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CRYPTIC SPECIES IN *GEMMULOBORSONIA* (GASTROPODA: CONOIDEA)

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Running title: Cryptic species in Conoidea

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ABSTRACT

During a broad molecular taxonomic and phylogenetic survey of the superfamily Conoidea 80 specimens of several species of the genus *Gemmuloborsonia* were sequenced for COI gene. The genus originally established for fossil species from the Plio-Pleistocene of the Philippines now includes living species from bathyal depths of the Indo-Pacific Oceans. The molecular data demonstrated the presence of five separate entities, while only four “morphospecies” can be isolated by visual examination. The two largest groups, representing separate species from the molecular data, were impossible to distinguish with certainty using shell or anatomical characters. The shape of the last whorl was analysed by Fourier analysis, Fourier coordinates were used in Canonical Variate Analysis. The majority of the specimens was separated into two groups but 21.6% of the specimens were impossible to distinguish by morphological characters. One of these two forms was attributed to the known species *Gemmuloborsonia moosai* Sysoev & Bouchet, 1996, while the other is described as a new species *G. clandestina*. *Bathytoma colorata* Sysoev & Bouchet, 2001 is transferred to *Gemmuloborsonia* on the basis of molecular analysis and radular morphology. Another species represented in our material by a single specimen, remains undescribed.

INTRODUCTION

The taxonomy of shell-bearing molluscs was and continues to be largely based on the shell characters. For more than 250 years of scientific malacology the shell has proven to be reliable species-level identifier, especially when including the protoconch. Similar characters have been used for the exceptionally good fossil record of molluscs. Furthermore intensive surveys in coral reef sites show that 28% of the species are simply never collected alive (Bouchet *et al.*, 2002).

For the overwhelming majority of described species of molluscs the primary name-bearing types are shells, these usually being the only part of the animal preserved in collections. This leaves conchological characters the major if not the only source of taxonomic decisions.

The conventional approach to documenting molluscan diversity or revisionary taxonomy is by sorting material to morphospecies on the basis of shell characters with subsequent testing of taxonomic hypotheses with all available data, such anatomy, biogeographic information and, more recently, with molecular analyses. The final and inevitable stage of any taxonomic decision in malacology is the critical re-evaluation of the shell characters in order to find and formalize the reliable discriminating features. In practice, the major task of a malacological taxonomist is the estimation and evaluation of the intraspecific variability of the shell.

Convergence and homoplasy render shell characters much less reliable predictors of relationships at higher taxonomic levels (family, genus) within the gastropod superfamily Conoidea (=Toxoglossa). Sometimes the incongruence between the shell and internal anatomy is startling and species with very similar shells may be very distantly or completely unrelated. For instance, shells of *Toxicochlespira* Sysoev & Kantor, 1990 (Conidae) strongly

resemble representatives of *Cochlespira* Conrad, 1865 (Turridae) (Sysoev & Kantor, 1990); shells of *Strictispira* McLean, 1971 (Strictispiridae), are hardly distinguishable from those of many species of *Crassispira* Swainson, 1840 (Turridae, Crassispirinae) (Tippett, 2006); and the radula-less species *Cenodagreutes aethus* Smith, 1967 is said to be conchologically indistinguishable from the radulate *Raphitoma leufroyi* (Michaud, 1828) (both Conidae, Raphitominae) (Fretter & Graham, 1985).

Cryptic, or sibling species of marine animals are ubiquitous and molluscs are no exception (see reviews by Knowlton, 1993, 2000). In reality most recently discovered cryptic species of Gastropoda are forms with superficially similar shells that can usually be reliably distinguished by anatomical characters. A recent example is the discovery of two conchologically very similar pairs of species initially placed in the genus *Xenuroturris* Iredale, 1929 but differing markedly in radular morphology (Kantor *et al.*, 2008).

Molecular techniques are now more frequently employed in taxonomic analysis and are revealing numerous cases of cryptic species in all groups, including molluscs (e.g. Williams & Reid 2004, Collin, 2005; Reid *et al.* 2006, Duda *et al.*, 2008; Malaquias & Reid, 2008). Molecular data now more often used in combination with shell and anatomical characters for taxonomic purposes and sometimes become the ultimate proof of the existence of separate species.

Cryptic species in molluscs pose significant nomenclatural problems since unambiguous assignment of older type specimens, which in molluscs are nearly inevitably represented by the empty shell, sometimes even atrociously "beach worn", often without good locality data, to one of several forms may be extremely difficult or impossible.

In course of a broad-scale taxonomic and phylogenetic survey of the superfamily Conoidea several cases were found where molecular data demonstrated conflict with hypotheses based on conventional shell and sometimes even anatomical characters (Puillandre

et al., 2008). A remarkable example is the genus *Gemmuloborsonia* Shuto, 1989, of which molecular data are now available for several species. The genus was established for four fossil species of Turridae from Plio-Pleistocene of Philippines, and the Late Miocene of Indonesia and Italy (Shuto, 1989). Five living species of the genus were described from bathyal waters of Indo-Pacific Oceans by Sysoev & Bouchet (1996). The genus *Gemmuloborsonia* was initially assigned to Borsoniinae (= Clathurellinae fide Taylor *et al.*, 1993), but transferred on the basis of radular characters to the subfamily Turrinae (Sysoev & Bouchet, 1996). However, recent molecular analyses do not confirm this result (Puillandre *et al.*, 2008).

The molecular analysis of 80 specimens of *Gemmuloborsonia* from the central Indo-Pacific using COI gene demonstrated the presence in our material of five separate entities, while only four “morphospecies” can be isolated by visual examination. The two largest groups, representing separate species (based on the molecular data) were initially impossible to distinguish by shell characters and it is not surprising that these forms avoided recognition even in the latest taxonomic revision of the genus (Sysoev & Bouchet, 1996). These discovery led us to make a more detailed examination of this *Gemmuloborsonia* species complex combining the molecular results with studies of the radula and multivariate analysis of shell form.

MATERIAL AND METHODS

Sampling

A total of 80 living specimens potentially belonging to the genus *Gemmuloborsonia* were collected between 2004 and 2007 in the Philippines, Solomon Islands and Coral Sea (Table 1). Specimens were preserved in 90 or 100% ethanol specifically for molecular

analysis by clipping pieces of the head-foot from anesthetized specimens, thus keeping the shell intact for morphological analyses.

All material is stored in the collections of Muséum National d'Histoire Naturelle, Paris (MNHN).

In order to test the monophyly of the genus *Gemmuloborsonia*, we used as outgroups several species of Turrinae (*Lophiotoma albina* Lamarck, 1822; *Turris babylonia* Linnaeus, 1758 and *Gemmula diomedea* E. A. Smith, 1894, *Lucerapex* sp. Iredale, 1936), but also several species belonging to other subfamilies of Conoidea (*Clavus* sp. Montfort 1810, *Raphitoma* sp. Bellardi 1848, *Conus orbigny* Kilburn, 1975). Additionally, one specimen included in our sampling was identified as *Bathytoma colorata* Sysoev & Bouchet, 2001, but this species is thought to belong to the genus *Gemmuloborsonia* (see below a more detailed discussion of this point). To test this hypothesis, we also included three specimens of the genus *Bathytoma* Harris & Burrows, 1891. A specimen of *Harpa* Röding, 1798 (Neogastropoda, Harpidae) was used as a distant outgroup.

Extraction and sequencing

DNA was extracted from a piece of foot, using 6100 Nucleic Acid Prepstation system (Applied Biosystem). A fragment of 658 bp of Cytochrome Oxidase I (COI) mitochondrial gene was amplified using universal primers LCO1490 and HCO2198 (Folmer *et al.*, 1994). All PCR reactions were performed in 25 μ l, containing 3 ng of DNA, 1X reaction buffer, 2.5 mM MgCl₂, 0.26 mM dNTP, 0.3 μ M of each primer, 5% DMSO and 1.5 units of Q-Bio Taq (MPBiomedicals). Amplifications were performed according to Hebert *et al.* (2003). PCR products were purified and sequenced by a sequencing facility (Genoscope). In all cases, both directions were sequenced to confirm accuracy of each haplotype sequence (GenBank accession numbers: see Table 1).

Phylogenetic analysis

COI sequences were manually aligned, as no ambiguous indels were found. Genetic distances (p-distances) between sequences were calculated using MEGA 3.1 (Kumar, Tamura & Nei, 2004). Phylogenetic reconstructions were conducted using Bayesian Analysis (BA), consisting of two Markov chains (10000000 generations each with a sampling frequency of one tree each thousand generations) run in four parallel analyses using Mr. Bayes (Huelsenbeck, Ronquist & Hall, 2001). When the log-likelihood scores were found to stabilize, a consensus tree was calculated after omitting the first 25% trees as burn-in. Only the number of nucleotide substitution rates categories (6) was fixed, the other parameters of the substitution model being estimated during the Bayesian analysis.

Fourier analysis

Morphometric analyses were performed in an attempt to identify morphological differences between two groups recognized genetically but indistinguishable morphologically using traditional characters. The shape of the last whorl was analysed by Fourier analysis, as previously described in Puillandre *et al.* (2009).

Shells were placed horizontally, aperture up, and digitized using a macro stand at the same magnification to reduce the possible optical distortions. As the outer apertural lip of some shells was broken, this part of the whorl was not included in the analysis, as described in Figure 1. Five landmarks were defined, corresponding to adapical and abapical margins of the peripheral keel on both sides of the shell, and to the tip of the siphonal canal (Fig. 1). The five landmarks, as well as the outlines, were digitized using TpsDig (Rohlf, 1996). The same starting point, corresponding to the first landmark, was always used. All pictures and outlines were taken by the same manipulator (NP).

Figure 1

Outlines were used as input for an EFA (Elliptic Fourier Analysis – Dommergues *et al.*, 2003; Baylac & Friess, 2005). The five landmarks were used as control points to rotate the outlines into the same orientation. The images were then centred and normalised for size (using square roots of the surface). A visualization of Fourier reconstructions using different numbers of harmonics, compared to the original outline, was used to estimate that 40 harmonics was sufficient to reconstruct the outlines with high accuracy (Fig. 1).

The obtained Fourier coordinates were used in CVA (Canonical Variate Analysis) analyses, using two different grouping variables: (i) the genetic groups as defined by the molecular analysis and (ii) the cruise of collection (Table 1). Visualizations of the outline deformations along the canonical axes were made using the procedure described in Monti *et al.* (2001). Assignment of a specimen to one or another genetic group was tested by a “leave-one-out” cross-validation (1000 bootstrap replicates). Several type specimens, not preserved in alcohol and thus not analysed molecularly, were added in the CVA analyses and assigned successively to each of the genetic groups analysed. All analyses were performed using specially devised MATLABv5.2 functions implemented by Michel Baylac.

Institutional abbreviations used in the text:

MNHN – Muséum National d’Histoire Naturelle, Paris, France; NM -- Natal Museum, Pietermaritzburg, South Africa; NMNZ – National Museum of New Zealand, Wellington, New Zealand; PPPO-LIPI – Pusat Penelitian dan Pengembangan Oseanologi LIPI, Jakarta, Indonesia; ZMMSU – Zoological Museum of Moscow State University, Moscow, Russia

RESULTS

Eighty specimens were sequenced for COI, resulting in a 658 bp fragment. The tree resulting from the Bayesian analysis supports the monophyly of *Gemmuloborsonia* (Posterior Probability PP = 0.99), and shows up five different groups, numbered from 1 to 5 in the Figure 2. Each of them includes from one to 49 specimens. Groups 3, 4 and 5, each including several specimens, are well supported (PP > 0.95). Mean genetic distance between groups ranges from 5.6% (between groups 1 and 3) to 10% (between groups 1 and 2).

Figure 2

The high genetic distances found between the different groups within *Gemmuloborsonia* are generally interpreted as interspecific distances (see e.g. Hebert *et al.*, 2003; Smith, Fisher & Hebert, 2005; more specifically for molluscs: Mikkelsen, Schander & Willassen, 2007; Malaquias & Reid, 2008; Puillandre *et al.*, 2009). Furthermore, all the groups that include several specimens are reciprocally monophyletic. These two findings suggest that these five entities certainly correspond to different species (Samadi & Barberousse, 2006).

Taxonomic position of studied forms

Group 1

This group is represented by a single specimen.

Gemmuloborsonia sp.

(Fig. 3 F)

Material examined: Solomon Islands (sta. 2850), MNHN 41918, 1 live specimen, shell length 25.3 mm.

Figure 3

Remarks: The single specimen examined was an immature female. The radula was studied (Fig. 4B) and is typical for the genus. It is formed by only 42 rows of teeth, 1.75 mm in length (0.20 of AL = aperture length). The marginal teeth are duplex, about 110 μ m long (1.25% of AL), with the central formation (Kantor, 2006) nearly rectangular, formed of fused central and lateral teeth. The cusp (= central tooth) is rather weak and narrow.

Figure 4

The specimen lacks a protoconch and is characterized by very prominent, bulging subsutural fold and peripheral keel. Nevertheless in nearly all studied species of *Gemmuloborsonia* the degree of prominence of fold and keel decreases with age and therefore it is difficult to predict the definitive shell form. Therefore, despite the fact that it is rather distinct from other species we refrain from description of a new species until additional fully grown specimens become available.

Group 2

Group 2 consists of a single adult specimen from New Caledonia. Its generic assignment posed little problem.

Gemmuloborsonia colorata (Sysoev & Bouchet, 2001) comb. nov.

(Fig. 3 A-E)

Bathytoma colorata Sysoev & Bouchet, 2001: 294, 296, Figs. 97-98.

Types: Holotype and paratype: MNHN.

Type locality: Vanuatu, NE of Tanna, 19°22'S, 169°26'E, 408-410 m (Expedition MUSORSTOM 8, sta. CP982).

Material examined: type material, New Caledonia, Lansdowne Bank, 20°06'S, 160°23'E, 490-550 m (Expedition EBISCO, sta. DW 2619, 20.10.2005), 1 specimen sequenced, MNHN 17849.

Remarks: This species was described in the genus *Bathytoma* (Conidae, Borsoniinae) on the basis of three empty shells from Vanuatu. Due to the lack of data on protoconch and radula the authors did not attribute it to any recognized subgenus of *Bathytoma*. Later additional material was collected off New Caledonia (Norfolk Ridge), in the Coral Sea (Chesterfield Plateau) and French Polynesia.

The specimen analysed (shell length 45.5 mm) (Fig. 3D-E) was collected alive from the Lansdowne Bank. Conchologically it is very similar to the holotype (Fig. 3A) but differs in the much paler coloration. Similarly coloured specimens were found in French Polynesia (Fig. 3C), with intermediate ones from New Caledonia (Fig. 3B). The protoconch appears typical of the subfamily Turrinae of Turridae. It is dark-brown, multispiral, formed by 3.25 whorls, diameter 790 µm. It consists of approximately 1.75 smooth whorls of protoconch I and 1.5 whorls of protoconch II covered with arcuate strongly prosocline ribs not reaching the low suture. In its general shape, size and ornamentation it is very similar to the protoconchs illustrated and described for *Gemmuloborsonia neocaledonica* Sysoev & Bouchet, 1996 and *G. moosai* Sysoev & Bouchet, 1996.

The radula of *Gemmuloborsonia colorata* (Fig. 4A) is typical for subfamily Turrinae and is extremely similar to that of other examined species of *Gemmuloborsonia*. It is formed by about 60 rows of teeth, 22 immature, 3.75 mm in length (0.23 of AL). Marginal teeth are

duplex, about 210 µm long (1.3% of AL). The central formation is rather short, and strongly notched anteriorly. The cusp is strong and curved in profile.

The molecular analysis groups the species unambiguously within *Gemmuloborsonia* (Fig. 2).

The species is widely distributed in the Indo-Pacific from French Polynesia through Vanuatu, New Caledonia and westward to Madagascar and Reunion. It is illustrated as *Lucerapex indagarotis* (Finlay, 1927) on the web site <http://vieocean.free.fr/>, dedicated to the molluscs of Reunion Island.

Group 4

Group 4 contains four specimens collected off New Caledonia and in all respects similar to *Gemmuloborsonia neocaledonica* Sysoev & Bouchet, 1996.

Gemmuloborsonia neocaledonica Sysoev & Bouchet, 1996

(Fig. 3G)

Gemmuloborsonia neocaledonica Sysoev & Bouchet, 1996: 76-78, Figs. 1; 2A,D; 3A-D.

Types: Holotype and nine paratypes in MNHN, 1 paratype in ZMMSU, one paratype in NM, 1 paratype in NMNZ.

Type locality: Southern New Caledonia, 24°40'S, 168°38'E, 650 m (Expedition CHALCAL 2, sta. DW74).

Material examined: Holotype and nine paratypes in MNHN, also see Table 1.

Remarks: Our specimens match the types and were collected in close proximity to the type locality at similar depths.

The species is distributed in New Caledonia, Loyalty Islands, southern New Hebrides Arc, at depths from 420-550 m.

Groups 3 and 5

These are the most numerous groups, containing 25 and 49 specimens respectively. In general shell shape and in multispiral protoconch both of them resemble *Gemmuloborsonia moosai* Sysoev & Bouchet, 1996. The similarity between two forms is striking; nevertheless the molecular data suggested the presence of two separate species. Both groups are reciprocally monophyletic, and the average genetic distance between them is 6.2%. Moreover, both forms were sympatric in a single dredge haul (400-500m) from the Philippines. Studies of the radulae revealed no significant differences, nor did standard measurements of the shell.

Therefore, a Fourier analysis was performed on the 74 specimens included in the genetic groups 3 and 5. Using CVA analysis, the two genetic groups are separated along the axis, although not completely (Fig. 5). Among 74 specimens, 16 are not assigned to the correct genetic group (Table 1). Using the collection locality (cruise) as a discriminant variable (Fig. 6), specimens collected during the Salomon 2 cruise are separated from the others on the first axis (representing 48.07% of the variance). On the second axis (39.44% of the variance), specimens collected during Aurora 07 (Philippines) and Salomon 3 (Solomon Islands) expeditions are discriminated, but the two groups overlap. Results of the CVA analysis

Figure 5

Figure 6

obtained both using genetic groups or collection locality as discriminant variable are not surprisingly similar, as genetic group 3 is exclusively in Philippines, and genetic group 5 is exclusively in Solomon Islands and Chesterfield Plateau, except for two specimens collected in the Philippines.

The axes discriminating genetic groups 3 and 5 (Fig. 5) and specimens from Solomon Islands and Philippines (Fig. 6) show up an opposition between forms with stouter shells with lower last whorled shells compared with forms with more elongated shells and taller last whorls.

The presence of two forms poses the question on the applicability of the names. One form is broadly distributed from the Coral Sea to Solomon Islands and Philippines, while the other is found only in the Philippines. The multivariate analysis demonstrated that the holotype of *Gemuloborsonia moosai* falls within the group 5 (Table 2). Thus, the name *moosai* can be attributed to Group 5.

Table 2

Gemuloborsonia moosai Sysoev & Bouchet, 1996

(Fig. 7A-H)

Figure 7

Gemuloborsonia moosai Sysoev & Bouchet, 1996: 82, 84-85, Fig. 2C, E; 5A-G.

Types: Holotype and 48 paratypes in MNHN, two paratypes in PPPO-LIPI, 2 paratypes in M, 2 paratypes in ZMMSU.

Type locality: Indonesia, E of Palau Jamdena Island, 08°20'S, 132°11'E, 405-399 m (Expedition KARUBAR, sta. CP59).

Material examined: Holotype and 48 paratypes in MNHN, also see Table 1.

Remarks: Sysoev & Bouchet (1996) remarked on the high variability of shell characters, including sculpture, shell outline and relative height of the last whorl. The holotype is one of the most slender specimens examined. Some of the paratypes from Indonesia match well with our specimens collected around the Solomon Islands at similar depths.

The species is extremely similar to *Gemmuloborsonia clandestina* sp. nov. and cannot be distinguished visually. The Fourier analysis of the shell outline showed that in general the specimens of *G. moosai* have slightly narrower and slightly taller last whorls. These differences are easily obscured by the shell sculpture. Besides, there is overlap in characters and not all of specimens can be distinguished even morphometrically.

The two species co-occur in the Philippines and were found in a single dredge haul (sta. CP2658). Contrary to usual phenomenon of character displacement where in the zone of co-occurrence close species differ more than in allopatric populations, those *Gemmuloborsonia* that co-occurred were very similar. Most of specimens from that station which were molecularly identified as *Gemmuloborsonia clandestina* new species were placed in the wrong group (that is *G. moosai*) by CVA (Table 1).

We examined the radulae of both species, including those of sympatric specimens (Fig. 4C-F). No significant differences of specific value can be found. The radula of *G. moosai* (Fig. 4 C-D) is typical for the genus. The marginal teeth are duplex, about 145 µm long (1.84% of AL), while the central formation is rather short, notched anteriorly. The cusp is strong and curved in profile.

Shell morphometry of the two paratypes of *G. moosai* from the Philippines revealed that they belong to the Group 3 (*G. clandestina*) (Table 2).

There is a possibility that the Indonesian population of *G. moosai* (the type locality) represents *a separate* species from Groups 3 and 5. In this case we are dealing with three species, but until material suitably preserved for molecular analysis becomes available from the type locality of *G. moosai*, we prefer to use this name for gastropods of Group 5.

Gemmuloborsonia moosai is distributed off the Tanimbar Islands (Banda and Arafura seas), Indonesia, Philippines (our material) and Solomon Islands (our material). The species was also thought to inhabit the Mozambique Channel, although the specimens from this area differ significantly in having a rather different shell outline, in particular the much taller last whorl. They are much more different from the specimens from Indonesia and Solomons than those from *G. clandestina*. We consider the Mozambique Channel should be excluded from the distributional range area of this species, as these specimens perhaps constitute maybe a different taxon.

Gemmuloborsonia clandestina new species

(Fig. 8)

Figure 8

Types: Holotype: MNHN 41937; 13 paratypes: MNHN 41941, 41942, 41943, 41944, 41945, 41946, 41947, 41948, 41949, 41950, 41951, 41952, 41953.

Type locality: Philippines, Philippine Sea, E of Luzon Island, 15°58'N, 121°49.1'E, 422-431 m (Expedition Aurora, sta. CP2658), holotype and 13 paratypes.

Material examined: Type material; Philippines, Philippine Sea, E of Luzon Island, 16°00.9'N, 121°51.2'E, 342-348 m (Expedition Aurora, sta. CP2657), 1 lv, MNHN 41929; 15°56.4'N, 121°48.9'E, 460-480 m (Expedition Aurora, sta. CP2659), 1 lv, MNHN 41936; 15°52.2'N,

121°48.8'E, 506-542 m (Expedition Aurora, sta. CP2660), 3 lv, MNHN 41938, 41939, 41940; 15°01.4'N, 121°44.8'E, 431-493 m (Expedition Aurora, sta. CP2673), 1 lv, MNHN 41932; 15°04.1'N, 121°41.1'E, 368-442 m (Expedition Aurora, sta. CP2707), 3 lv, MNHN 41933, 41934, 41935; 15°19'N, 121°33.9'E, 300-318 m (Expedition Aurora, sta. CP2727), 1 lv, MNHN 41931; 15°58.1'N, 121°49.2'E, 418-456 m (Expedition Aurora, sta. CP2744), 1 lv, MNHN 41930; Philippines, 13°49'N, 120°28'E, 441-550 m (Expedition MUSORSTOM 2, sta. CP78), 2 dd (paratypes of *Gemmuloborsonia moosai* Sysoev & Bouchet, 1996); Philippines, 11°58'N, 121°06'E, 448-466 m (Expedition MUSORSTOM 3, sta. CP118), 1 dd (paratype of *Gemmuloborsonia moosai* Sysoev & Bouchet, 1996).

Etymology: *clandestinus* – Latin, means hidden, concealed, with reference to the extreme similarity of the species to *G. moosai*.

Description (holotype): The shell is elongate-biconic, strong, medium-sized, slightly glossy, covered by thin light yellowish smooth periostracum. Protoconch eroded, brown, multispiral, consists of approximately 2.6 whorls, diameter 670 µm. Transition from protoconch to teleoconch is clearly marked by the change in color. Teleoconch consists of 9.75 low whorls separated by shallow channeled suture. Whorls bear well developed subsutural fold and peripheral keel. Subsutural fold appears on first teleoconch whorls and is narrower than the keel, although its relative width progressively enlarges with the shell growth. The subsutural fold is covered by rounded blunt gemmules, which occupy the whole fold on early whorls, but on last and most of penultimate whorl they are confined to narrowing cord in the middle of the fold which becoming more flat on the last whorl. There are 39 gemmules on the last whorl and 28 on the penultimate whorl. On the 7th teleoconch whorl the cord at the upper edge of subsutural fold appears and within one whorl is split in two, that are more convex and well

developed on the last whorl. The peripheral keel bears longitudinally elongate gemmules that are arcuate on the last and penultimate whorls. There are 36 gemmules on the last whorl and 28 on the penultimate whorl. The interspace between subsutural fold and peripheral keel is very narrow and smooth on upper 5 teleoconch whorls. Later there appears an initially narrow cord, becoming progressively broader and more pronounced. On the last whorl the interspace between the fold and the keel is broad and have 3 narrow but distinct spiral cords. Body whorl occupies 0.61 of the shell length. Periphery of the whorl below the keel, shell base and canal are covered by narrow granulated cords slightly differing in width. There are in total 22 such cords, with interspaces not exceeding the cord width. The aperture is narrow and its width slowly decreases to rather broad and obliquely truncated canal. The inner lip is smooth and convex in its parietal part and nearly straight at the columellar part. It is covered with a thin off-white glossy callus. The weak columellar pleat encircles the columellar obliquely. The outer lip projects strongly forward below the anal sinus. The sinus is deep, U-shaped, slightly adapically directed.

Shell length 25.3 mm, body whorl length 15.6 mm, aperture length 8.5 mm, canal length 3.0 mm, shell diameter 8.5 mm.

Remarks: Although there is clear conchological similarity among all specimens that are attributed to the new species on the basis of molecular data, *G. clandestina* is rather variable in terms of shell outline, especially in terms of shell slenderness. The type locality is very remarkable in this respect, since the variability within the type series equals the maximal variability within the species (shell width/shell length ratio varies from 0.34 to 0.40, average 0.36 ± 0.01 , $n=24$).

The radula was examined in three specimens, including two paratypes (Fig. 4E-F). The radula is formed by about 48 (paratype MNHN 41943) to 60 rows of teeth (MNHN 41934),

12-20 nascent, 2.51 to 2.87 mm in length (0.32-0.34 of AL). The marginal teeth are duplex, about 105-137 μm long (1.75-1.37% of AL) and the central formation is rather short, with the anterior border indistinct and fused with the membrane. The cusp is strong and curved in profile.

The species is extremely similar conchologically to *Gemmuloborsonia moosai* and some of the specimens cannot be distinguished even by the morphometric analysis. For discussion and comparison see the Remarks section of the previous species. The holotype of the new species is distinguished from the holotype of *G. moosai* in having a smaller and broader shell. Both species can be readily distinguished by COI sequences.

The species is so far found only in the Philippines, at the depths 342-542 m.

DISCUSSION

The conventional practice of distinguishing species is to find the gaps in the morphological continuum. Therefore, until the discrete differences (at least in some of the parameters) are found, entities are usually not considered as separate species. Prior to use of molecular techniques the status of allopatric forms was, in reality, decided arbitrarily.

In our analysis, two discrete entities, revealed by the DNA analysis, are not morphologically distinguishable. Before conducting time consuming Fourier analysis we tried the more standard morphometric parameters that were proven to be operational for different groups of marine gastropods (Bouchet & Kantor, 2004; Kantor & Bouchet, 2007) but we were not able to delimit the species. Similarly, the radular morphology and gross anatomy did not reveal any significant differences. Finally, Fourier analysis allowed us to attribute most, but not all specimens to one of the two groups.

However, COI sequences clearly suggested that two different species (*G. moosai* and *G. clandestina*) were included in what was considered before as single “*G. moosai*”. Genetic distances between *G. moosai* and *G. clandestina* are similar to that found between others unquestioned species included in *Gemmuloborsonia* (Fig. 2). Although our conclusion was based on a single gene, it is unlikely that these two species exchange genes. This hypothesis is supported by the fact that the two species co-occur sympatrically in the Philippines at the same site. We also sequenced an nuclear gene (28S rRNA – results not shown) to test if the genetic differences found the mitochondrial marker was reflecting the species boundaries (see e.g. Nichols, 2001; Funk and Omland, 2004), but all the specimens were sharing the same 28S sequence. A more variable nuclear marker would confirm the hypotheses proposed with the COI gene.

The described above situation with *Gemmuloborsonia moosai* and *G. clandestina* is presently very uncommon for molluscs. Although species are now commonly delimited using molecular data (e.g. Meyer & Paulay, 2005; Mikkelsen, Schander & Willassen, 2007; Campbell *et al.*, 2008), species limits are most of the time illustrated by morphological differences, *a priori* known or *a posteriori* found. Even when cryptic species are revealed by DNA surveys, morphological differences can usually be identified.

In several cases, morphologically indistinguishable entities have been recognized as separate species in molluscs. One is the recognition of two sister pairs of species of *Bulla* Linnaeus, 1758 (Bullidae) (Malaquias & Reid, 2008). The other is a recognition of a cryptic speciation of the genus *Bostrycapulus* Olsson & Harbison, 1953 (Calyptraeidae) (Collin, 2005). In both cases the specific status was proven on the basis of molecular data for allopatric forms. Using COI sequences Gittenberger & Gittenberger (2006) demonstrated the existence of several morphologically unrecognizable parasitic species of the genus *Leptoconchus* Rüppell, 1834 (Coralliophilidae). In this case, sympatric species inhabited

different species of the hosts – scleractinian corals of the family Fungiidae. The authors refrained from formal introduction of 14 recognized new species.

Our case is different from the above mentioned. Firstly, the unexpected diversity was found without any clue in conchology, anatomy, or ecology. Secondly, comparison of syntopic specimens of *G. moosai* and *G. clandestina*, found in the same dredge haul, revealed that they are more similar to each other than the specimens of allopatric populations. Most of specimens from that station which molecularly were shown to belong to *Gemmuloborsonia clandestina* new species were placed in the wrong group (that is *G. moosai*) by CVA (Table 1). Usually the situation is the opposite and the sympatric specimens of different species are much easier recognizable than those from allopatric populations.

Although we were unable to demonstrate that these species are morphologically discrete, we feel that it was necessary to formally recognize two clades within what was previously considered as *G. moosai* as separate species, even if DNA constitutes the only tool to separate them. We agree with Collin (2005) that there is no theoretical reason to expect that mechanisms of speciation should always result in species that can be distinguished visually, especially for recent speciation events.

For the practical purposes of the discrimination of *G. moosai* from *G. clandestina* only the specimens from Philippines constitute a problem (as far as our sampling revealed). 100% of the specimens collected in Solomon Islands or Chesterfield Plateau belonged to *G. moosai* and 92.6% of the specimens collected in Philippines were *G. clandestina* (only 2.7% of the specimens are not correctly assigned). Morphological characters failed to distinguish a significant 21.6% of specimens.

Although discriminating morphological (or anatomical) characters in *Gemmuloborsonia* species were not found, this does not mean that some discrete differences might not be identified, most probably by detailed anatomical study. At the same time such an intensive

search may not prove to be operational. Empty shells cannot be identified with certainty (at least from Philippines). At present, even the examination of the radulae on the scanning electron microscope (not to mention serial histological sectioning) is probably more costly and labour intensive than molecular sequencing. Molecular analysis in contrary is becoming more and more a standard procedure with rapidly decreasing costs that can be performed by the personnel without taxonomic expertise.

Current developments in malacology clearly demonstrate that the recognition of cryptic species, indistinguishable by shell characters and anatomy is becoming a more common phenomenon. This highlights a general problem of traditional taxonomic malacology – the absence of reliable link to the overwhelming majority of existing name-bearing types of molluscs which are represented by material unsuitable for molecular sequencing. The problem exists not only for the species described many decades ago, but it can happen even with mostly recently described ones (*G. moosai* was described slightly over decade ago) but recognised prior to common usage of molecular techniques.

At present while describing new species the preference when designating the types is given to well preserved adult shells. It is advisable that future preference will be given to specimens for which either a sequence exists, or at least the samples are suitable for future molecular analysis.

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Figure captions.

Figure 1. Outline reconstructions with increasing number of harmonics indicated within outlines. In black, original outline. The five landmarks are represented on the shell picture.

Figure 2. Bayesian tree obtained with the COI gene. Posterior Probabilities (superior to 0.5) are given for each node. Groups are numbered top downwards from 1 to 5. For each group and for each cruise within a group, one shell is illustrated (numbered from 1 to 7).

Figure 3. Examined species of *Gemuloborsonia*. **A-E.** *Gemuloborsonia colorata* (Sysoev & Bouchet, 2001). **A.** Holotype, MNHN, shell length 42.5 mm. **B.** Specimen from New Caledonia, Norfolk Ridge, MNHN, shell length 30.0 mm. **C.** Specimen from French Polynesia, E off Rapa, MNHN, shell length 44.7 mm. **D.** Specimen from New Caledonia, Lansdowne Bank, MNHN 17849, shell length 45.5 mm. **F.** Undescribed species, Solomon Islands (sta. 2850), MNHN 41918, shell length 25.8 mm. **G.** *Gemmuloborsonia neocaledonica* Sysoev & Bouchet, 1996, specimen from New Caledonia, Norfolk Ridge (sta. 2097), MNHN 41921, shell length 25.2 mm. **A-E.** shells at the same scale, **F-G.** not to scale.

Figure 4. Radula of examined species. **A.** *Gemuloborsonia colorata* (Sysoev & Bouchet, 2001), MNHN 17849, shell see Fig. 3D-E. **B.** Undescribed species, Solomon Islands (sta. 2850), MNHN 41918, shell see Fig. 3F. **C-D.** *Gemmuloborsonia moosai* Sysoev & Bouchet, 1996, Philippines, Aurora07, sta. CP2658, MNHN 41993, shell see Fig. 7 D. **E-F.** *Gemuloborsonia clandestina* sp. nov. **E.** Paratype, MNHN 41952, shell see Fig. 8 E. **F.** Paratype, MNHN 41943, shell length 18.7 mm. Scale bars 50 μ m, for D – 10 μ m.

Figure 5. CVA for the two groups identified as *G. moosai*, using genetic groups as grouping variable. **A.** Genetic group 1. **B.** Genetic group 2. **C.** Superimposed outlines for minimum (grey line) and maximum (full line) projections onto the axis are represented.

Figure 6. CVA for the two groups identified as *G. moosai*, using cruise of collection as grouping variable. Superimposed outlines for minimum (dotted line) and maximum (full line) projections onto the two principal axes are represented.

Figure 7. A-H. *Gemmuloborsonia moosai* Sysoev & Bouchet, 1996. **A-C.** Holotype, MNHN, shell length 32.4 mm. **D.** Philippines, Aurora 07, sta. CP2658, MNHN 41993, shell length 25.2 mm. **E.** Coral Sea, EBISCO, DW2546, MNHN 41996, shell length 20.1 mm. **F.** Philippines, Aurora07, sta. CP2660, MNHN 41992, shell length 20.9 mm. **G.** Solomon Islands, Salomon 2, sta. 2177, MNHN 41922, shell length 28.6 mm. See radula on Fig. 4C-D. **H.** Solomon Islands, Salomon 3, sta. 2857, MNHN 41927, shell length 27.4 mm. **I.** *G. clandestina* sp. nov. – paratype of *Gemmuloborsonia moosai*, shell length 32.2 mm.

Figure 8. *Gemuloborsonia clandestina* sp. nov. **A-C.** Holotype, MNHN 41937. **D-J.** Paratypes, sta. CP2658. **D.** Shell length 24.9 mm, MNHN 41949. **E.** Shell length 22.4 mm, MNHN 41952. **F.** Shell length 22.3 mm, MNHN 41953. **G.** Shell length 26.3 mm, MNHN

41950. **H.** Shell length 21.4 mm, MNHN 41948. **I.** Shell length 24.8 mm, MNHN 41947. **J.** Shell length 24.8 mm, MNHN 41946. Paratypes H-J were erroneously attributed to *Gemmuloborsonia moosai* with Fourier analysis (see explanations in the text).

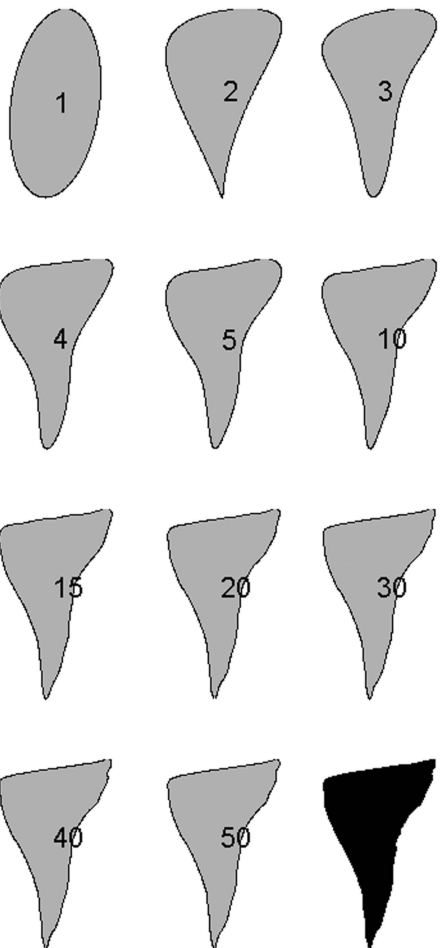
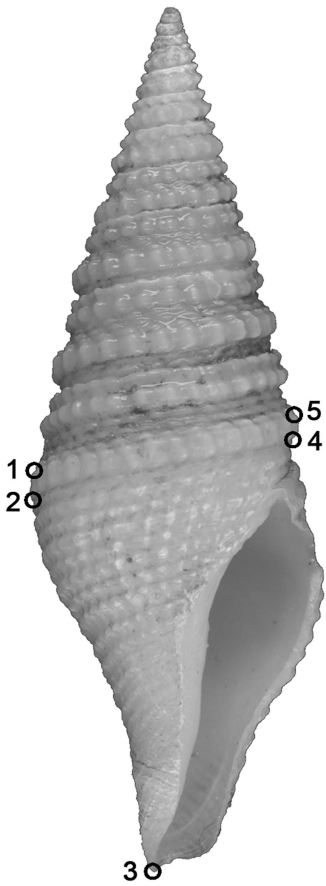
Table 1. Identification number (MNHN ID), cruise, station, species identification, % of assignment obtained with the CVA analysis for the two groups identified as *G. moosai* (% are provided only when the specimens was assigned to the wrong group) and BOLD (Barcode Of Life Database) and GenBank numbers are given for each specimen.

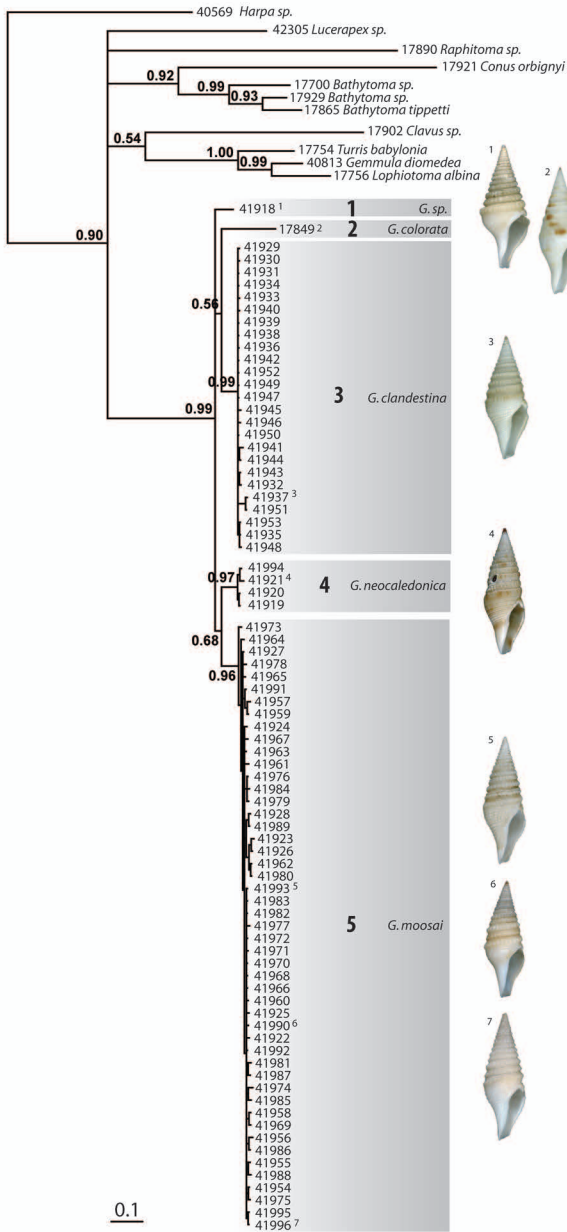
ID	BOLD	GenBank	Cruise	species	% wrong group assignment
17849	CONO192-08	EU015658	EBISCO (Chesterfield Islands)	<i>colorata</i>	
41918	CONO841-08	FJ462616	Salomon 3 (Solomon Islands)	<i>sp.</i>	
41919	CONO597-08	FJ462589	Norfolk 2 (Norfolk ridge)	<i>neocaledonica</i>	
41920	CONO598-08	FJ462588	Norfolk 2 (Norfolk ridge)	<i>neocaledonica</i>	
41921	CONO599-08	FJ462587	Norfolk 2 (Norfolk ridge)	<i>neocaledonica</i>	
41922	CONO758-08	FJ462590	Salomon 2 (Solomon Islands)	<i>moosai</i>	
41923	CONO780-08	FJ462593	Salomon 2 (Solomon Islands)	<i>moosai</i>	
41924	CONO822-08	FJ462602	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41925	CONO811-08	FJ462595	Salomon 2 (Solomon Islands)	<i>moosai</i>	
41926	CONO798-08	FJ462594	Salomon 2 (Solomon Islands)	<i>moosai</i>	0.733
41927	CONO812-08	FJ462596	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41928	CONO844-08	FJ462619	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41929	CONO534-08	FJ462557	Aurora 07 (Philippines)	<i>clandestina</i>	
41930	CONO560-08	FJ462583	Aurora 07 (Philippines)	<i>clandestina</i>	
41931	CONO559-08	FJ462582	Aurora 07 (Philippines)	<i>clandestina</i>	
41932	CONO555-08	FJ462578	Aurora 07 (Philippines)	<i>clandestina</i>	0.7025
41933	CONO556-08	FJ462579	Aurora 07 (Philippines)	<i>clandestina</i>	
41934	CONO557-08	FJ462580	Aurora 07 (Philippines)	<i>clandestina</i>	
41935	CONO558-08	FJ462581	Aurora 07 (Philippines)	<i>clandestina</i>	
41936	CONO547-08	FJ462570	Aurora 07 (Philippines)	<i>clandestina</i>	0.6995
41937	CONO542-08	FJ462565	Aurora 07 (Philippines)	<i>clandestina</i>	
41938	CONO548-08	FJ462571	Aurora 07 (Philippines)	<i>clandestina</i>	
41939	CONO549-08	FJ462572	Aurora 07 (Philippines)	<i>clandestina</i>	
41940	CONO550-08	FJ462573	Aurora 07 (Philippines)	<i>clandestina</i>	
41941	CONO537-08	FJ462560	Aurora 07 (Philippines)	<i>clandestina</i>	
41942	CONO546-08	FJ462569	Aurora 07 (Philippines)	<i>clandestina</i>	
41943	CONO554-08	FJ462577	Aurora 07 (Philippines)	<i>clandestina</i>	
41944	CONO540-08	FJ462563	Aurora 07 (Philippines)	<i>clandestina</i>	0.5562
41945	CONO538-08	FJ462561	Aurora 07 (Philippines)	<i>clandestina</i>	0.7968
41946	CONO536-08	FJ462559	Aurora 07 (Philippines)	<i>clandestina</i>	0.9879
41947	CONO539-08	FJ462562	Aurora 07 (Philippines)	<i>clandestina</i>	0.9565
41948	CONO553-08	FJ462576	Aurora 07 (Philippines)	<i>clandestina</i>	0.6838
41949	CONO541-08	FJ462564	Aurora 07 (Philippines)	<i>clandestina</i>	
41950	CONO535-08	FJ462558	Aurora 07 (Philippines)	<i>clandestina</i>	
41951	CONO552-08	FJ462575	Aurora 07 (Philippines)	<i>clandestina</i>	
41952	CONO545-08	FJ462568	Aurora 07 (Philippines)	<i>clandestina</i>	
41953	CONO544-08	FJ462567	Aurora 07 (Philippines)	<i>clandestina</i>	
41954	CONO813-08	FJ462597	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41955	CONO814-08	FJ462598	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41956	CONO815-08	FJ462599	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41957	CONO816-08	FJ462600	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41958	CONO817-08	FJ462601	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41959	CONO824-08	FJ462603	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41960	CONO825-08	FJ462604	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41961	CONO826-08	FJ462605	Salomon 3 (Solomon Islands)	<i>moosai</i>	0.8906
41962	CONO829-08	FJ462606	Salomon 3 (Solomon Islands)	<i>moosai</i>	0.9887
41963	CONO830-08	FJ462607	Salomon 3 (Solomon Islands)	<i>moosai</i>	0.6045
41964	CONO831-08	FJ462608	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41965	CONO832-08	FJ462609	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41966	CONO833-08	FJ462610	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41967	CONO834-08	FJ462611	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41968	CONO835-08	FJ462612	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41969	CONO836-08	FJ462613	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41970	CONO837-08	FJ462614	Salomon 3 (Solomon Islands)	<i>moosai</i>	

41971	CONO840-08	FJ462615	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41972	CONO842-08	FJ462617	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41973	CONO843-08	FJ462618	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41974	CONO846-08	FJ462620	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41975	CONO847-08	FJ462621	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41976	CONO848-08	FJ462622	Salomon 3 (Solomon Islands)	<i>moosai</i>	0.9973
41977	CONO849-08	FJ462623	Salomon 3 (Solomon Islands)	<i>moosai</i>	0.9068
41978	CONO850-08	FJ462624	Salomon 3 (Solomon Islands)	<i>moosai</i>	0.9572
41979	CONO851-08	FJ462625	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41980	CONO853-08	FJ462626	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41981	CONO854-08	FJ462627	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41982	CONO855-08	FJ462628	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41983	CONO856-08	FJ462629	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41984	CONO857-08	FJ462630	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41985	CONO858-08	FJ462631	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41986	CONO859-08	FJ462632	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41987	CONO860-08	FJ462633	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41988	CONO861-08	FJ462634	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41989	CONO862-08	FJ462635	Salomon 3 (Solomon Islands)	<i>moosai</i>	
41990	CONO762-08	FJ462592	Salomon 2 (Solomon Islands)	<i>moosai</i>	
41991	CONO759-08	FJ462591	Salomon 2 (Solomon Islands)	<i>moosai</i>	
41992	CONO551-08	FJ462574	Aurora 07 (Philippines)	<i>moosai</i>	
41993	CONO543-08	FJ462566	Aurora 07 (Philippines)	<i>moosai</i>	0.8149
41994	CONO571-08	FJ462584	EBISCO (Chesterfield Islands)	<i>neocaledonica</i>	
41995	CONO580-08	FJ462585	EBISCO (Chesterfield Islands)	<i>moosai</i>	0.9999
41996	CONO581-08	FJ462586	EBISCO (Chesterfield Islands)	<i>moosai</i>	
17700	CONO147-08	EU015643	Vanuatu	<i>Bathytoma sp.</i>	
17754	CONO226-08	EU015677	Philippines	<i>Turris babylonia</i>	
17756	CONO481-08	EU127882	Vanuatu	<i>Lophiotoma albina</i>	
17865	CONO242-08	EU015687	Philippines	<i>Bathytoma tippetii</i>	
17890	CONO279-08	EU015713	Philippines	<i>Raphitoma sp.</i>	
17902	CONO225-08	EU015676	Philippines	<i>Clavus sp.</i>	
17921	CONO296-08	EU015721	Philippines	<i>Conus orbigny</i>	
17929	CONO363-08	EU015742	Solomon Islands	<i>Bathytoma sp.</i>	
40569		EU685626	Vanuatu	Harpidae, <i>Harpa</i>	
40813	FRANZ270-08	EU820609	Philippines	<i>Gemmula diomedea</i>	
42305	CONO570-08	FJ462636	Chesterfield Islands	<i>Lucerapex sp.</i>	

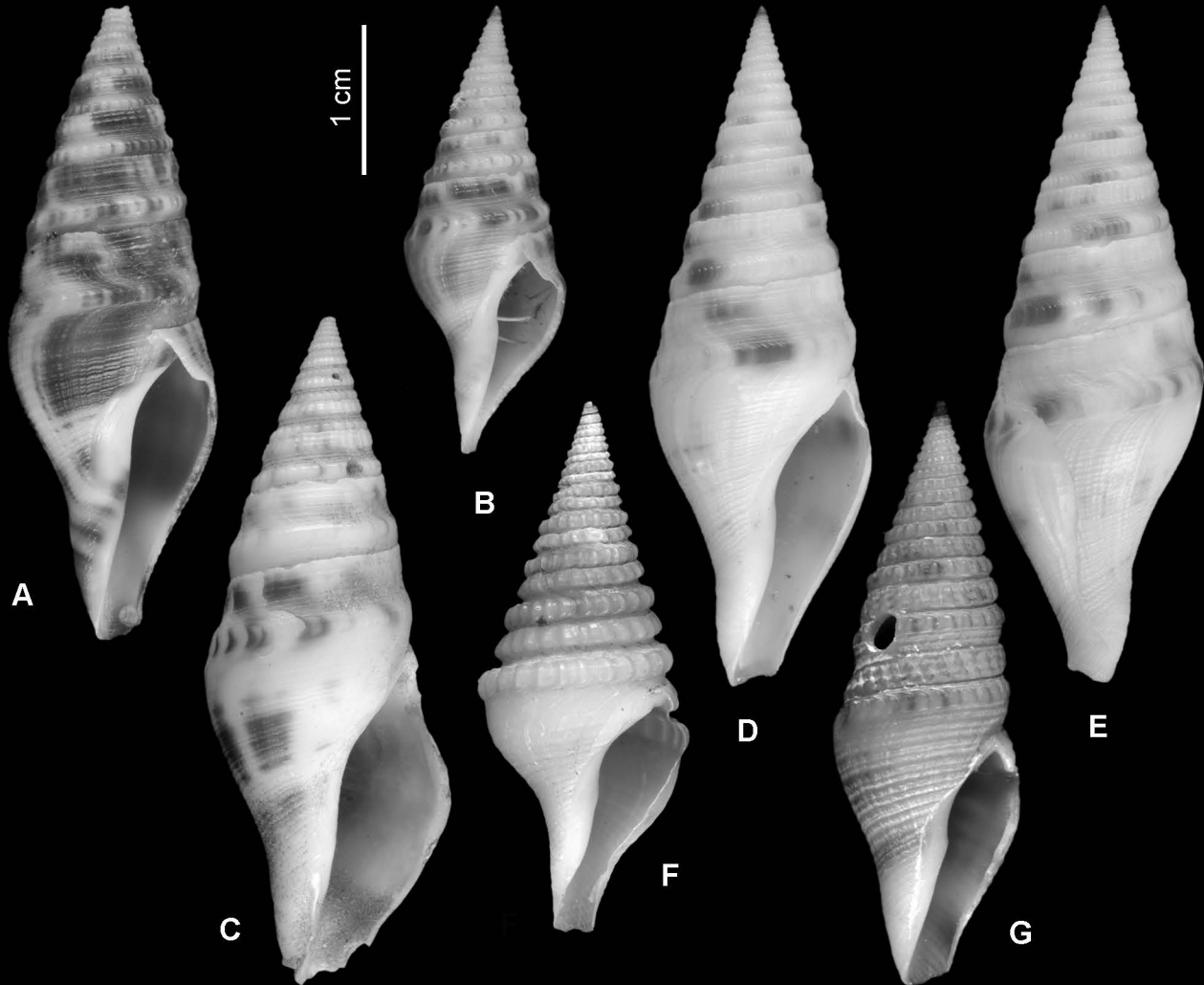
Table 2. assignation of the holotype and the two paratypes of *G. moosai* obtained with the CVA analysis.

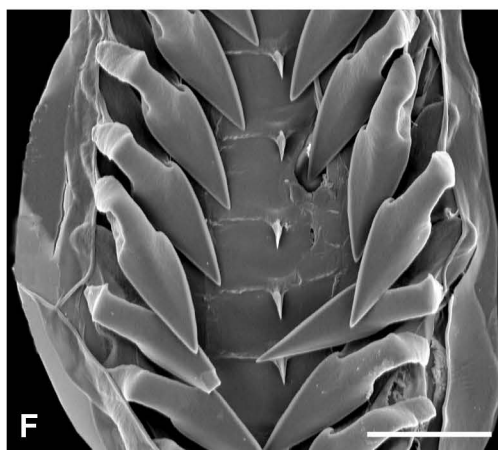
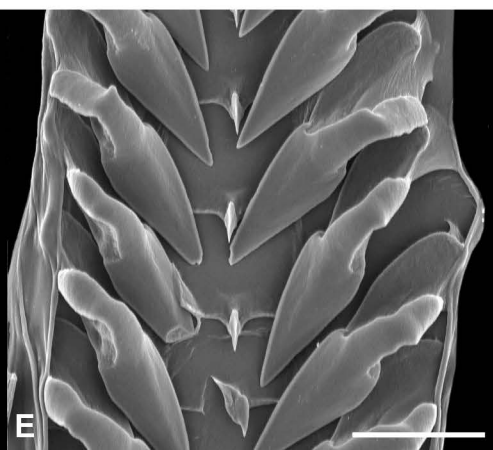
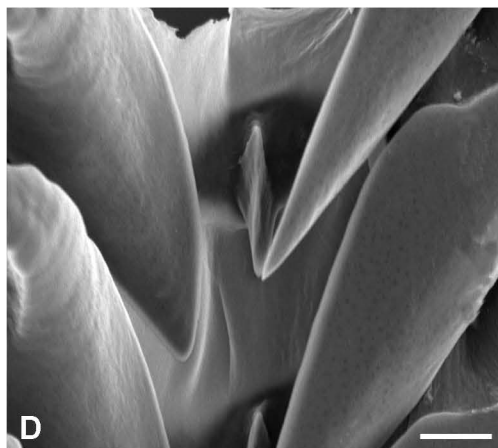
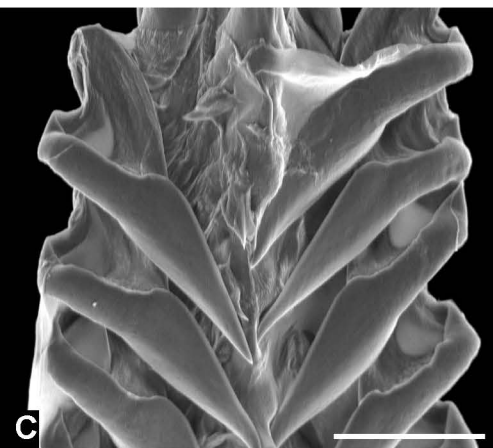
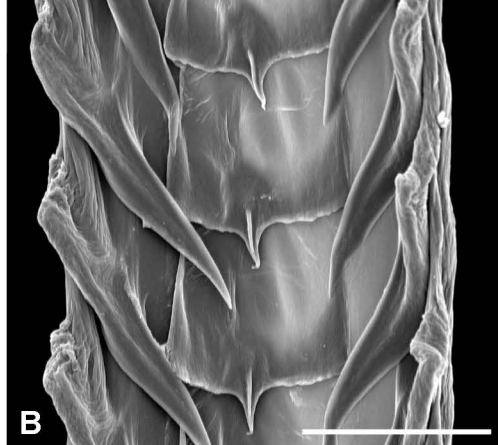
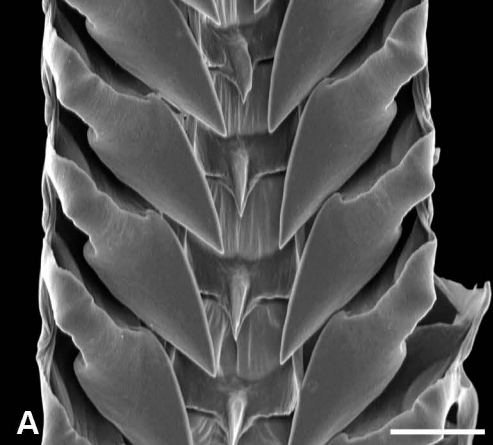
	Localization	<i>G. moosai</i>	<i>G. clandestina</i>
Holotype	Indonesia	0.982	0.018
Paratype 78	Philippines	0.0003	0.9997
Paratype 118	Philippines	0.0823	0.9177

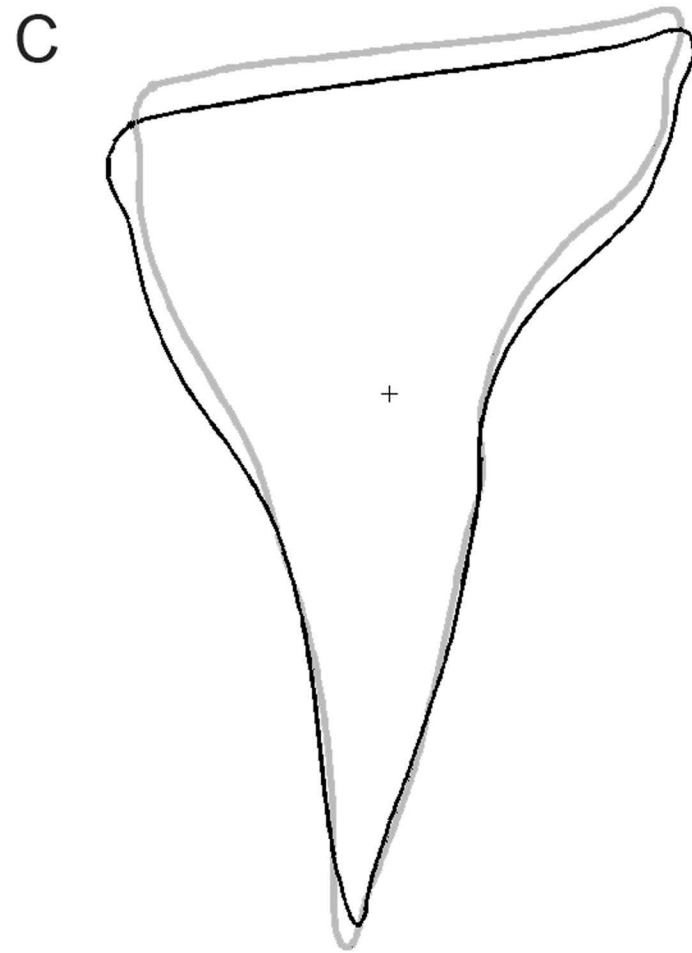
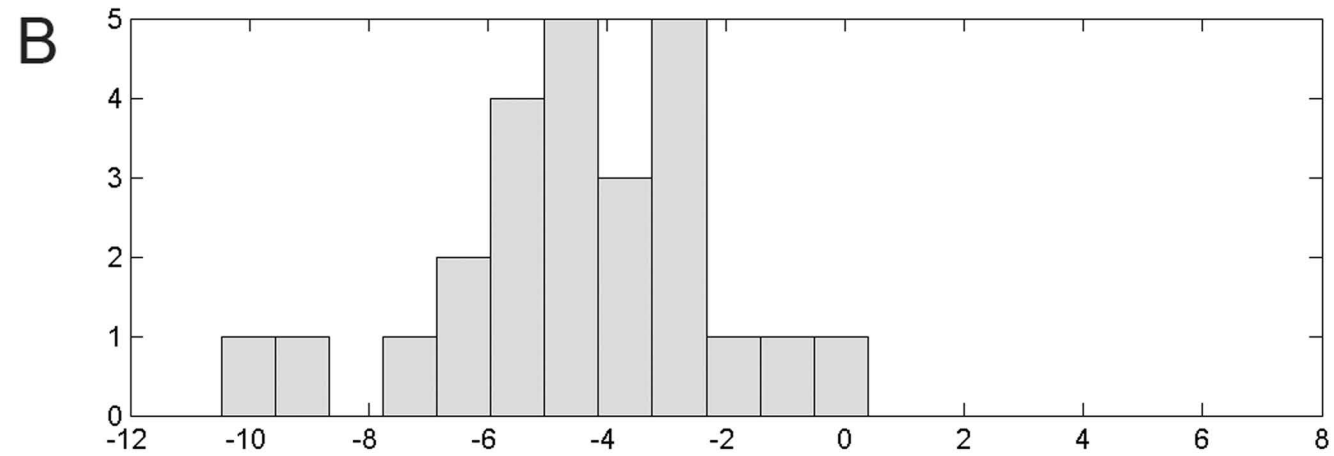
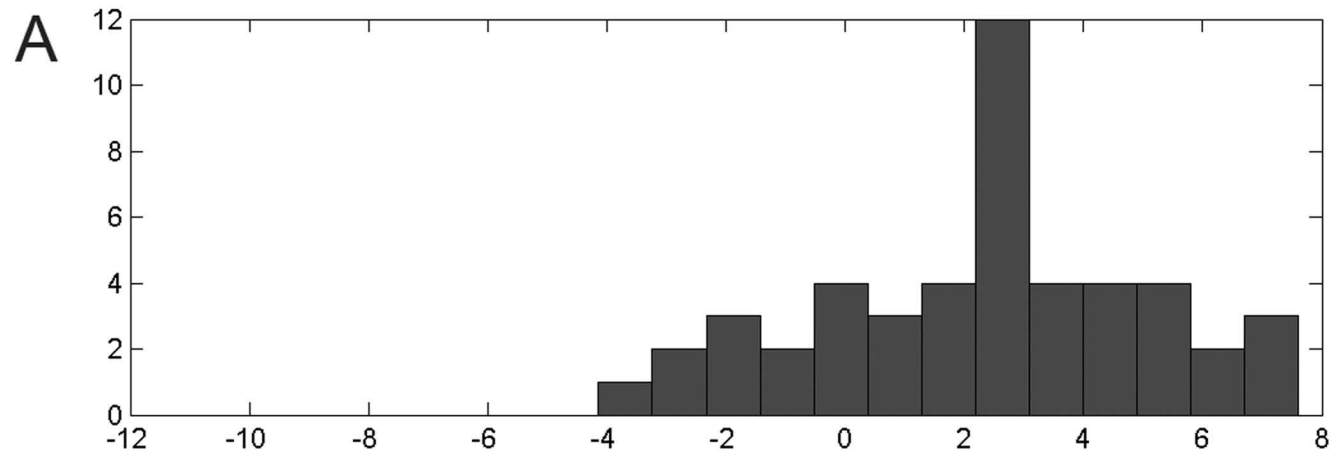


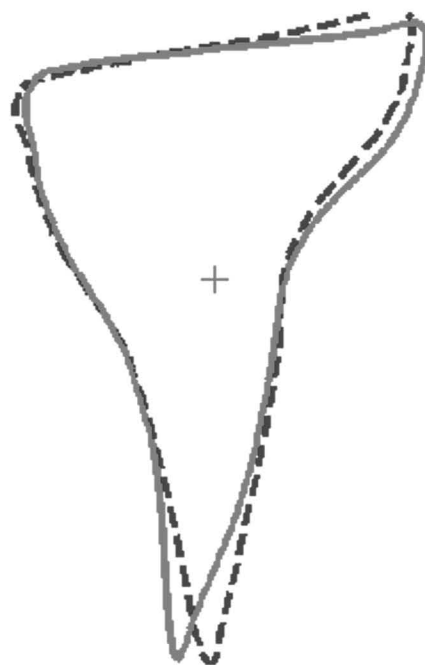
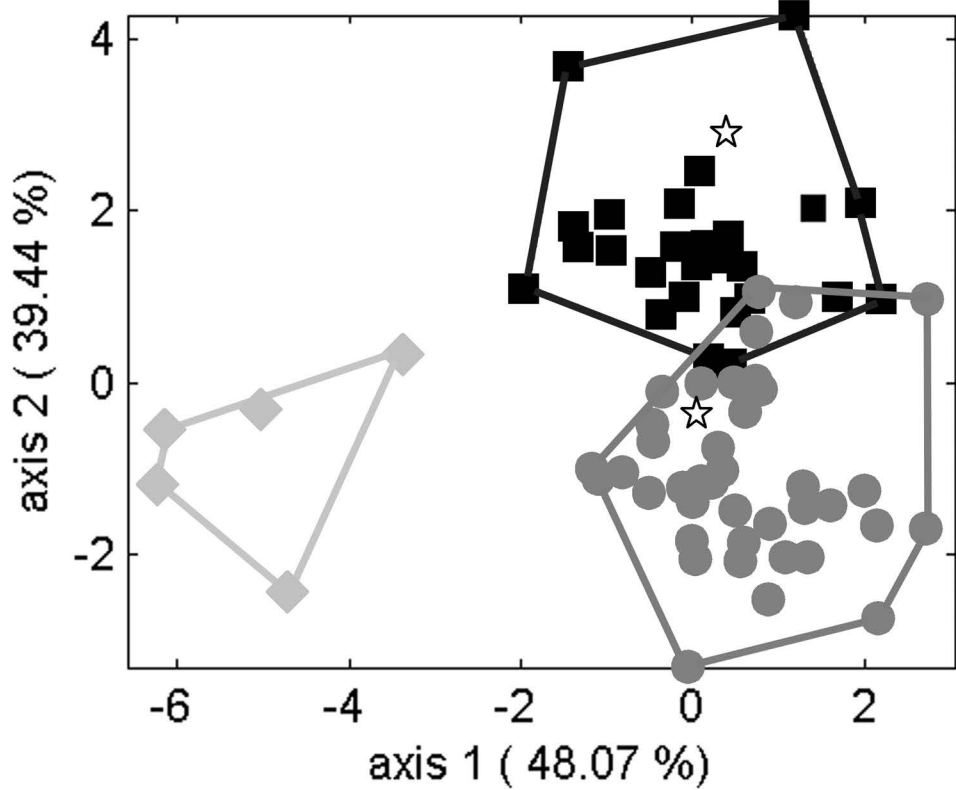
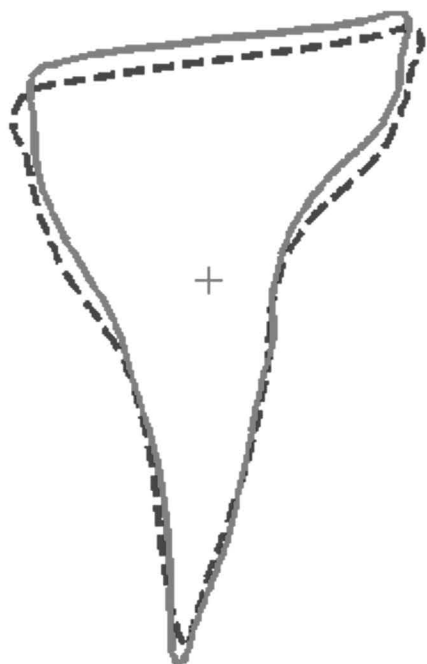


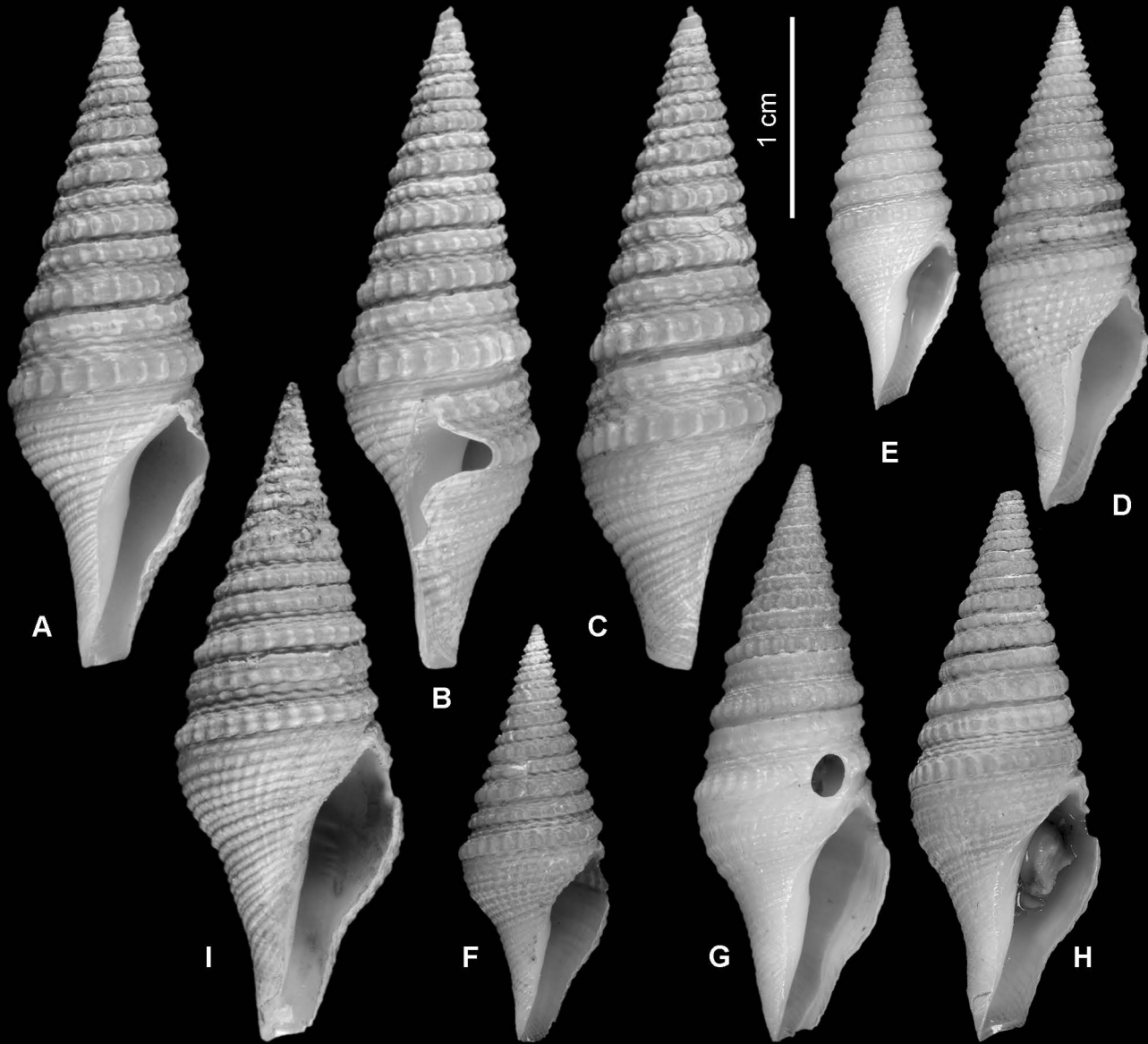
0.1













A



B



C



D



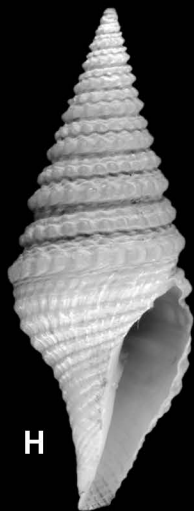
E



F



G



H

1 cm



I



J