

TOXOGLOSSAN GASTROPODS OF THE SUBFAMILY CRASSISPIRINAE (TURRIDAE) LACKING A RADULA, AND A DISCUSSION OF THE STATUS OF THE SUBFAMILY ZEMACIINAE

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ABSTRACT

Two new species of *Horaiclavus*, lacking radula, venom gland and proboscis, are described. The genus is placed in the subfamily Crassispirinae (Turridae). Both species possess a peculiar foregut structure, the muscular rhynchodaeal outgrowth situated in the rhynchocoel. The possible function of the rhynchodaeal outgrowth is discussed. Other studied species of *Horaiclavus* possess a radula of a typical 'crassispirine' type but lack the outgrowth. The anatomy of the foregut of the new species is superficially similar to that of *Zemacies excelsa* (Turridae: Zemaciinae), which also possesses an additional structure of the rhynchocoel, namely the 'pyriform gland'. Conchologically, there is no resemblance between *Zemacies* and *Horaiclavus* and it is concluded that similar foregut arrangement appeared independently in both lineages. A new monotypic subfamily Zemaciinae was erected mostly on the basis of the unique foregut arrangement of *Zemacies excelsa*. We express doubts concerning the importance of these characters in establishing a new taxon of subfamilial rank and therefore the validity of the subfamily Zemaciinae.

INTRODUCTION

The crucial stage in the evolution of the neogastropod superfamily Conoidea was probably the origin of the unique feeding mechanism whereby single radular marginal teeth are held at the end of the proboscis for stabbing and envenomation of prey (Taylor, Kantor & Sysoev, 1993). This development led to transformations of both radular (e.g. reduction of the subradular membrane, origin of the hollow marginal teeth) and foregut morphology.

By contrast, a remarkable tendency to complete loss of the radula has been documented in several lineages of 'higher' Conoidea (subfamilies Raphitomininae and Mangeliinae of Conidae) and in Terebridae (Taylor *et al.*, 1993; Oliverio, 1995; Kantor & Taylor, 2002). Usually, loss of the radula is accompanied by reduction of other foregut organs, leading to complete loss of proboscis, venom apparatus and salivary glands.

Within the family Turridae loss of the radula is very rare and presently known only in a single species, *Zemacies excelsa* Sysoev & Bouchet, 2001, that lacks both radula and venom apparatus (Medinskaya & Sysoev, 2003). A most unusual character of the foregut anatomy in *Z. excelsa* is the presence of the so-called 'pyriform gland', a distinct glandular structure, located at the ventral wall of the rhynchocoel. The pyriform gland resembles a 'hollow flask', opening into the rhynchocoel and containing a muscular bulb, covered by folded glandular epithelium. Homologies and function of this structure are unclear, but a glandular function has been suggested. Based on the presence of this unusual character in *Z. excelsa*, a new nominotypical subfamily Zemaciinae Sysoev, 2003 was erected (Medinskaya & Sysoev, 2003). However, it was mentioned that conchologically Zemaciinae is most similar to species classified in the subfamily Cochlespirinae (Turridae).

Until now the foregut morphology of *Z. excelsa* was considered to be unique. Moreover, no other representatives of Turridae lacking a radula were known.

A vast quantity of conoidean gastropods has been collected by recent expeditions exploring the New Caledonia area and is housed in the Muséum National d'Histoire Naturelle, Paris (MNHN). While examining the radular morphology of a number of turrids, several species (all still unnamed), tentatively placed in the genus *Horaiclavus* Oyama, 1954, were found to lack the radula, while seven other undoubtedly congeneric species possessed a radula. For two of the radular-less species preserved material suitable for anatomical studies was available.

These two still unnamed species are described by A.V. Sysoev in the appendix to this paper. Examination of the foregut anatomy of these species (*Horaiclavus phaeocercus* Sysoev, n. sp. and *Horaiclavus anaimus* Sysoev, n. sp.) showed a close similarity to the foregut of *Zemacies excelsa*, particularly in the presence of a structure similar to the 'pyriform gland'.

In this paper we describe the foregut anatomy of the two species of *Horaiclavus* lacking a radula and compare them with *Zemacies excelsa*.

MATERIAL AND METHODS

Material for this study was collected from bathyal depths off the southern coast of New Caledonia. One paratype of *Horaiclavus phaeocercus* from the type locality (BIOCAL, stn DW44, 22°47'S, 167°14'E, 440–450 m, 30.08.1985) (Fig. 5D) and one paratype of *Horaiclavus anaimus* (BATHUS 2, stn DW739, 22°35'S, 166°27'E, 465–525 m, 14.05.1993) (Fig. 5K) were examined anatomically. Due to the small size of the specimens, their foregut anatomy was studied by serial longitudinal sections of the anterior part of the body.

For histological preparations, the bodies were dehydrated and embedded in paraplast; subsequently, serial sections were cut at 7 µm thickness and stained with Masson's trichrome.

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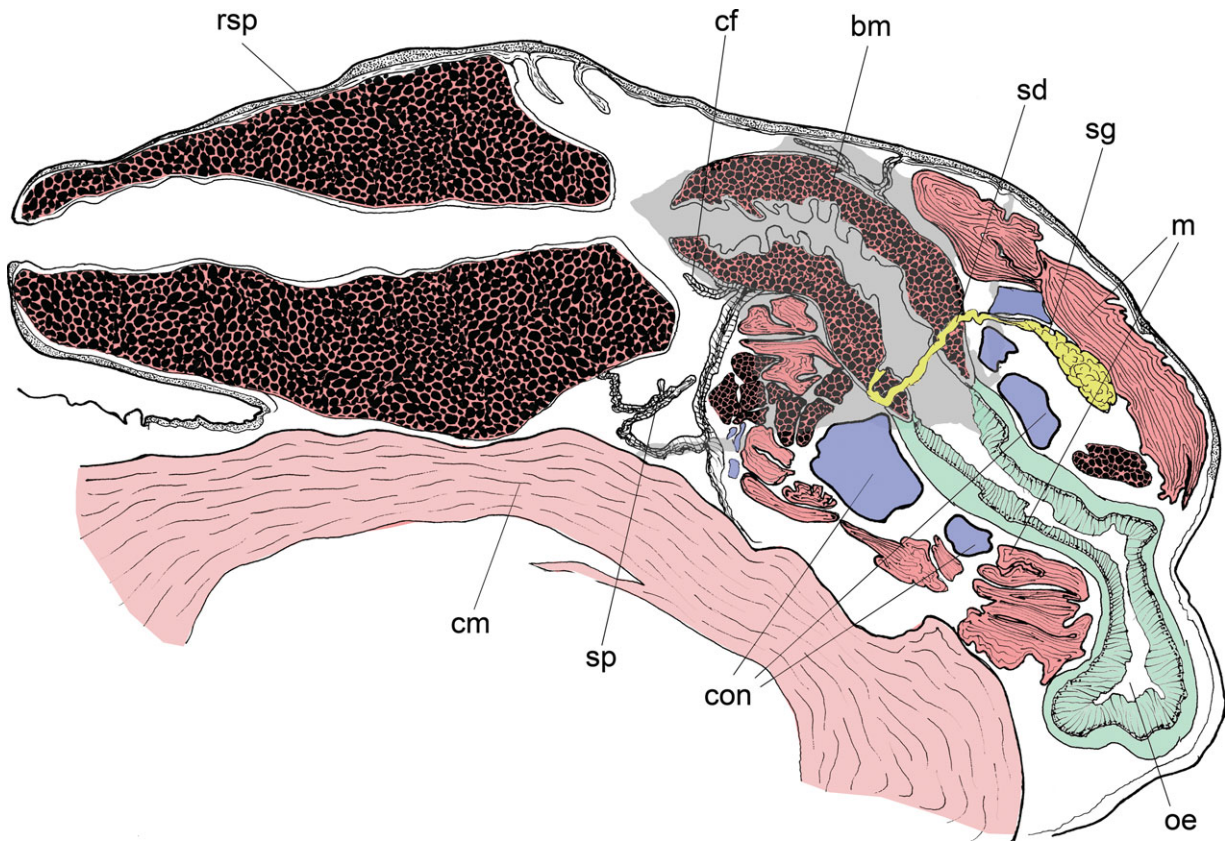


Figure 1. *Horaiclavus phaeocercus* n. sp. Semidiagrammatic longitudinal section of the foregut. Position of the rhynchodaeal outgrowth shown by gray colour. Abbreviations: bm, buccal mass; cf, circular fold surrounding the buccal mass; cm, columellar muscle; con, circumoesophageal nerve ring; m, retractor muscles of rhynchodaeal outgrowth; oe, oesophagus; rsp, rhynchostomal sphincter; sd, salivary duct; sg, salivary gland; sp, septum.

RESULTS

Foregut anatomy of Horaiclavus phaeocercus n. sp.

The rhynchostomal sphincter is extremely large, as long as the rhynchocoel (Fig. 1). The rhynchocoel is partitioned by two rhynchodaeal septa, which are located close to each other just behind the rhynchostomal sphincter. The septa are thin, with large orifices, around 3/4 of the rhynchocoel width. In the ventral part the septa are fused, so that in most sections they appear single, while they remain always separate on the dorsal surface of the rhynchodaeum.

The rhynchocoel is lined by an epithelium formed by cubic or rectangular cells, and obviously non-secretory. The epithelium of the rhynchocoel anterior to the septa is underlined by a medium-thin layer of muscle fibres, which becomes much thinner posterior to the septum, especially in the dorsal part.

The muscular buccal mass opens directly into the rhynchocoel, strongly protruding into the cavity (Figs 1, 2A – bm). The anterior part of the buccal mass is surrounded by thin epithelial fold (Figs 1, 2A – cf), which may represent the remnant of a highly reduced proboscis. It is difficult to establish its homology, since even detailed examination of fine structure of this fold did not reveal any additional characters.

The buccal mass is long, with thick muscular walls and a narrow lumen. The inner walls of the buccal mass form numerous longitudinal folds. The circum-oesophageal nerve ring (Fig. 1 – con) is positioned at the border between the buccal mass and anterior oesophagus. The oesophagus (Fig. 1 – oe) lacks the loop. Paired salivary ducts (Fig. 1 – sd) open laterally into the anterior part of the buccal mass. These are short, not

convoluted, with the inner epithelium formed by ciliated cells. Salivary glands are compact and acinous (Fig. 1 – sg). Both the radular apparatus and venom gland are entirely absent.

The ventral right wall of the rhynchodaeum forms a massive tongue-shape outgrowth (Fig. 2B, C – ro) that occupies the right half of the rhynchocoel. The surface of this outgrowth is covered by a uniform columnar epithelium forming numerous circular folds and consisting of cells with large, intensely coloured nuclei, and a cytoplasm devoid of any inclusions, granular structures or vesicles. This epithelium is underlain by thin, but well developed, layers of circular and longitudinal muscle fibres, exceeding in thickness the muscle layer in the rest of the rhynchodaeum. The entire lumen of the outgrowth, which is confluent with the cephalic haemocoel, is filled by numerous thick muscles, attached to its walls and following to the cephalic haemocoel. These muscles are long, winding, and fill most of cephalic haemocoel. In longitudinal sections they were sectioned at varying angles, so they may appear oblique or transverse. The majority of muscles traced are attached to the lateral walls of the cephalic haemocoel.

The foregut of *Horaiclavus anaimus* n. sp. (Fig. 2D–F), is nearly identical to that of *Horaiclavus phaeocercus*. Some insignificant differences are: a smaller rhynchodaeal septum (Fig. 2F – sp), and slightly different shape of the buccal mass. In *H. anaimus* the buccal mass has thinner walls and forms a noticeable circular fold in its middle part (Fig. 2D). Also, there are some differences in the position of the rhynchodaeal outgrowth. In *H. phaeocercus* it is contracted and located wholly on the right side of the buccal mass, while in *H. anaimus* it is extended and curved, so that its distal part lies in front of the buccal mass.

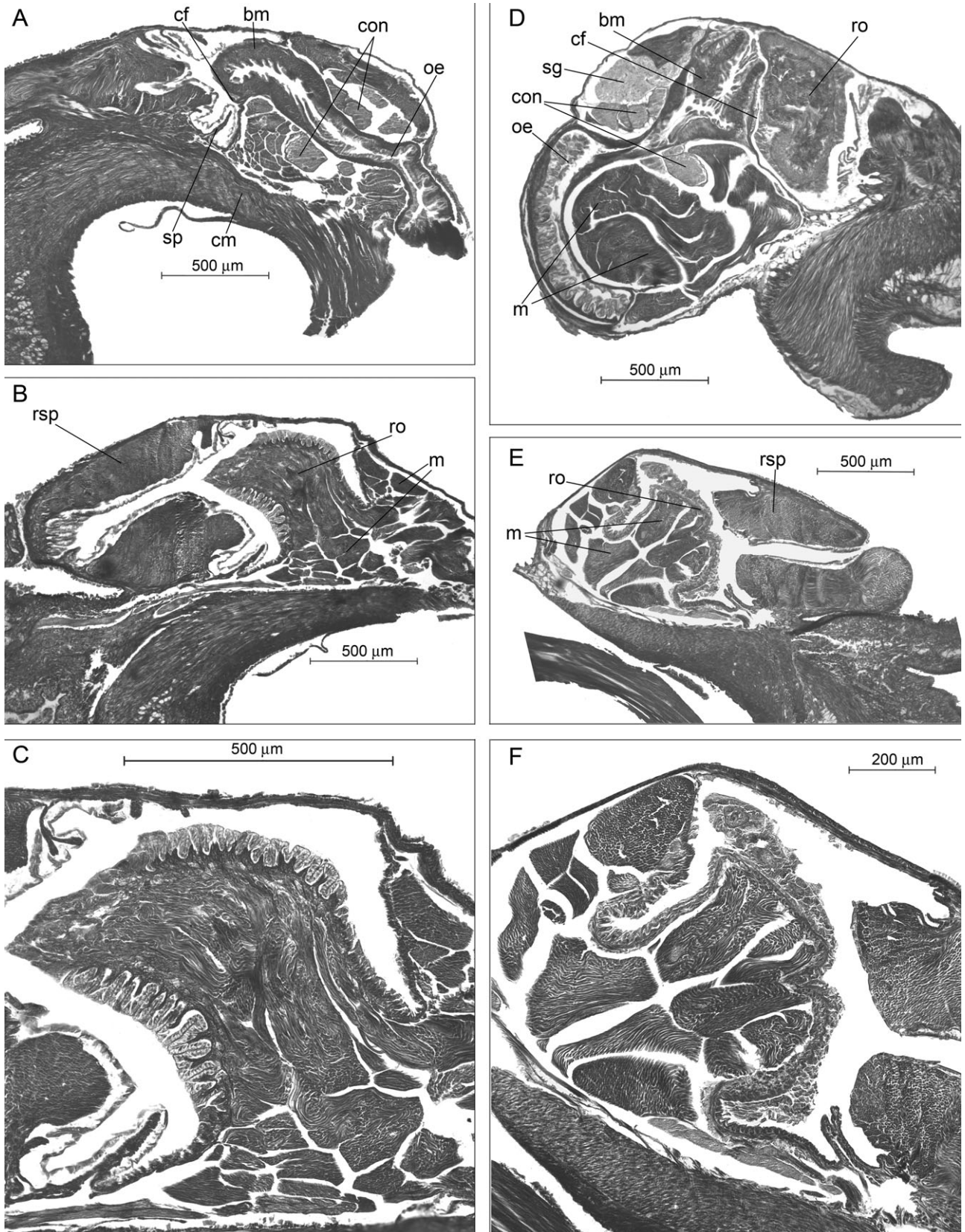


Figure 2. Histological sections of the anterior part of the digestive system. **A–C.** *Horiaclavus phaeocercus*. **A.** Section through the buccal mass and oesophagus. **B. C.** Sections through the rhynchodaeal outgrowth. **D–F.** *Horiaclavus anaimus*. **D.** Section through the buccal mass and oesophagus. **E, F.** Sections through the rhynchodaeal outgrowth. Abbreviation: ro, rhynchodaeal outgrowth, other abbreviations as in Figure 1.

It is possible that most of the observed differences (especially the relative length of the outgrowth) are the results of preservation artifacts.

DISCUSSION

Possible function of rhynchodaeal outgrowth of Horaiclavus

The morphology of the outgrowth, with its combination of muscles in the wall and large muscles filling the lumen of the outgrowth suggests a function as a muscular hydrostat, similar to a typical proboscis. Contraction of circular muscles in the wall should cause a decrease in diameter and elongation of the outgrowth. The large muscles most probable act as retractors and their contraction should lead to shortening and widening of the outgrowth. The structure of the epithelium, covering this rhynchodaeal outgrowth suggests capacity for considerable extension. It is highly possible that the outgrowth is capable of protrusion through the rhynchostome.

The epithelium of the rhynchodaeal outgrowth does not contain any identifiable secretory cells and, as there are no glands connected to it, we conclude that secretory functions are unlikely for this organ. Therefore it is logical to suggest that a mechanical function is likely for this structure. Unfortunately, there is no information on the diet of any species of *Horaiclavus* (due to very limited material). If these radula-less species feed on animals with a rigid cuticle or shell, then the

rhynchodaeal outgrowth could possibly act as pestle to crush integumental structures prior to swallowing. Additionally, the huge rhynchostomal sphincter may hold the prey, facilitating its destruction. Preliminary crushing of prey allows more rapid digestion, making prey tissues accessible to digestive enzymes.

Taxonomic position of Horaiclavus Oyama, 1954 and newly described species within Conoidea

The taxonomic position of the genus *Horaiclavus* Oyama, 1954 (type species by original designation *Mangilia splendida* A. Adams, 1867; Fig. 3B) has been uncertain. Powell (1966) hesitated in attributing it to Turridae and considered the possibility of placement in Buccinidae. Later the genus was classified within Drilliidae (Sysoev, 1993, 1996; Higo, Callomon & Goto, 1999). Recently, the junior author examined the radula of *Horaiclavus splendidus* and its morphology (Fig. 3A) undoubtedly places the genus within the turrid subfamily Crassispirinae McLean, 1971. Distinguishing characters include the absence of the central tooth, and long and relatively narrow marginal teeth, with small, narrow accessory limbs.

The two new species described here lack a radula and possess a very specialized morphology of the foregut, comparable only with *Zemacies excelsa* and therefore their taxonomic position is ambiguous.

Here (Appendix) they are conditionally assigned to the genus *Horaicavus*. Nevertheless, the junior author examined several other species of this group (all still unnamed) (Fig. 3D), on

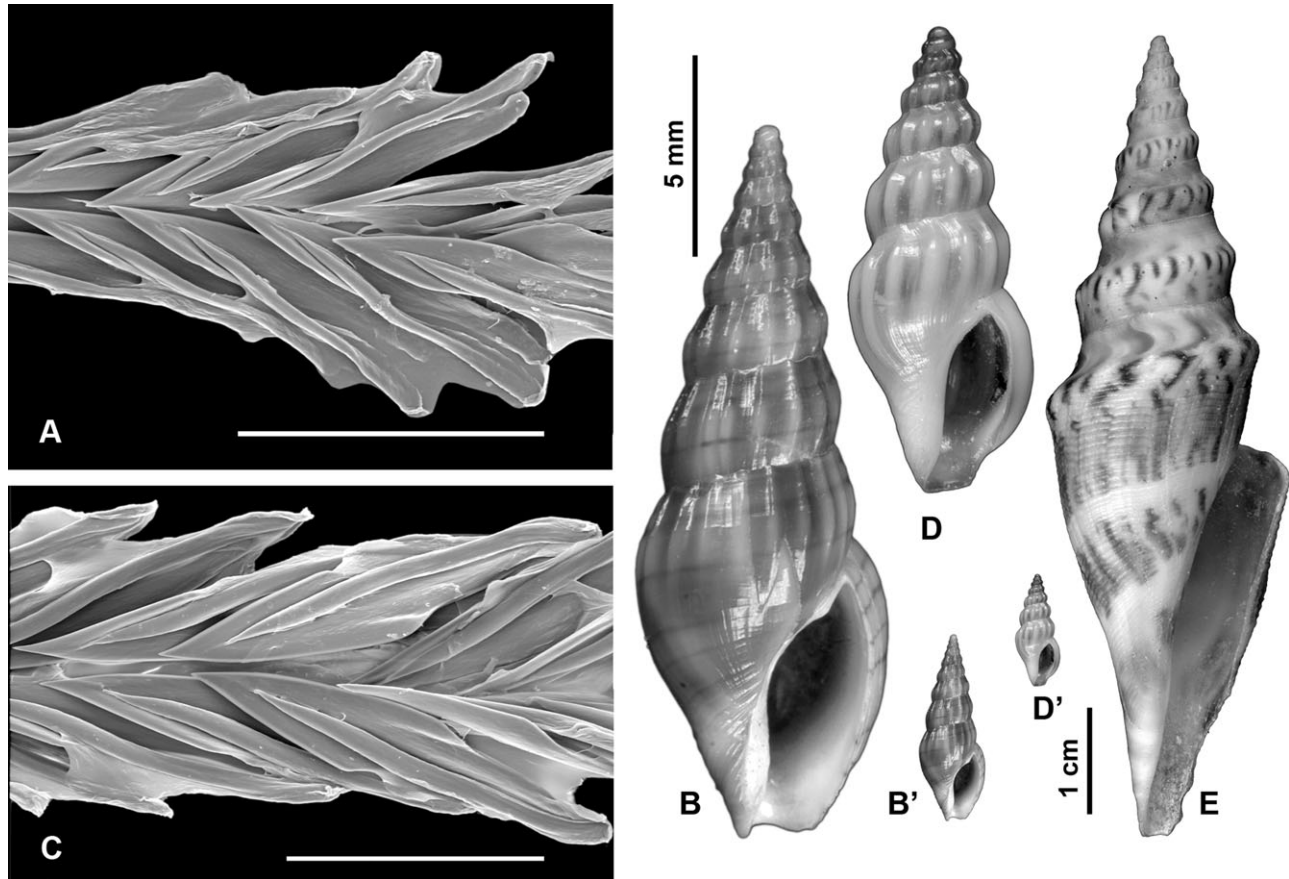


Figure 3. A–B. *Horaiclavus splendidus* (A. Adams, 1867): **A.** Dorsal view of the radula. **B, B'.** southern Vanuatu, VOLSMAR stn DW59, 21°00'S, 170°17'E, 320 m, shell length 17.6 mm. **C, D.** *Horaiclavus* sp., one of still unnamed species of *Horaiclavus*, closely related to studied species, New Caledonia. BIOCAL stn DW44, 22°47'S, 167°14'E, 440–450 m, shell length 11.6 mm. **C.** Dorsal view of the radula. **D, D'.** shell. **E.** *Zemacies excelsa* Sysoev & Bouchet, 2001, holotype (MNHN) shell length 74.8 mm. Scale bars: **A, C** = 100 μ m; **B, D** at same scale; **B', D', E** at same scale.

shell features extremely similar to two species treated here (compare Fig. 5 with Fig. 3D) and there is little doubt that they are congeneric with *Horaiclavus phaeocercus* n. sp. and *Horaiclavus anaimus* n. sp. Some of the studied species possess a radula very similar to that of *H. splendidus* (Fig. 3C). This evidence would place these new species (even if they belong to a new genus) into Crassispirinae.

The anatomy of two radulate species of *Horaiclavus* (*H. splendidus* and *Horaiclavus* sp., shell in Fig. 3D) has been examined by dissection. Both species possess ‘normal’ foregut anatomy, having proboscis, venom and salivary glands, but lack the rhynchodaeal outgrowth.

Comparison of Horaiclavus Oyama, 1954 with other Crassispirinae and Turridae

The diversity of foregut configurations within the Crassispirinae has been studied by Kantor, Medinskaya & Taylor (1997), where the high morphological disparity allowed identification of 13 different types. Some foregut organs in Crassispirinae are prone to variation, while others are similar in all species studied. The proboscis in particular appears to be very variable, in contrast to the conservative structure of the venom gland.

A proboscis is well developed in the majority of investigated Crassispirinae species, but in some a reduction of size and structural simplification was observed. However, no Crassispirinae species was found without proboscis, other than the radular-less species. Thus, the foregut morphology of the two *Horaiclavus* species described here is so far unique in Crassispirinae, since it is characterized by complete loss of the radula, proboscis and venom apparatus. Loss of these organs is accompanied by development of a very large rhynchostomal sphincter and rhynchodaeal outgrowth. This enigmatic, highly muscular outgrowth on the right-ventral side of the rhynchodaeum is the most unusual foregut structure in both species of *Horaiclavus*.

Several cases of somewhat similar structures have been described in representatives of two unrelated clades of Conoidea:

the accessory proboscis structure (APS) in some species of Terebridae (Taylor, 1990; Taylor & Miller, 1990) and the pyriform gland in *Zemacies excelsa* of the subfamily Zemaciinae (Turridae) (Medinskaya & Sysoev, 2003).

The APS has been recorded in a number of Terebridae and consists of a very long and narrow, sometimes branching outgrowth [*Hastula bacillus* (Deshayes, 1859) – Taylor & Miller, 1990]. It was found both in radular-less (e.g. *Terebra affinis* Gray, 1834) and radulate species (e.g. *Hastula bacillus*). Morphologically, it is rather different from the outgrowth found in *Horaiclavus*. It is much less muscular with a few thin and short muscles leaving the APS to fuse with the walls of the body haemocoel.

The foregut anatomy of *Zemacies excelsa* is very similar to that of both species of *Horaiclavus*. The common characters are complete loss of radula, venom apparatus and proboscis, and a massive buccal mass that opens directly to the rhynchocoel and is surrounded by circular fold. This semitransparent fold was believed to be the remnant of highly reduced proboscis in *Zemacies* (Medinskaya & Sysoev, 2003). Both species of *Horaiclavus* and *Z. excelsa* possess a large rhynchostomal sphincter, and salivary gland(s) (single in *Zemacies*), which is unusual in species lacking radula and venom apparatus.

At the first sight, the pyriform gland of *Z. excelsa* (Fig. 4) has little in common with the rhynchodaeal outgrowth of *Horaiclavus*. The pyriform gland represents a large flask of pyriform shape, hollow inside, lying on the distal surface of the rhynchodaeum (Medinskaya & Sysoev, 2003). Its cavity communicates with the rhynchocoel through a large opening, and bears a bulb-like structure covered by small tentacles with a folded surface on its base. The inner cavity of this bulb contains a well-developed system of muscles, which are attached mainly to the apical part of the structure (Fig. 4B). Nevertheless, comparison of the rhynchodaeal outgrowth of *Horaiclavus* and the bulb-like structure situated inside the pyriform gland of *Z. excelsa*, shows their similarity in morphology. Both have a roughly conical shape and complex system of muscles that leave the inner cavity of the organ and fill a significant part

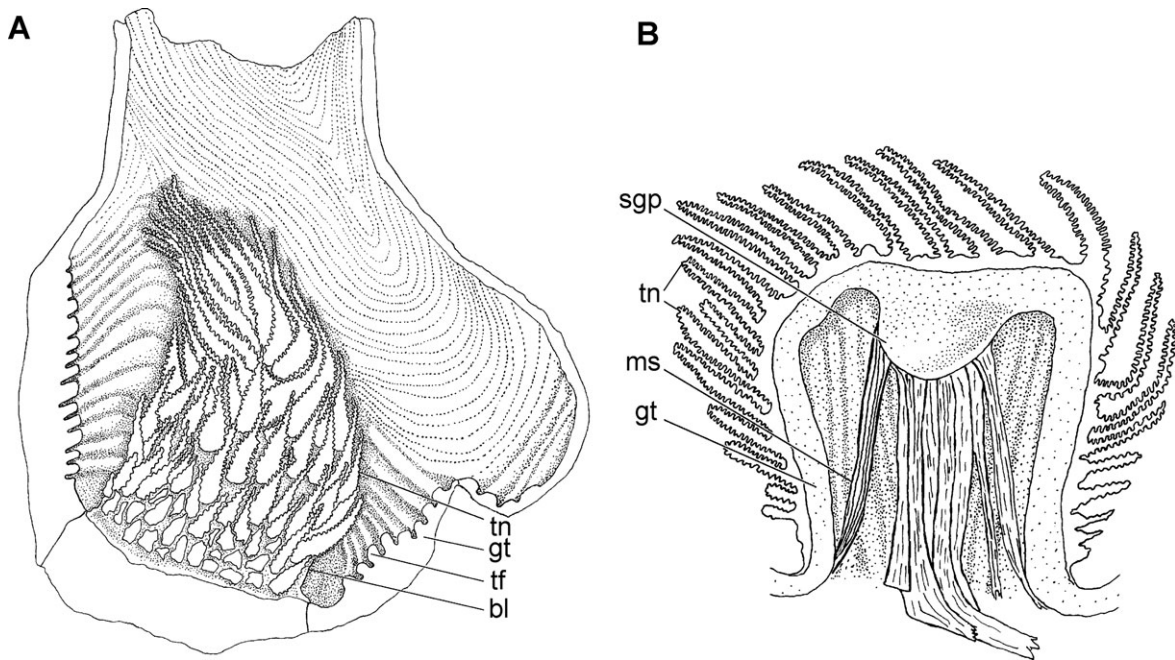


Figure 4. Pyriform gland of *Zemacies excelsa* (after Medinskaya & Sysoev, 2003). **A.** General view. **B.** Section through the bulb-like structure. Abbreviations: bl, bulb-like structure; gt, glandular tissue; ms, muscles; sgp, semicircular glandular pad; tn, tentacles.

of the body haemocoel. Both structures probably function as muscular hydrostats and are capable of elongation and contraction. The main differences between these structures are that the bulb of the pyriform gland is pulled inside the cavity formed by the rhynchodaeum, and that it is lined by glandular epithelium forming long and thin tentacles, as is stated by Medinskaya & Sysoev (2003). This glandular structure of the bulb of the pyriform gland of *Z. excelsa* probably explains differences in morphology between the former and the rhynchodaeal outgrowth. The wall separating the cavity of the pyriform gland from the rest of the rhynchocoel perhaps facilitates accumulation of the secretion within the gland. Since the rhynchodaeal outgrowth does not act as a secretory organ, the surrounding wall is unnecessary. However, it is possible that the wall of the pyriform gland is eversible and the mentioned difference represents a different stage of contraction. Thus, the foregut anatomy of *Z. excelsa* appeared to be rather similar to that of the two *Horaiclavus* species described above.

Conoidean taxonomy is currently based mostly on conchological and radular characters, although the shell is well known to show remarkable cases of homeomorphism. For example, the shells of species of *Strictispira* McLean, 1971 (Conoidea, Strictispiridae) are hardly distinguishable from many species of *Crassispira* Swainson, 1840 (Turridae, Crassispirinae) (Tippett, 2006), although radular and morphological characters clearly place both genera in different families.

Where major taxonomic characters have been lost, as in the species of *Horaiclavus* and *Zemacies*, and in the absence of molecular data, shell characters give the main clues to relationship. *Zemacies* and both *Horaiclavus* species are very different conchologically (Fig. 3). *Zemacies excelsa* is several times larger than *Horaiclavus* (Fig. 3B', D', and E represent shells at the same scale). The shell of *Zemacies* conforms in major details with that of representatives of the subfamily Cochlespirinae, and particular is similar to some species of *Leucosyrinx* Dall, 1889 in shell outline, subsutural position of the sulcus and strongly angulated shoulder. Sysoev (in Medinskaya & Sysoev, 2003) admitted the strong similarity of *Zemacies* to Cochlespirinae, but nevertheless erected the new monotypic subfamily Zemaciinae, based mostly on what he considered the unique foregut anatomy of *Z. excelsa*. He mentioned that 'The new subfamily is conchologically very similar to Cochlespirinae Powell, 1942 (Turridae). . . . A direct anatomical comparison with other groups is hampered by the absence of most part of typical conoidean characters (proboscis, radula and poison gland), whereas there is an autapomorphic feature (pyriform gland) having no analogues among conoidean gastropods' (Medinskaya & Sysoev, 2003: 86).

The shells of *Horaiclavus* have rather strong resemblances to those of the family Drilliidae and until radulae were examined the genus was placed in this family. The radula, on the contrary, provides good evidence that the genus *Horaiclavus* should be placed in the subfamily Crassispirinae.

Judging from the shell characters *Horaiclavus* and *Zemacies* are clearly not closely related and thus the unusual foregut anatomy likely appeared independently, with the implication that the peculiar rhynchodaeal outgrowth and pyriform gland are not homologous structures.

At present, in the absence of molecular data both for radular-less species of *Horaiclavus* and *Zemacies*, it is difficult to evaluate the taxonomic value of the rhynchodaeal outgrowth and the pyriform gland. Using a conventional approach we conclude that the outgrowth appeared within the single genus *Horaiclavus*, in which some species possess a normal toxoglossan foregut morphology, while others have a very specialized one. Equally, it is reasonable to suggest that in the case of *Zemacies* it is doubtful whether the similar foregut arrangement should be considered as having high enough significance for establishing a new taxon of subfamilial rank (and morphology was essentially the

only reason for establishing the new subfamily). However, pending molecular data and taking into account the ambiguity of taxonomic decisions based purely on conchological characters in such a diverse and variable group as Turridae, we refrain from reducing the taxonomic status of subfamily Zemaciinae and synonymizing it with Cochlespirinae.

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APPENDIX

Description of new species (by A.V. Sysoev)

Genus *Horaiclavus* Oyama, 1954

Type species: Mangilia splendida E.A. Smith, 1867 (by original designation).

The species described below belong to a group of small to medium-sized SW Pacific crassispirines characterized by a claviform shell sculptured with axial folds, but otherwise smooth and glossy (rarely with obsolete spiral sculpture); the anal sinus is weakly expressed or nearly lacking. This group actually consists of at least 2–3 genera, though only one of them – *Horaiclavus* (with the subgenus *Anguloclavus* Shuto, 1983) – is presently formally known. The species considered differ from typical *Horaiclavus* in having a less stout shell with a proportionally lower spire and larger aperture and a somewhat longer siphonal canal. However, it seems preferable to refrain from describing a new genus here. Both considered species lack a radula, whereas at least seven other species (still undescribed) do possess it, so choosing a non-typical representative as a type species may cause taxonomic confusion in future.

***Horaiclavus phaeocercus* Sysoev new species**

(Fig. 5A–G)

Types: Holotype, MNHN, New Caledonia, R/V *Jean-Charcot*, BIOCAL, stn DW44, 22°47'S, 167°14'E, 440–450 m, 30.08.1985; 6 live collected paratypes (from the same lot), MNHN; 1 dead collected paratype, MNHN, New Caledonia, R/V *Vauban*, MUSORSTOM 4, sta. DW230, 22°52'S, 167°12'E, 390–420 m, 30.09.1985; 1 dead collected paratype, MNHN, South New Caledonia, R/V *Alis*, SMIB 8, sta. DW168, 23°38'S, 168°43'E, 433–450 m, 29.01.1993; 1 dead collected paratype, MNHN, South New Caledonia, R/V *Alis*, SMIB 8, sta. DW193–196, 22°59'–23°S, 168°21'–168°23'E, 491–558 m, 01.02.1993; 1 dead collected paratype, MNHN, New Caledonia, R/V *Alis*, BATHUS 3, sta. CP805, 23°41'S, 168°01'E, 278–310 m, 27.11.1993; 1 dead collected paratype, MNHN, North New Caledonia, R/V *Alis*, BATHUS 4, sta. DW923, 18°52'S, 163°24'E, 470–502 m, 06.08.1994.

Etymology: Greek *phaios* (*phaeo-*, adj.: brown, dusky) and *kerkos* (*cercus*, latinized form, noun: tail, appendage), referring to the characteristic dark staining of the end of the siphonal canal.

Referred material: New Caledonia, Atoll de Surprise, sta. 444, 18°15'S, 162°59'E, 300–350 m, 28.02.1985, 1 dead; New Caledonia, R/V *Jean-Charcot*, BIOCAL, sta. DW77, 22°15'S, 167°15'E, 440 m, 05.09.1985, 2 dd; Coral Sea, R/V *Coriolis*, MUSORSTOM 5, sta. 361, 19°53'S, 158°38'E, 400 m, 19.10.1986, 1 dd; Loyalty Basin, R/V *Coriolis*, BIOGEOCAL, sta. DW307, 20°35'S, 166°55'E, 470–480 m, 01.05.1987, 2 dd; South Vanuatu, R/V *Alis*, VOLSMAR, sta. DW51, 20°59'S, 170°03'E, 400 m, 04.07.1989, 1 dd; Loyalty Rise, R/V *Alis*, MUSORSTOM 6, sta. DW410, 20°38'S, 167°07'E, 490 m, 15.02.1989, 2 dd; South New Caledonia, R/V *Alis*, SMIB 8, sta. DW197–199, 22°51'–22°52'S, 167°12'–168°12'E, 408–436 m, 01.02.1993, 1 lv; North New Caledonia, R/V *Alis*, BATHUS 4, sta. DW925, 18°55'S, 163°24'E, 370–405 m, 07.08.1994, 1 dd; South New Caledonia, R/V *Alis*, NORFOLK 1, sta. DW1733, 22°56'S, 167°15'E, 427–433 m, 28.06.2001, 1 dd.

Description: Shell claviform, consisting of ca. 7.5 whorls, with rather acute apex and moderately high spire, ratio shell diameter to shell height 0.50, aperture height to shell height 0.52, spire height to shell height 0.35. Protoconch turbiniform, of

about 2.5 smooth whorls, last half whorl slightly angulated. Teleoconch of 5 gradate, moderately convex whorls with flattened lateral side. Whorls with prominent shoulder angulation at 0.6 whorl height on early whorls and at 0.7 whorl height on latter whorls. Suture shallowly impressed, slightly wavy. Subsutural ramp narrow, clearly expressed, strongly inclined. Axial sculpture represented by strong, rounded, slightly arcuate and weakly opisthocline folds, running from suture to suture but fading on subsutural ramp and lower shell base, varying in number from 11 per whorl on early whorls to 12 on last whorl. Folds of about same width as intervals between them. Spiral sculpture represented by thin, poorly visible spiral threads covering adapical half of whorl side and seen as white lines on semi-transparent shell surface. Ridged spiral ribs represented on abapical part of shell base and canal. Base evenly convex, curved in passing to canal. Aperture oval, with short, obliquely truncated basal canal. Anal sinus weak, just slight insinuation of thin lip edge. Inner lip evenly curved, columellar part straight, parietal callus forming a narrow ridge-like pad; outer lip with heavy varix behind thin lip edge. Axial folds behind varix strongly smoothed. Shell glossy, yellowish-white, with chestnut-brown end of siphonal canal and pale-brown spiral elements on varix: three narrow lines adapically, one wider band below periphery, and one line abapically. Abaxial part of protoconch last whorl and two initial teleoconch whorls reddish-brown.

Shell height (holotype) 11.2 mm, shell diameter 5.6 mm, last whorl height 7.3 mm, aperture height 5.8 mm.

Distribution: SW Pacific: New Caledonia, Loyalty Basin, and Coral Sea; northward to 18°S, southward to 23°S, westward to 158°E, eastward to 170°E; living at 408–450 m, empty shells at 300–558 m.

Remarks: Maximum shell dimensions: 12.5 × 6.65 at 5.2 teleoconch whorls. Variation of shell indices: shell diameter to shell height 0.47–0.54, aperture height to shell height 0.49–0.54, spire height to shell height 0.34–0.40 (commonly 0.34–0.37). Number of folds rather stable during shell growth; 9–11 folds on last whorl. Anal sinus from not expressed to very poorly developed. Shell from Vanuatu (not included in type series) characterized by less angulated whorls and longer axial folds, not strongly smoothed on lower shell base (Fig. 5G). All fresh shells with dark upper whorls and brownish end of canal; sometimes there is a pale-brown spiral line running abapically of whorl angulation.

Operculum was examined in one of the paratypes from type locality. It is large, occupying entire aperture, thin, transparent, leaf-shaped, with terminal nucleus.

The species differs from *H. anaimus* in having more angulated whorls, fewer axial folds and in details of shell coloration.

***Horaiclavus anaimus* Sysoev new species**

(Fig. 5H–M)

Types: Holotype, MNHN, South New Caledonia, R/V *Alis*, BATHUS 2, sta. DW730, 23°03'S, 168°58'E, 397–400 m, 12.05.1993; 1 live collected paratype, MNHN, South New Caledonia, R/V *Alis*, BATHUS 2, sta. DW739, 22°35'S, 166°27'E, 465–525 m, 14.05.1993; 1 dead collected paratype, MNHN, New Caledonia, R/V *Alis*, NORFOLK 1, sta. DW1679, 24°43'S, 168°10'E, 298–324 m, 22.06.2001; 1 dead collected paratype, MNHN, Norfolk Rise, R/V *Alis*, NORFOLK 1, sta. DW1707, 23°43'S, 168°16'E, 381–493 m, 25.06.2001; 1 live collected paratype, MNHN, Norfolk Rise, R/V *Alis*, NORFOLK 1, sta. DW1727, 23°17'S, 168°14'E, 190–212 m, 27.06.2001.

Etymology: Greek *anaimos*, meaning pale and referring to the generally light coloration of the shell.

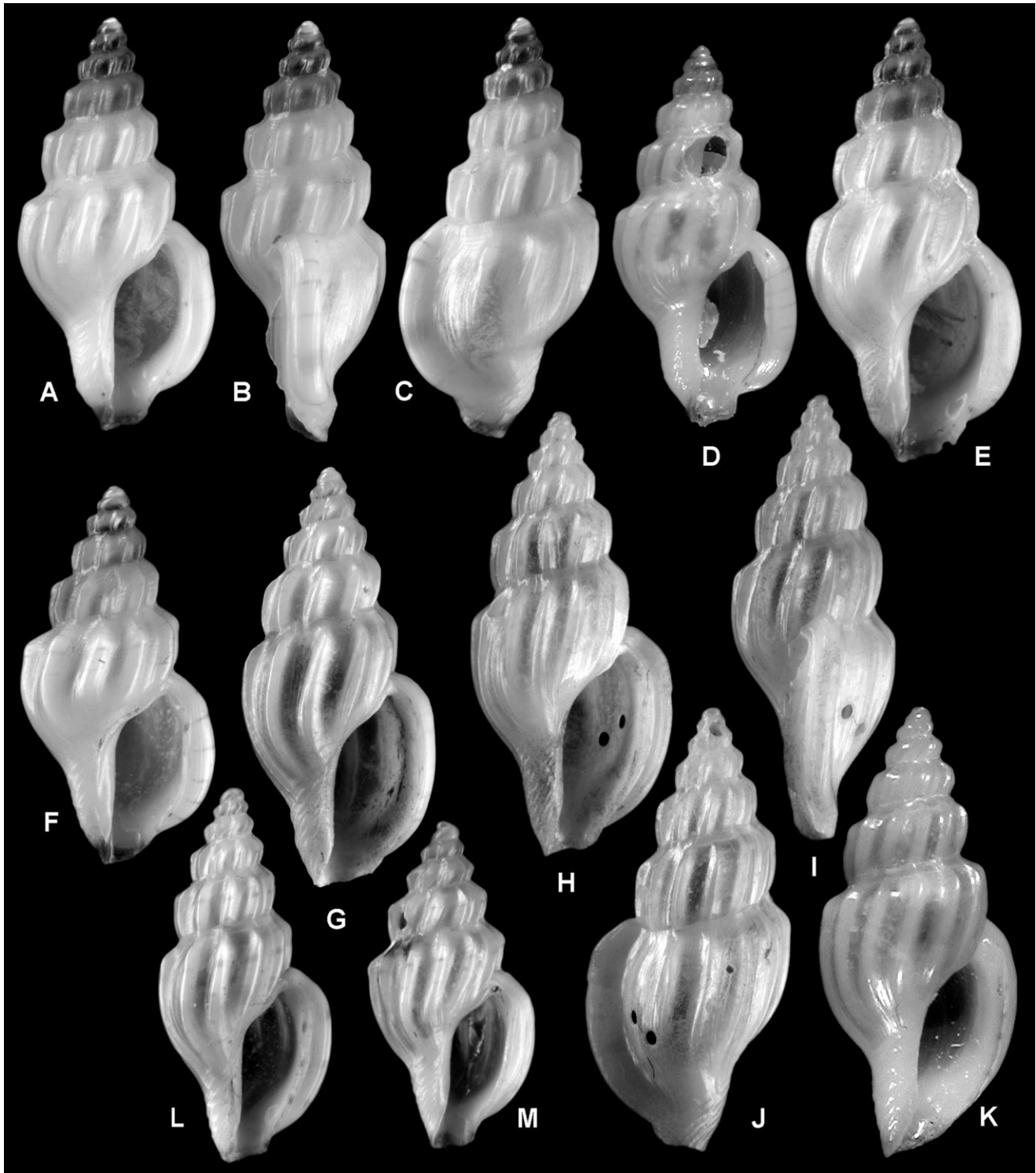


Figure 5. **A–G.** *Horaiclavus phaeocercus*. **A–C.** Holotype. **D.** Paratype, BIOCAL stn DW44, shell height 10.2 mm (anatomy examined). **E.** Paratype, SMIB 8, stn 193–196, shell height 12.0 mm. **F.** Paratype, MUSORSTOM 4, stn DW 230, shell height 10.2 mm. **G.** Paratype, VOLSMAR, stn DW 51, shell height 11.3 mm. **H–M.** *Horaiclavus anaimus*. **H–J.** Holotype, shell height 12.0 mm. **K.** Paratype, BATHUS 2, stn DW739, shell height 12.1 mm (anatomy examined). **L.** paratype, NORFOLK 1, stn DW1679, shell height 10.2 mm. **M.** Paratype, NORFOLK 1, stn. DW1727, shell height 8.8 mm. All shells at same scale.

Referred material: New Caledonia, R/V Vauban, MUSORSTOM 4, sta. DW226, 22°47'S, 167°22'E, 390 m, 30.09.1985, 1 dd; Loyalty Basin, R/V Coriolis, BIOGEOCAL, sta. DW253, 21°32'S, 166°29'E, 310–315 m, 16.04.1987, 1 dd; South

New Caledonia, R/V Alis, BERYX 11, sta. DW11 + CP 23, 24°44'–24°43'S, 168°10'–168°08'E, 270–350 m, 16–17.10.1992, 1 dd; New Caledonia, R/V Alis, BATHUS 3, sta. DW838, 23°01'S, 166°56'E, 400–402 m, 30.11.1993, 1 dd.

Description: Shell claviform, consisting of ca. 7 whorls, with moderately high spire, shell diameter to shell height 0.43, aperture height to shell height 0.49, spire height to shell height 0.36. Protoconch pupilliform, of about 1.5 smooth whorls. Teleoconch of 5.2 convex, weakly gradate, bluntly angulated whorls. First teleoconch whorl with median angulation, subsequent whorls angulated in adapical part due to asymmetrically thickened folds; maximal width of whorls in place of angulation. Suture shallowly impressed, slightly wavy. Subsutural ramp narrow, weakly concave. Axial sculpture represented by strong, acute, slightly arcuate and weakly opisthocline folds, running from suture to suture, much weakening on subsutural ramp and fading on lower shell base, varying in number from 10 per whorl on early whorls to 12 on last whorl. Folds slightly narrower than intervals between them. Spiral sculpture represented only by weak spiral ribs covering abapical part of shell base and siphonal canal. Base weakly convex, slightly curved in passing to canal. Aperture oval, with short, obliquely truncated basal canal. Anal sinus weak, just insinuation of thin lip edge. Inner lip evenly curved, columellar part straight, parietal callus forming a weak pad; outer lip with heavy varix behind thin lip edge. Area behind varix smoothed. Shell glossy and white.

Shell height (holotype) 12.0 mm, shell diameter 5.2 mm, last whorl height 7.7 mm, aperture height 5.9 mm.

Distribution: A rather small area in the SW Pacific between New Caledonia, Loyalty Basin, and Norfolk Rise; northward to 21°S, southward to 24°S, westward to 166°E, eastward to 168°E; living at 190–525 m, empty shells at 270–493 m.

Remarks: Holotype is the largest specimen. Variation of shell indices: shell diameter to shell height 0.43–0.49, aperture height to shell height 0.48–0.52, spire height to shell height 0.34–0.37. Number of plicae slightly increasing with shell growth: from 9–10 on early whorls to 11–12 on last whorl. Most expressed shell coloration represented by diffuse brownish-yellow spots on subsutural ramp, one or two indistinct narrow pale-brown spiral bands running abapically of whorl angulation, and 3–4 bands seen on abapertural part of varix.

Operculum was examined in one of the paratypes (Fig. 5M). It is large, occupying entire aperture, thin, transparent, leaf-shaped, with terminal nucleus.

The species differs from *H. phaeocercus* in having more rounded whorls with more numerous axial folds, and in a protoconch with a smaller number of whorls.