterior-most part before transition to teleoconch with few narrow arcuate axial ribs.

Radula (Fig. 4E–H): duplex marginal teeth with sharp-edged major limb with rather deep socket in which relatively large accessory limb inserts; length of accessory limb about 2/3 of major limb. Lateral teeth irregularly trapeziform, with thickened anterior margin and shallowly notched posterior margin, which is elevated producing blunt outer cusp and narrower and more pointed inner cusp. Central teeth trapeziform in dorsal view, with shallowly notched anterior margin. Basal plate in side view (Fig. 4H) forming two transverse elevated ridges, one at anterior margin, another close to posterior margin, which is weakly irregularly serrated.

***Paraclavatula christiana* (Nolf, 2011) n. comb.**
(Fig. 5)

Clavatula christiana Nolf, 2011: 25–26, pl. I, figs 1–6, pl. II, figs 7–12, pl. III, figs 13–18 (holotype RBINS IG.31835; Cacuaco, Bengo Province, Angola, on intertidal rocks).

Material examined: Cacuaco Bay, Angola, from very low tide to 1 m, coll. J. Horro, 1 specimen (Fig. 5A–C, radula Fig. 5E–G); Sacomar, Angola, 2–5 m., coll. E. Rolán, 1 specimen (radula Fig. 5H).

The figured shell was taken from the type locality. Similar specimens from different locations from Ghana to Angola are also possession of one of authors (JH). Although the studied specimen differs from the photograph of the holotype in having a shorter siphonal canal, it falls within the intraspecific variability of the species as defined by Nolf (2011); its identification was confirmed by F. Nolf.

Description: Protoconch (Fig. 5D): multispiral, of about 3 whorls, upper ones smooth and weakly convex, posterior-most part before transition to teleoconch with few narrow arcuate axial ribs.

Radula (Fig. 5E–H): marginal teeth duplex, with sharp-edged major limb with pronounced socket in which relatively large accessory limb inserts; length of accessory limb about 2/3 of major limb. Lateral teeth irregularly trapeziform, with thickened anterior margin and nearly straight oblique posterior margin, which is elevated producing blunt outer cusp and narrower and more pointed

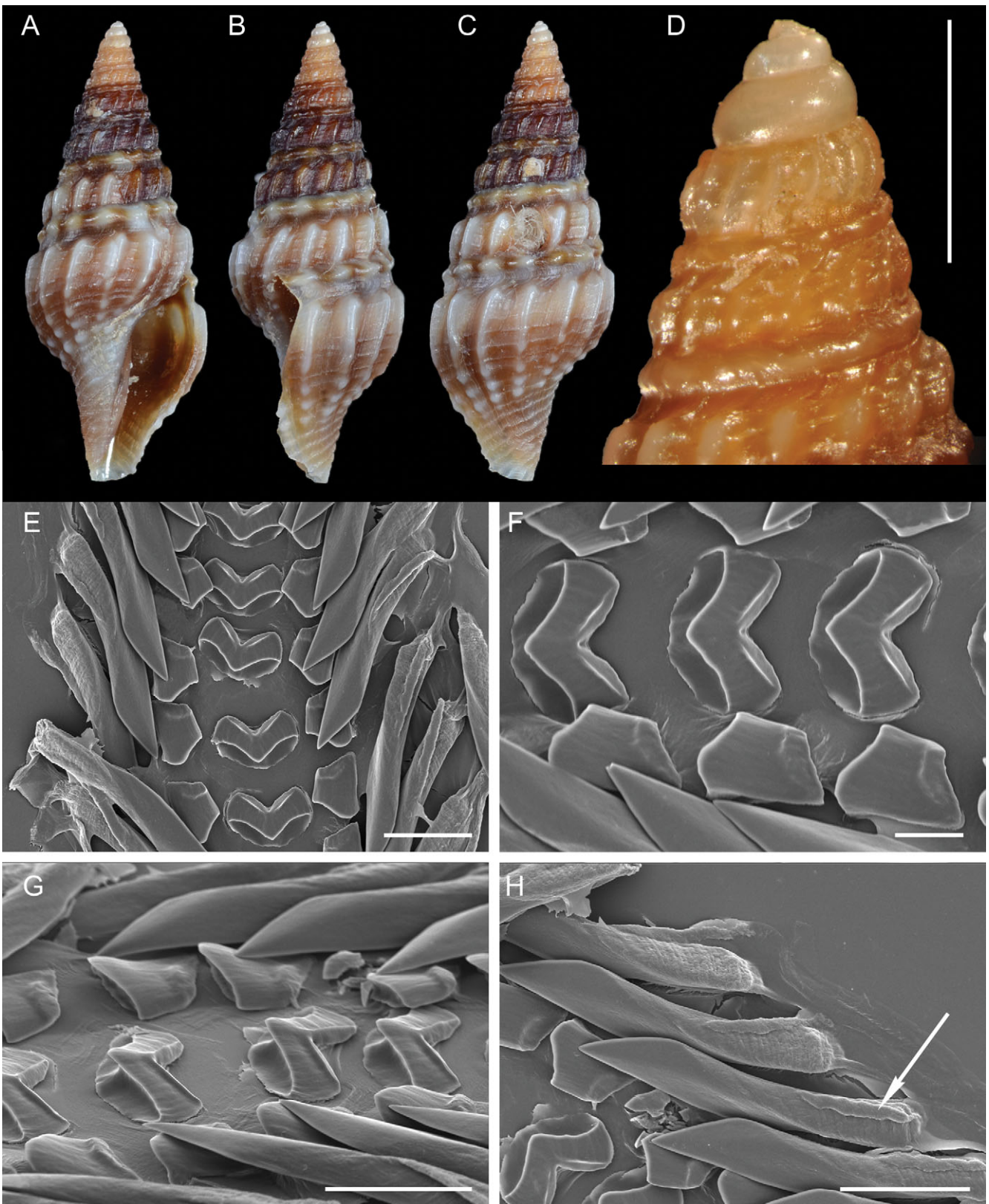


Figure 2. *Paraclavatulula delphinae* (Nolf, 2008), Pointe-Noire, Republic of the Congo (MNHN IM-2009-26535). **A–C.** Shell, SL 11.4 mm. **D.** Protoconch. **E–H.** Radula. **E.** Dorsal view of central part. **F.** Enlarged central portion. **G.** Lateral view of central portion. **H.** Enlarged marginal teeth; arrow marks accessory limb. Scale bars: **D** = 0.5 mm; **E, G, H** = 50 μm; **F** = 20 μm.

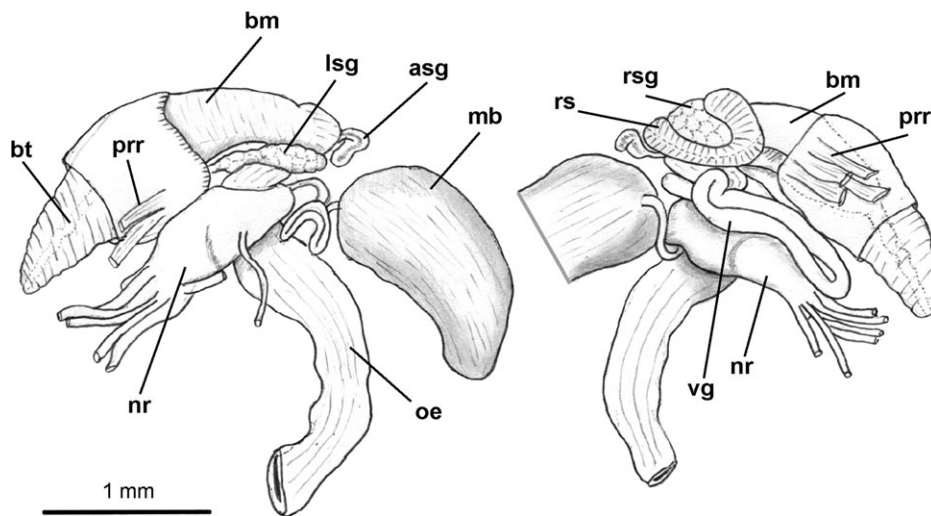


Figure 3. Left and right views of foregut of *Paraclavatula delphinae* (Nolf, 2008), Pointe-Noire, Republic of the Congo (MNHN IM-2009-26535). Abbreviations: asg, accessory salivary gland; bm, buccal mass; bt, buccal tube seen through proboscis wall; lsg, left salivary gland; mb, muscular bulb of the venom apparatus; nr, circumoesophageal nerve ring; oe, oesophagus; prr, proboscis retractors; rs, radular sac; rsg, right salivary gland; vg, venom gland.

inner cusp. Central teeth in dorsal view crescent shaped, with arcuate notched anterior margin. In side view (Fig. 5G) basal plate of central teeth forms three transverse parallel elevated arcuate ridges, on both anterior and posterior margins and in central part of tooth.

DISCUSSION

Powell (1966) considered the conoidean radula with five teeth in a transverse row as the ‘prototypic form’ confined to Drilliidae (as Clavinae). In this family of Conoidea, well-defined lateral teeth are arcuate, comb-shaped and multicuspid (Taylor, Kantor & Sysoev, 1993; Bouchet et al., 2011). The viewpoint of radular morphology in Drilliidae as ‘least derived’ was accepted also by Taylor et al. (1993). At the same time, it was suggested that in Turridae and Clavatulidae, usually with a broad central tooth, the ‘insubstantial, lateral ‘wings’ [of the central tooth] may represent vestiges of lateral teeth that have fused with the central tooth’ (Taylor et al., 1993: 135). Later, Taylor (1994: 195, pl. 5) illustrated the radula of *Turricula javana* (Clavatulidae) and commented that the broad central tooth may be formed by fusion of the plate-like lateral teeth with the smaller true central tooth. Finally, Kantor (2006) illustrated a number of different radular morphologies in Turridae s. s. and concluded that, in this family, the ‘central tooth’ is also formed by complete or incomplete fusion of central and plate-like lateral teeth. The term ‘central formation’ was proposed for this composite structure. to distinguish it from the true central tooth. The homology of the elements of the central portion of the radula in Conoidea is not always easy to establish. In Cochlespiridae there is no evidence that the central tooth is a composite structure (Bouchet et al., 2011: fig. 12).

Nevertheless, in addition to Drilliidae, *Paraclavatula* is the second case among the Conoidea of a radula having five well defined separate teeth in a transverse row.

The radulae of the species assigned to *Paraclavatula* are unique for Clavatulidae and Conoidea in general. In Clavatulidae, the central formation is variously developed, sometimes appearing as a pronounced tooth (e.g. *Turricula nelliae*, Fig. 6C), sometimes it looks like three incompletely fused elements (*Clionella sinuata*; Taylor et al. 1993: fig. 18A, B; *Tomellana lineata*, Fig. 6B). In some clavatulids the central formation is very reduced and is probably represented

by a central tooth alone (*Perrona xanteni*, Fig. 6D). Finally it may be nearly completely reduced (*Pusionella compacta*, Bouchet et al., 2011: fig. 18C). On the contrary, in *Paraclavatula* central and lateral teeth are completely separate; the lateral teeth are very well defined, rather broadly spaced and of a strange trapeziform shape without distinct cusps. Somewhat similar lateral teeth were found only in some species of *Turridrupa* (Turridae; Kantor, 2006: fig. 4C, D, as *Turridrupa* n. sp.), but they are less defined, with an inner margin fused to the radular membrane, while the central teeth are narrowly cuspidate. In *Paraclavatula* all sides of the lateral teeth are well defined and the central tooth has a very different morphology. These two families, Clavatulidae and Turridae, are not closely related as demonstrated by molecular phylogeny (Puillandre et al., 2011). Thus, the similarity between the shape of the lateral teeth in *Paraclavatula* and *Turridrupa* is superficial.

The central tooth of *Paraclavatula* is very different from that in other Conoidea. The central tooth in other Conoidea, when present, is always narrow, monocuspid and with a pointed cusp. In *Paraclavatula*, although being variable in shape, the central tooth is plate-like, broad, cusplless and with two or three characteristic elevated transversal ridges. So far, the central tooth of *Paraclavatula* can be considered a synapomorphy of the genus. The radula of *Paraclavatula* is unique in the shape not only of the central, but of the lateral teeth as well, since such well defined plate-like laterals with an elevated posterior margin have not been recorded either in Clavatulidae or in Conoidea. The discovery of another group of Conoidea (in addition to Drilliidae) with five well defined teeth in a transverse radular row is evidence that this condition is more broadly distributed within Conoidea than previously anticipated.

The radular morphology is widely used in the taxonomy of Conoidea (as well as other Neogastropoda), since in many demonstrated cases the shell characters are not sufficient for revealing relationships and the radula is usually a good morphological proxy for taxonomic decisions, at least at the family level. Nevertheless, in case of a very unusual or unique radula its morphology is not sufficient for attribution. For example, the genus *Strictispira* was assigned to its own family Strictispiridae based on an unusual radula and foregut anatomy (Taylor et al., 1993; Puillandre et al., 2011), but molecular phylogenetic analysis has recently placed the genus in Pseudomelatomidae (N. Puillandre, unpublished).

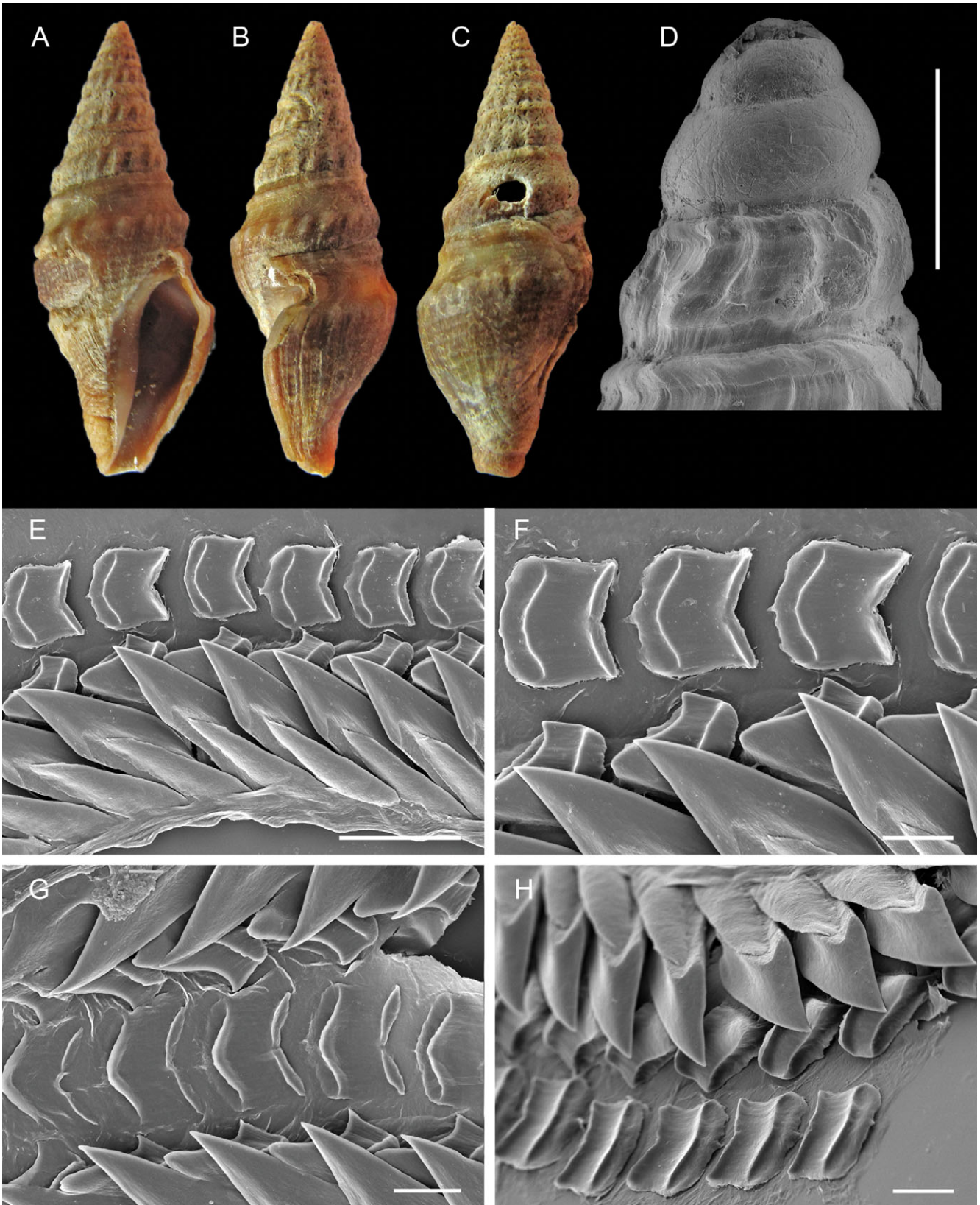


Figure 4. *Paraclavatula pseudomystica* (Nolf, 2008), Cacuaco Bay, Angola (collection of J. Horro). **A–C.** Shell, SL 18.3 mm. **D.** Protoconch. **E–H.** Radula. **E.** Dorsal view of the central part. **F.** Enlarged central portion. **G.** Developing posterior part. **H.** Enlarged marginal teeth, lateral view of central portion. Scale bars: **D** = 0.5 mm; **E** = 50 μ m; **F, G, H** = 20 μ m.

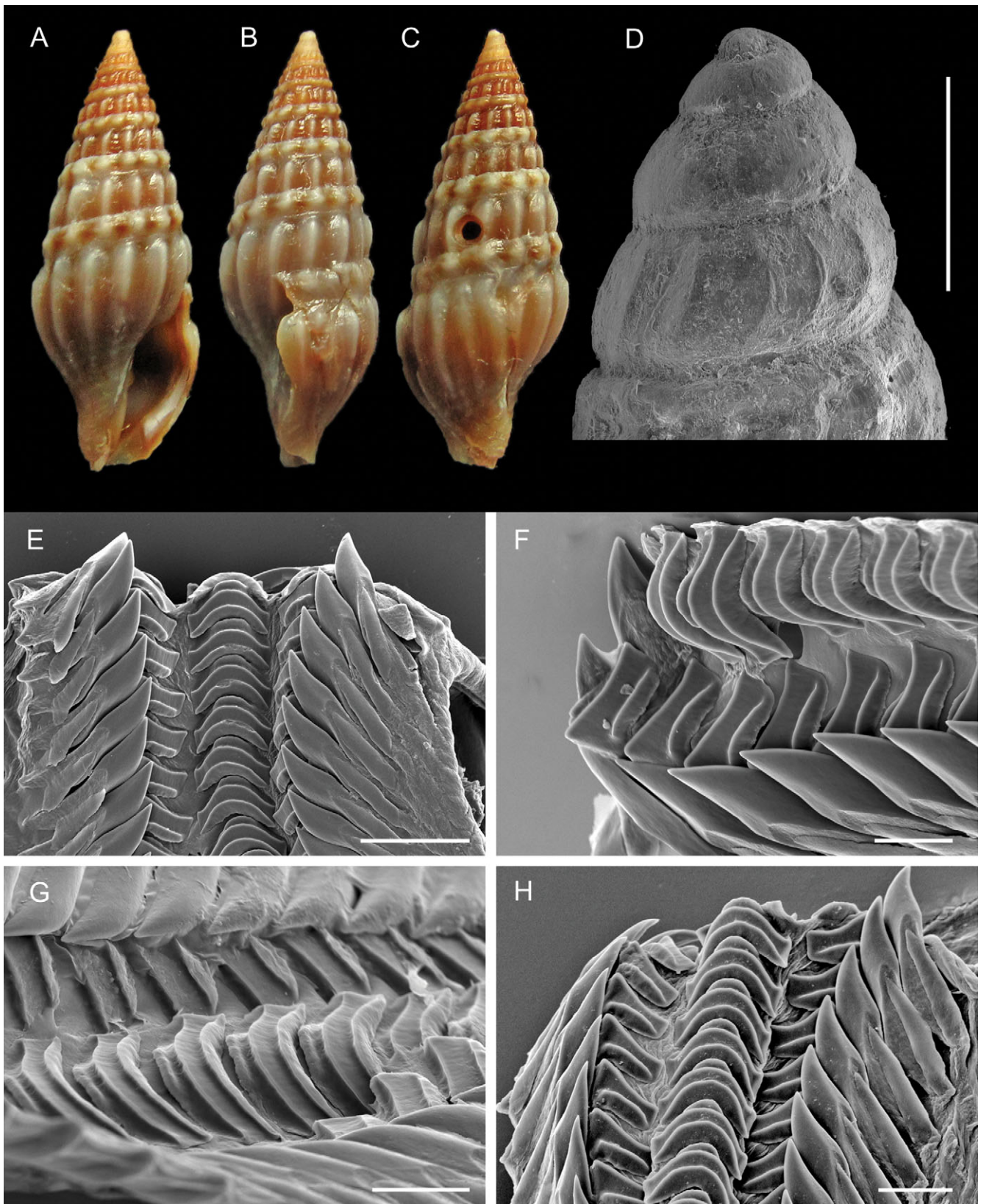


Figure 5. *Paraclavatula christiana* (Nolf, 2011), **E–G.** Cacuaco Bay, Angola (collection of J. Horro). **H.** Sacomar, Angola (collection of J. Horro). **A–C.** Shell, SL 14.6 mm. **D.** Protoconch. **E–H.** Radulae. **E.** Dorsal view of bending plane. **F.** Enlarged central portion. **G.** Lateral view of central portion. **H.** Anterior part. Scale bars: **D** = 0.5 mm; **E** = 50 μ m; **F, G, H** = 20 μ m.

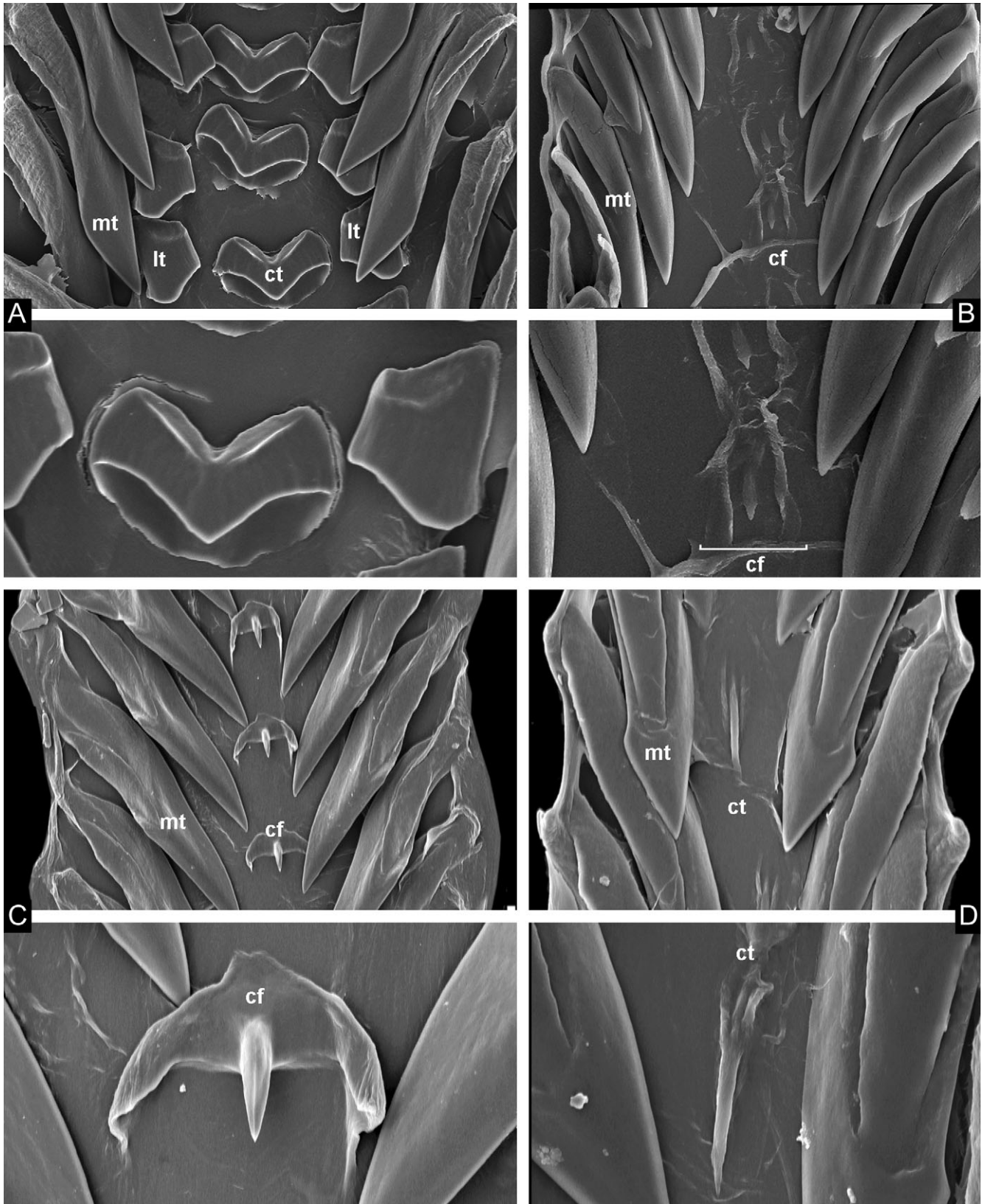


Figure 6. Comparative morphology of radulae of Clavatulidae. For each species, upper panel shows dorsal view of entire transverse radula row, lower panel the enlarged central portion. **A.** *Paraclavatulata delphinae* (Nolf, 2008), Pointe-Noire, Republic of the Congo (MNHN IM-2009-26535). **B.** *Tomellana lineata* (Lamarck, 1818), Pointe-Noire (Port ZANAGA stn CP510), Republic of the Congo (MNHN uncatalogued). **C.** *Turricula nelliae* (E.A. Smith, 1877), Danang, Vietnam (NHMUK MOEA 20100551). **D.** *Perrona xanteni* (Nolf & Verstraeten, 2006), Loanda I., Angola (MNHN IM-2007-17829). Abbreviations: cf, central formation; ct, central tooth; lt, lateral tooth; mt, marginal tooth.

Similarly, inclusion of *Paraclavatula* in Clavatulidae would have been difficult on the basis of the radula alone and required confirmation by molecular analysis.

ACKNOWLEDGEMENTS

We would like to thank Peter Ryall (Maria Rain, Austria) for sharing material and opinions about described species, and Frank Nolf for his help in identification.

The material in this paper originates from several shore-based expeditions and deep-sea cruises, conducted respectively by MNHN and Pro-Natura International (PNI) as part of the Our Planet Reviewed programme (ATIMO VATAE) and/or by MNHN and Institut de Recherche pour le Développement (IRD) as part of the Tropical Deep-Sea Benthos programme (TAIWAN 2004, NANHAI 2014, EBISCO). Scientific partners included the Université de Tuléar, Madagascar, and the Madagascar bureau of the Wildlife Conservation Society (WCS). Additional fieldwork included PANGLAO 2004 and 2005 (Joint Projects of MNHN, University of San Carlos, Cebu City, and the Philippines Bureau of Fisheries and Aquatic Research). Special thanks to Bernard Thomassin, who invited Alexander Fedosov to participate in the Port ZANAGA field survey and to A. Fedosov himself, who collected the sequenced material during this survey. All expeditions operated under the regulations then in force in the countries in question and satisfy the conditions set by the Nagoya Protocol for access to genetic resources.

We thank, among others, Virginie Héros, Philippe Maestrati and Barbara Buge for their role in specimen processing during the expeditions and for their help in curating the specimens. We gratefully acknowledge two anonymous referees for their corrections and suggestions, which improved the manuscript. This project was partly supported by the Service de Systématique Moléculaire [UMS 2700 CNRS (Centre national de la recherche scientifique) -MNHN], the bilateral cooperation research funding from the Ministry of Science and Technology, Taiwan (grant number MOST 102-2923-B-002-001-MY3) and the French Agence Nationale de la Recherche (ANR) (grant number ANR 12-ISV7-0005-01) and by the CONOTAX project funded by the French ANR (grant number ANR-13-JSV7-0013-01). The contribution of Y.I. Kantor was funded by grant no. 16-14-10118 from the Russian Science Foundation.

And it is always a pleasure to deal with the friendly and meticulous editors of the Journal.

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