



***Lenticellaria* and *Hillerella*, new kraussinoid genera (Kraussinoidea, Brachiopoda) from Indo-Pacific and Red Sea waters: evolution in the subfamily Megerliinae**

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Abstract

Two new kraussinid brachiopod genera, namely *Lenticellaria* **gen. nov.** and *Hillerella* **gen. nov.** are described from Pacific waters in the sub-equatorial zone in the Indonesian Archipelago, from Indian Ocean waters in Madagascar and from Red Sea waters in Egypt (Gulf of Aqaba) and Sudan. This fills the equatorial gap in the distribution of the superfamily Kraussinoidea, known from higher latitudes in both hemispheres. The micromorphic new material described is an excellent example of homeomorphy in brachiopods. It also provides new information on the distribution of the genus *Megerlia sensu stricto* and illustrates subtle variations in the evolutionary process of the reduced brachidium in Kraussinoidea.

Key words: Brachiopoda, Kraussinoidea, *Lenticellaria*, *Hillerella*, Indo-Pacific, Red Sea

Résumé

L’article décrit de nouveaux genres de brachiopodes kraussinides (Kraussinoidea) à savoir *Lenticellaria* **gen. nov.**, et *Hillerella* **gen. nov.**, découverts dans les eaux pacifiques de l’archipel indonésien, dans l’Océan Indien à Madagascar et dans

les eaux de la Mer Rouge (Egypte et Soudan). Ceci permet de combler la lacune équatoriale dans la distribution de ce groupe connu jusqu'ici de latitudes plus élevées dans les deux hémisphères. Ces espèces micro-morphiques sont un excellent exemple d'homéomorphie chez les brachiopodes. Ce travail précise la distribution du genre *Megerlia sensu stricto* et illustre la subtile variation dans le processus d'évolution du brachidium réduit chez les Kraussinoidea.

Mots-clefs: Brachiopodes, Kraussinoidea, *Lenticellaria*, *Hillerella*, Indo-Pacifique, Mer Rouge

Ringkasan

Ini adalah pertama kalinya bahwa Kraussinid genus baru *Lenticellaria* digambarkan dari zona hamper khatulistiwa di kepulauan Indonesia, dan dari Laut Merah. Ada juga genus baru lain *Hillerella* digambarkan dari Madagascar dan Laut Merah. Mengisi kesenjangan dalam distribusi Kraussinoidea yang istimewa ini diketahui dari lintang yang lebih tinggi di kedua belahan. Bahan micromorphic adalah bahan baru yang digambarkan dengan contoh yang sangat baik untuk homeomorphy di Brachiopoda. Ini juga memberikan peluang baru untuk meningkatkan batas dari genus *Megerlia* dan menggambarkan variasi dalam evolusi dengan mengurangi brachidium di Kraussinoidea.

Kata kunci: Brachiopoda, Kraussinoidea, *Lenticellaria*, *Hillerella*, Indo-Pacific, Laut Merah

Introduction

Brachiopods of the superfamily Kraussinoidea erected in 2006 by Lee and MacKinnon constitute a very homogeneous taxonomic group, easily identified by their reduced brachidium with a typical Y-form, their tuberculate inner valve floor, their thick shell, generally costate, and their large foramen.

The latter feature allows the passage of a strong pedicle useful for ensuring very strong fixation to the substrate in high-energy environments. In such conditions, the foramen is often abraded because the thick pedicle is relatively short. At the family and superfamily levels these brachiopods are easily identified. However since the nineteenth century, many studies have been undertaken to try to understand their peculiar taxonomic position within the phylum Brachiopoda. Dall (1870), Eudes-Deslongchamps (1884), Davidson (1852, 1880, 1886), Oehlert (1887), Allan (1940), Jackson (1952), Hatai (1965) and Lee & MacKinnon (2006) are among the most important contributors to our modern concept of this special group. Their respective contributions have been summarized by Hiller *et al.* (2008) who published an exhaustive synthesis of the most current knowledge in the field of the Kraussinoidea. The superfamily is represented by one family, the Kraussinidae Dall, 1870 which comprises four genera: *Kraussina* Davidson in Suess, 1859, *Megerlia* King, 1850, *Megerlina* Eudes-Deslongchamps, 1884 and *Pumilus* Atkins, 1958. The diagnoses of these genera are described in Lee & Mackinnon (2006) and important characters are emphasised in Hiller *et al.* (2008). The latter authors also discussed the taxonomic status of some of the genera and species, most notably the case of *Pantellaria* Dall, 1919, later discarded by Logan (1979, 2007) and others, and *Megerlia echinata* (Fischer & Oehlert, 1890) which is accepted by several authors and considered as invalid by others. Hiller *et al.* (2008) pointed out important conclusions concerning the study of the ontogeny of the brachidia in kraussinid brachiopods. A phylogenetic relationship between the Kraussinoidea and the Laqueoidea is clearly suggested by comparison of early stages of development which are reminiscent of the ontogeny of *Terebratalia transversa* (Sowerby, 1846). They also erected the subfamily Megerliinae which was included within the family Kraussinidae Dall, 1870. Although the relationships between Kraussinoidea and other brachiopod superfamilies were sometimes difficult to clarify due to methodological problems (Endo *et al.*, 1994), the close relationship between the Laqueoidea and Kraussinoidea has been shown by Cohen (2001). A confirmation of the proximity of these two superfamilies has again been discussed by Bitner & Cohen (2015).

This paper described new kraussinid specimens initially discovered in 2009 among sediments collected in a shipwreck in Bali at a depth of 25 m. The material was not abundant and at first glance was considered as juvenile *Megerlia* sp. Two years later, in the Strait of Makassar, at a depth of 30 m, more identical specimens at different stages of growth were found, including a living specimen attached to a shell of a pteriod bivalve: *Isognomon* sp. Among the specimens found were juveniles demonstrating the ontogeny of their brachidium. SEM studies revealed several peculiar morphological characters which lead us to separate these specimens from *Megerlia* and to erect a new species belonging to a new genus. This is also the first time that a kraussinid brachiopod has been found in

sub-equatorial waters from the Indo-Pacific region, filling an enormous gap in the global distribution of this superfamily (Zezina, 1985; Logan, 2007; Hiller *et al.*, 2008). Furthermore, after revising kraussinid material collected from the Red Sea it appears that the same genus is also present there, represented by another new species. Moreover this revision led us to discover another new kraussinid genus and species in another part of the Red Sea and in Madagascar. The new species erected here greatly enlarge the subfamily Megerliinae (Hiller *et al.*, 2008). This paper raises the question of a precise diagnosis for the genus *Megerlia*, introduces some questions about the distribution of *Megerlia truncata* (Linné, 1767) and further illustrates the significance of homeomorphy in this group of brachiopods. For the first time SEM illustrations of the type material of *Megerlia echinata* (Fischer & Oehlert, 1890) are published, making it possible to investigate the morphological characters for this species in more detail.

The development of the brachidium in *Megerlia* species was drawn in detail by Atkins (1961). However, when using scanning electron microscopy, more details of the ontogeny are seen and they are useful for comparison with the ontogeny of the newly-described species. Thus the ontogeny of *M. truncata*, using a population from Italy which represents all growth stages, is illustrated here.

As homeomorphy is common in brachiopods, we listed and analyzed the material presented as *Megerlia* in Indo-Pacific waters. A further revision of some of these specimens seems useful.

Material and methods

Specimens studied in this paper are housed at the following institutions:

MNHM	Muséum National d'Histoire Naturelle, Paris, France.
NBM	New Brunswick Museum, Saint John, New Brunswick, Canada.
NHMW	Natural History Museum of Vienna, Austria.
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

All Indonesian brachiopod specimens used in this study were collected in August 2009 and 2011 by our friend and colleague the late Gregory Willems (La Chaux-de-Fond, Switzerland), a very experienced biologist and scuba diver (Fig. 1) who had the opportunity to pay visits to old shipwrecks in Tulamben (Bali, Indonesia) and in Makassar (South Sulawesi), Indonesia (Fig. 2). G. Willems sent me these specimens for study. During many years he collected much interesting material in which numerous brachiopods were discovered. Without his collaboration this work would not be possible. This paper and a new species are dedicated to him in recognition of his invaluable cooperation.

In Tulamben, east coast of Bali, the shipwreck is the US army cargo vessel *Liberty* which was torpedoed in 1942. It lies on a sand bank just 30 m off the beach (8°14'53.84"S / 115°37'07.66"E). The top of this wreck is 3 m below the surface and the bottom is at 29 m depth. Inside one of the dark holds of the wreck, situated at a depth of 25 m, the upper part of the muddy sediment accumulated on the floor was carefully collected.

In Makassar (South Sulawesi Province), material was collected from a shipwreck of a tanker which was sunk during World War II in the Spermonde Archipelago, west of Makassar, near the small island of Kodingareng (5°06'17.43" S / 119°17'03.92"E). The ship lies on the bottom at a depth of 30 m. The holds of the ship, which are under the influence of a relatively strong current, the "Throughflow" (Gordon *et al.*, 2008) were accessible even though they were very dark. Samples from the upper part of the sediment on the floor were collected. Additionally, several living *Isognomon* and *Malleus* specimens were collected from the ceiling to obtain living specimens of brachiopods. This provided us with a specimen of the newly-described species in living position. Sediments collected in wreck store-holds have been washed and sieved. A sieve of 0.5 mm was used for the smallest fraction. The sieved material was air dried and the brachiopods were picked out under a binocular microscope. The living specimen obtained was preserved in pure ethanol diluted at 70% allowing for future DNA analysis.

For the study of *Megerlia truncata*, specimens dredged off Anzio (Rome, Italy) at a depth of 100 m during April 2006 were used. The sieved sediment was extremely rich in *M. truncata* with all age classes represented, permitting precise SEM observations of the development of the brachidium.



TEXT-FIGURE 1. Photo of our late colleague Gregory Willems (La Chaux-de-Fond, Switzerland) who contributed many times to the discovery of new species of brachiopods.

The material from the Red Sea (Fig. 3) was collected almost entirely by Martin Zuschin (see Grill & Zuschin, 2001 for localities and depths) from the coasts of Egypt and the Sudan and this collection of kraussinids from the Dahab region in the Gulf of Aqaba and from Port Sudan was invaluable in this study.

The material from Madagascar, comprising a single specimen, was dredged by Jacques Picard in 1965 from western coral reefs at Toliara (23°, 21' S / 43°, 41' E) at an unknown depth (general locality shown on Figure 3).

The type specimen of *Megerlia echinata* (Fischer & Oehlert 1890), preserved in the MNHN, has been observed for the first time in detail with scanning electron microscopy (Pl.10, Figs. 1–2).

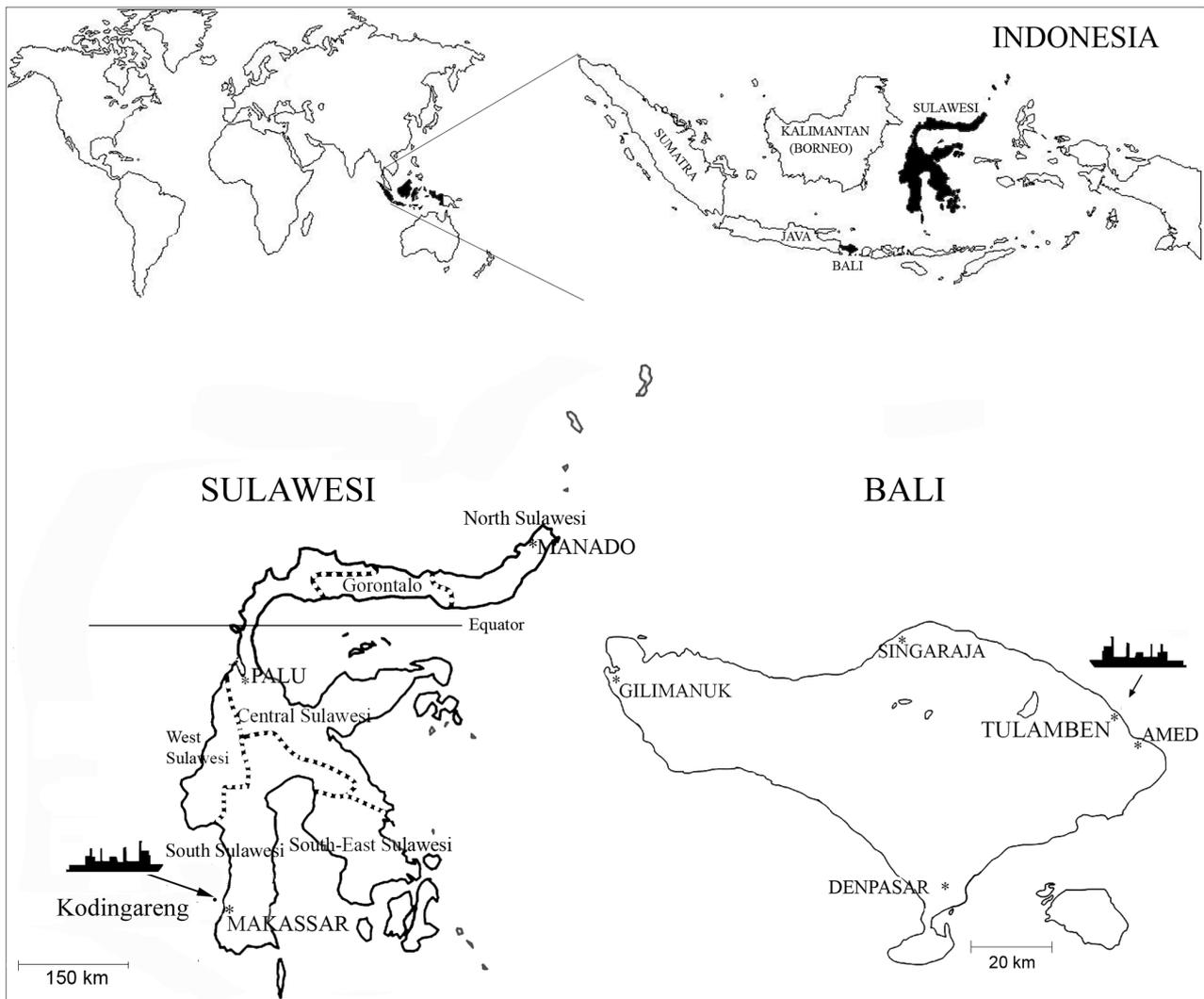
Digital macrophotography was carried out using a Pentax K20D camera. Shells of specimens selected for scanning electron microscopy were treated with household bleach (5% hypochlorite) to remove all remaining soft parts. All the samples were coated with gold and observed using a low vacuum SEM—an ESEM FEI Quanta 200.

Suprafamilial classification follows Williams *et al.* (1996) and Williams *et al.* (2000, pp. 22–27). The hierarchy within the superfamily Kraussinoidea Dall, 1870 follows Lee & MacKinnon (2006) and Hiller *et al.* (2008).

Specimens from Indonesia illustrated in this paper have been deposited under general number I.G. 33227 in the collections of the RBINS. Registered specimen numbers are given below in the text.

Specimens from the Red Sea illustrated in this paper have been deposited in the collections of the NHMW under general number NHMW 87192 and of the NBM with registered specimen numbers given below in the text.

This paper follows the Recommendation 13b of the International Code for Zoological Nomenclature related to the language. Therefore abstracts and diagnoses in French and Bahasa Indonesia have been added.



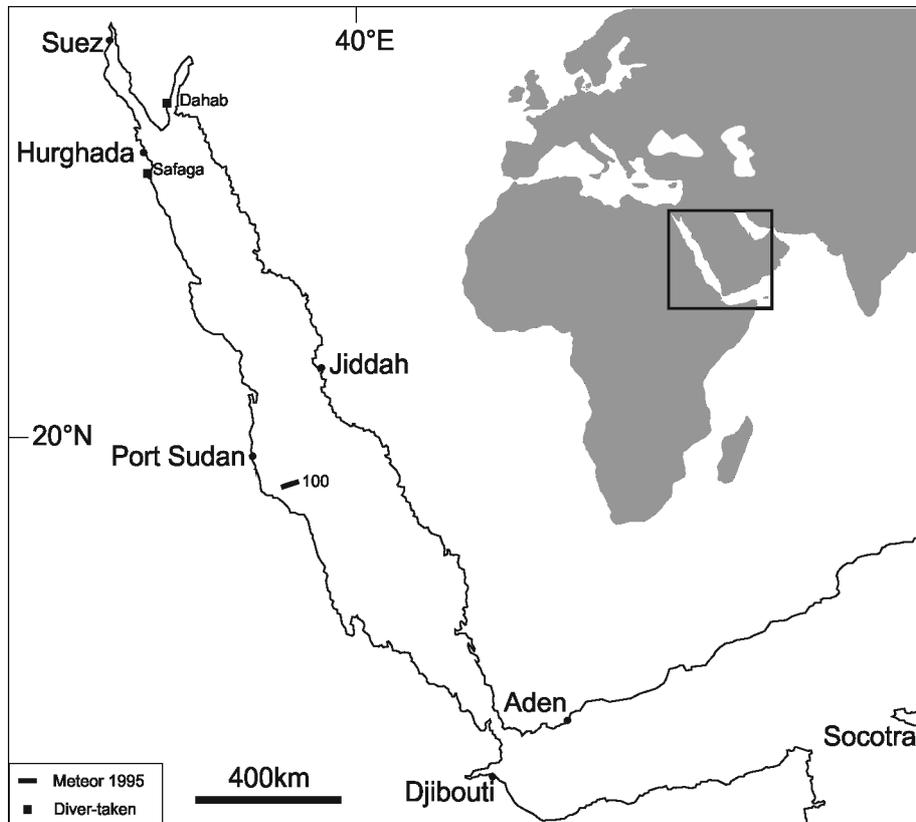
TEXT-FIGURE 2. Map of Indonesia and local maps of Sulawesi and Bali showing the collecting sites, the shipwreck “Liberty” (water depth: 25 m), which sank off Tulamben (Sea of Bali, Bali, Indonesia) and the tanker shipwreck at Kodingareng Island (Spermonde Archipelago, West of Makassar, South Sulawesi, Indonesia).

Results

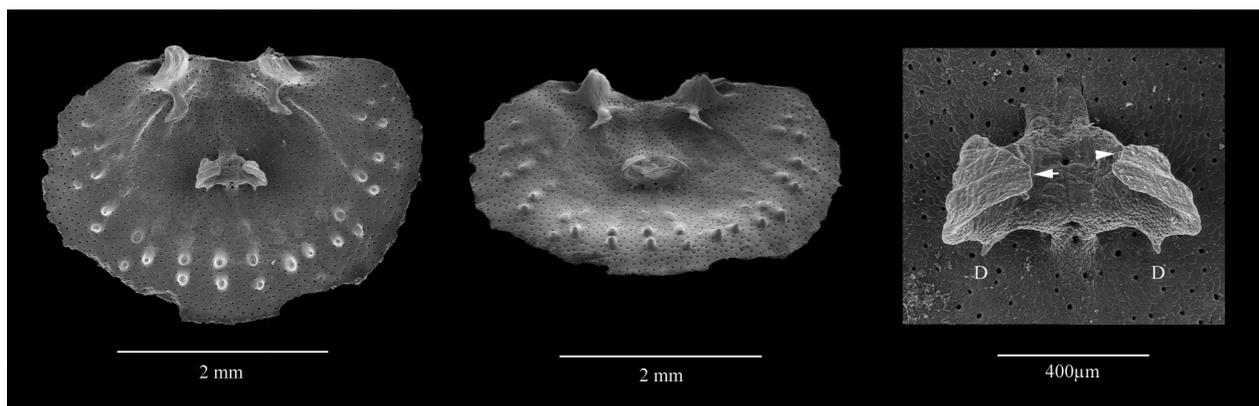
Several brachiopod species were obtained from the sediment collected in the *Liberty* wreck in Bali. The most abundant species is a new, quite large *Novocrania* Lee & Brunton, 2001 which will be described later. It is followed by *Joania arguta* (Grant, 1983) which has been described in Simon (2010). Some *Frenulina sanguinolenta* (Gmelin, 1790) and *Minutella* cf. *minuta* (Cooper, 1981b) are also present in the sample investigated. The last species found is a Kraussinidae represented by a single complete specimen and several fragments of dorsal and ventral valves. The appearance of this specimen, seemingly a juvenile, led us at first glance to determine it as a *Megerlia* sp.

Two years later, diving in the vicinity of Makassar provided us again with several brachiopods. Living *Discradisca stella* (Gould, 1862) was found attached to shells of dead oysters. Undetermined smooth living discinid brachiopods were observed and kept on shells of *Malleus* where they have been placed in ethanol for further study. *Ospreyella mutiara* Simon & Hoffmann, 2013 was also recovered from this wreck, widening the distribution of this thecideoid brachiopod. Also some *Novocrania* were observed on dead shells of *Isognomon* sp. Kraussinids that are identical to the Balinese specimens were collected more abundantly, including one living specimen. In the Makassar material different growth stages are present and the ontogeny of the brachidium can be

established. A careful observation of these specimens using SEM convinced us that these brachiopods could not be assigned to the genus *Megerlia*. When photographed using a macro-objective, the material collected from Bali and Makassar is very similar to a *Megerlia* sp. (Pl. 6, Figs. 1a–b, 2, 3a–c). Even when the specimens are observed with a SEM at a low magnification (Pl. 6, Figs. 4a–e) the “*Megerlia* impression” is sustainable. However, in these specimens the loop is made of two claws (Pl. 6, Figs. 3c, 4f).



TEXT-FIGURE 3. Map of the Red Sea and the Gulf of Aqaba with localities from which brachiopods were collected for the present paper.



TEXT-FIGURE 4. RBINS-INV.138512 Illustration of a juvenile stage of growth of *Megerlia truncata* (Linné, 1767) collected from La Palma, Canary Islands (Spain) with its ring of the loop broken. Note the asymmetrical extremities of the tips of the upper portion of the ring.

Initially we considered that the loop was incomplete or broken. A small *Megerlia* sp. from La Palma, (Canary Islands) with its ring broken on the top (Fig. 4) can be compared with our Indonesian material. In this broken specimen, the damaged ventral parts of the ring have ends showing asymmetrical breaks. In all Indonesian specimens from Bali and Makassar, the sharp claws are always symmetrical and the typical ring of *Megerlia* is

absent. Dead specimens occur in the sediment and no larger shells than those described here were recovered. This suggests that larger adult specimens do not exist and that this material is micromorphic. The small size is an adaptation quite common in brachiopods through time. Some limited examples confirm the fact that such small species were present from the Palaeozoic (Mottequin *et al.*, 2015) through the Mesozoic (Surlyk, 1972; Bitner & Pisera, 1979; Simon, 2000; Bitner & Motchurova-Dekova, 2005) and into the Tertiary (Bitner & Dulai, 2008). This led us to erect a new species placed in a new genus described below as *Lenticellaria gregoryi* **gen. nov.** and **sp. nov.**

When examining brachiopod material collected by M. Zuschin from the Red Sea in Dahab (Gulf of Aqaba) it appeared that other specimens of the genus *Lenticellaria* **gen. nov.** were also abundant there. While all the generic characters are found in this material, some specific details indicate that the Egyptian species is different from the Indonesian type and a new species has been erected here under the name *Lenticellaria marerubris* **sp. nov.**

Revisiting Red Sea material enabled us to review the specimens collected near Port Sudan by the Meteor cruises M5 (1987) and 31/2 (1995). Originally they were assigned by Logan *et al.* (2008) to juvenile stages of *Megerlia echinata* (Fischer & Oehlert 1890). The authors referred to Cooper (1973) but did not provide a detailed description of this material. This brachiopod has an outline similar to *Megerlia* representatives. However, SEM illustrations given on their fig. 2, P–T show several distinct characters which are not observed in *M. echinata sensu* Cooper (1973, pl. 1, figs. 1–3) or *sensu* Fischer & Oehlert (1890). The ventral valve is different, as acute spines all over the ventral outer surface are not visible (a specific feature in the original description of *M. echinata*). However in these specimens from the Red Sea the surface between the tuberculate radial rows is covered by a specific ornamentation. With the magnification used in the illustration by Logan *et al.* (2008) it was not possible to describe it precisely and a revision at higher magnification of this material has been made here. The septum in the ventral valve is not interrupted in its posterior part and that is a difference with *Lenticellaria*. The tuberculation of the dorsal valve floor is limited and tubercles are elongated. In *M. truncata* the tuberculation of the dorsal valve floor is much more developed at the same stage of growth (Pl. 4, Fig. 2a) and the tubercles are in concentric rows and are not elongate. The loop is made of a complete ring but no crural bases are developed. This material from the Red Sea must be considered as new material distinct from *M. truncata* and *M. echinata sensu stricto*, from *Lenticellaria* **gen. nov.** and also distinct from “*Megerlia*” *acrura* Hiller, 1986. These differences warrant the erection of a new genus and a new species *Hillerella bisepta* presented below.

The genus *Megerlia* King, 1850

The main question of this paper is “to be or not to be *Megerlia*”. The type species of this genus is *Megerlia truncata* (Linné, 1767). The original material described by Linné as *Anomia truncata* apparently consists of two dried specimens (as indicated in the Catalogue of Type specimens of the University of Uppsala: n°1907a and n°1907b) and should be Norwegian specimens (“*Habitat in Pelago Norvegico Supra corallia*” Linné, 1767; p. 1152, n° 229). However, the presence of this species off Norway was not mentioned by Logan (2007) or Hiller *et al.* (2008). The species was not found in northerly latitudes such as the Irish coasts by Massy (1925), Norway by Wesenberg-Lund (1939), the North Sea (Cori, 1933) and the Faroe Islands (Thomsen, 2001). In the 19th century *Megerlia* species were not recognized along the British coasts (Forbes & Hanley 1850, 1853). The original Linnaean specimens may have come from another area in the eastern Atlantic or even from the Mediterranean Sea. The current genus description provided by Lee & MacKinnon (2006, p. H2245) stresses the large foramen which is often abraded (considered submesothyrid to amphithyrid), the disjunct deltidial plates and the tuberculate internal valve floors. No cardinal process is developed. Crural bases are present and attached to the inner sides of socket ridges. Descending branches join the cardinalia with the posterior part of the ring of the loop. The brachidium is typically bifurcate (see MacKinnon & Lee, 2006, fig.1312) and a complete ring is built; this is unique among Kraussinoidea.

SEM observations show in detail the development in *M. truncata* and interpretation of the earliest growth stages is here discussed again. The smallest specimen collected from Anzio has a width of 1.4 mm (Pl.1, Figs. 1a, 1b). This specimen is slightly biconvex. The tip of the beak is abraded but the submesothyrid foramen is still intact on its dorsal side. The dorsal valve is smooth and the ventral valve presents some rare tubercles near the anterior commissure. The second specimen (Pl. 1, Figs. 2a, 2b) has a width of 1.73 mm. The shell becomes ventribiconvex

with a smooth dorsal valve whereas the external surface of the ventral valve presents a radial series of tubercles. Noteworthy is that the outer shell surface between the radial ornamentation is smooth. The beak is more abraded and the dorsal valve is affected as the foramen seems amphithyrid. This gradual change is quite continuous during growth as seen on Pl. 1, Figs. 3–7. It appears that the foramen is more and more abraded due to the shortness of the pedicle and the high energy environment where *M. truncata* is generally living. Another development is the appearance of radial costae with tubercles on the external side of the dorsal valve. This tuberculation becomes more important during growth (Pl. 2, Figs. 1–3) although the ventral tubercles always remain more developed in size. An underestimated character in *M. truncata* is the absence, at all growth stages, of secondary tubercles, spines or scales in the “intercostal” zones. In these zones the shell remains smooth and only concentric growth lines are perceptible (Pls. 1–5). This is not the case in *M. echinata* (Pl. 10, Figs. 1, 2a–d) as strong spines cover the whole external surface of the ventral valve (see also Fischer & Oehlert, 1891, pl. 7, figs 13a and b).

Examination of many specimens of *M. truncata* from the whole Mediterranean Sea also clearly shows that both valves are provided with radial tuberculation, the ventral tuberculation always being stronger than the dorsal one. Specimens with abraded dorsal tubercles are found but an entirely smooth dorsal valve without any tuberculation has not been observed. This feature is important for distinguishing *M. truncata* from *M. echinata* (see below).

The ontogeny of the brachidium in *Megerlia*

At the beginning (shell width: 1.4 mm), the brachidium (Pl. 3, Figs 1a–d) is supported by a very low septal pillar. In lateral view (Pl. 3, Figs. 1c, 1d), it is possible to see the earliest beginning of the bifurcate stage which is built by some fibers on each side of the anterior part of the septal pillar. No crura are produced at this stage (Pl. 3, Fig. 1e) and the tuberculation of the inner valve floor is very limited.

A little later (shell width: 1.73 mm), the brachidium (Pl. 3, Figs. 2a–f) shows clearly the bifurcate septum and the development of a cucullate phase. This structure is in fact a slightly posteriorly concave plate built by the two anterior parts of the bifurcate septal pillar (Pl. 3, Fig. 2c, anterior view). It has a quite different origin than the cucullate phase observed in terebratulid brachiopods, as explained by MacKinnon & Lee (2006). However, these authors pointed out that “the distal extremities of the Y-shaped median septum become united by a narrow transverse band to form a ring” (p. H1983). This stage presented as an annular phase (MacKinnon & Lee, 2006, p. H1983) is not observed in our material. For us, this is a “pseudo annular phase” that occurs later by a resorption process as described by Atkins (1961). The cucullate cone formed by the extremities of the bifurcate septal pillar is more deeply extended posteriorly. The valve floor is slightly more tuberculate. Crural bases are emerging (Pl. 3, Figs. 2a, 2c, 2g) from the anterior part of the inner side of the socket ridges.

At the next stage (shell width: 2.3 mm) the cucullate cone becomes still deeper and the medio-posterior part of the cone disappears by resorption (Pl. 3, Figs. 3a–e). However the ventro-anterior part of the cucullate cone remains completely intact. The “ring” begins to be constituted here. The inner valve floor has now two rows of tubercles. The next stage is very important (Pl. 3, Figs. 4a–c). The dissolution of the medio-posterior part of the cucullate structure is stronger and the anterior part of the cone produces the ring of the loop which is one of the most important loop features in *Megerlia* (shell width: 2.87 mm). The “pseudo annular” phase is now completed. The ring results only from the non-resorption of the anterior part of the cucullate structure (Pl. 3, Fig. 4c). At this stage of growth the descending branches are appearing from crural bases (Pl. 3, Fig. 4a) and the tuberculation of the inner valve floor is still increasing. Another view of this stage is given on Pl. 4, Figs. 1a–d. Just after, when the resorption process is completed, two “flanges” remain on each posterior side of the ring. Simultaneously, at the anterior edges of the dorsal side of the ring, the anterior portions of the descending branches are appearing (shell width: 4.8 mm). The posterior part of the descending branches is much more developed (Pl. 4, Figs. 2a–g).

The residual “flanges” disappear and the two parts of the descending branches are merged together. This step is well seen in Pl. 4, Figs. 3a–e (shell width: 5.6 mm). There are now five rows of concentric tubercles on the inner valve floor. The antero-lateral parts of the ring are thickening and projecting anteriorly (Pl. 5, Figs. 1a–g). This stage is also when an adult plectolophe lophophore is effective (Atkins, 1961). Crural processes are now well developed. They are still increasing during the last growth stage (Pl. 5, Figs. 2a–c). The adult loop stage is now completed.

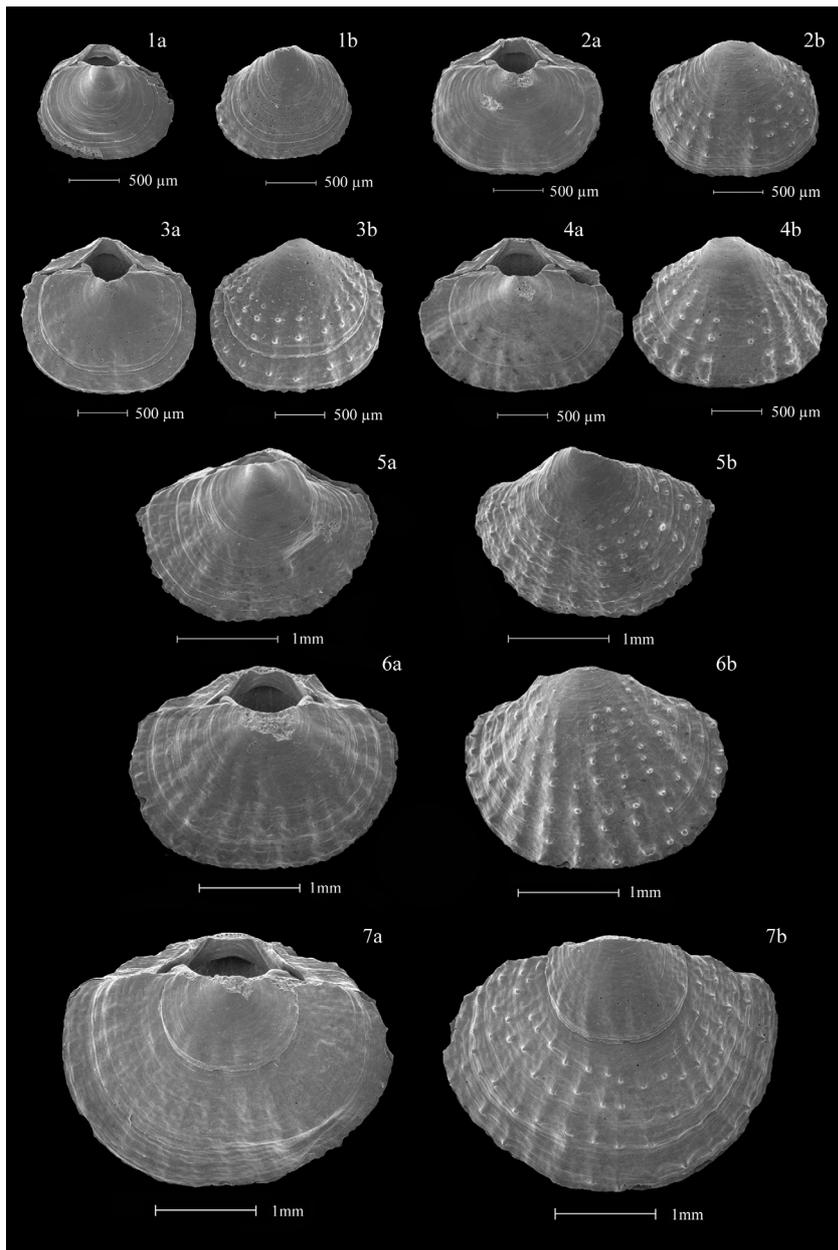


PLATE 1. Growth stages of *Megerlia truncata* (Linné, 1767). External views of early juvenile and juvenile specimens. The shell surface between the radial tubercles series on the ventral valve always remains smooth, without spines or scales. Material collected from Anzio (Roma, Italia) at a depth of 100 m. Size of the specimens indicated with scale bars. a: dorsal views; b: ventral views.

Fig. 1. RBINS-INV.138500. The smallest specimen observed. The dorsal valve is smooth and the ventral has few tubercles mainly in subcommissural position. The beak is intact and the foramen is submesothyrid.

Fig. 2. RBINS-INV.138501. The beak begins to be abraded and the umbo of the dorsal valve is affected by abrasion. The tuberculation of the ventral is stronger with more radial rows.

Fig. 3. RBINS-INV.138502 This specimen is a little larger with a similar number of radial rows of tubercles. The foramen is better preserved and remains hypothyrud.

Fig. 4. RBINS-INV. 138503. Larger well-preserved specimen. The tubercles are stronger but the number of radial rows of tubercles remains the same.

Fig. 5. RBINS-INV.138504. At this stage of growth the dorsal valve is smooth but “pseudo costae” are emerging like undulations. The beak is abraded and the umbo of the dorsal valve is affected.

Fig. 6. RBINS-INV.138505 The number of radial rows of tubercles on the ventral valve is increasing. The undulate “pseudo costae” of the dorsal valve are more visible. The foramen begins to be “amphithyrud” due to the stronger attrition of the beak.

Fig. 7. RBINS-INV.138506 Increasing of the tuberculation of the ventral valve and increasing of the smooth undulate costellation of the dorsal valve. Foramen “amphithyrud” due to strong attrition of both ventral and dorsal umbos.

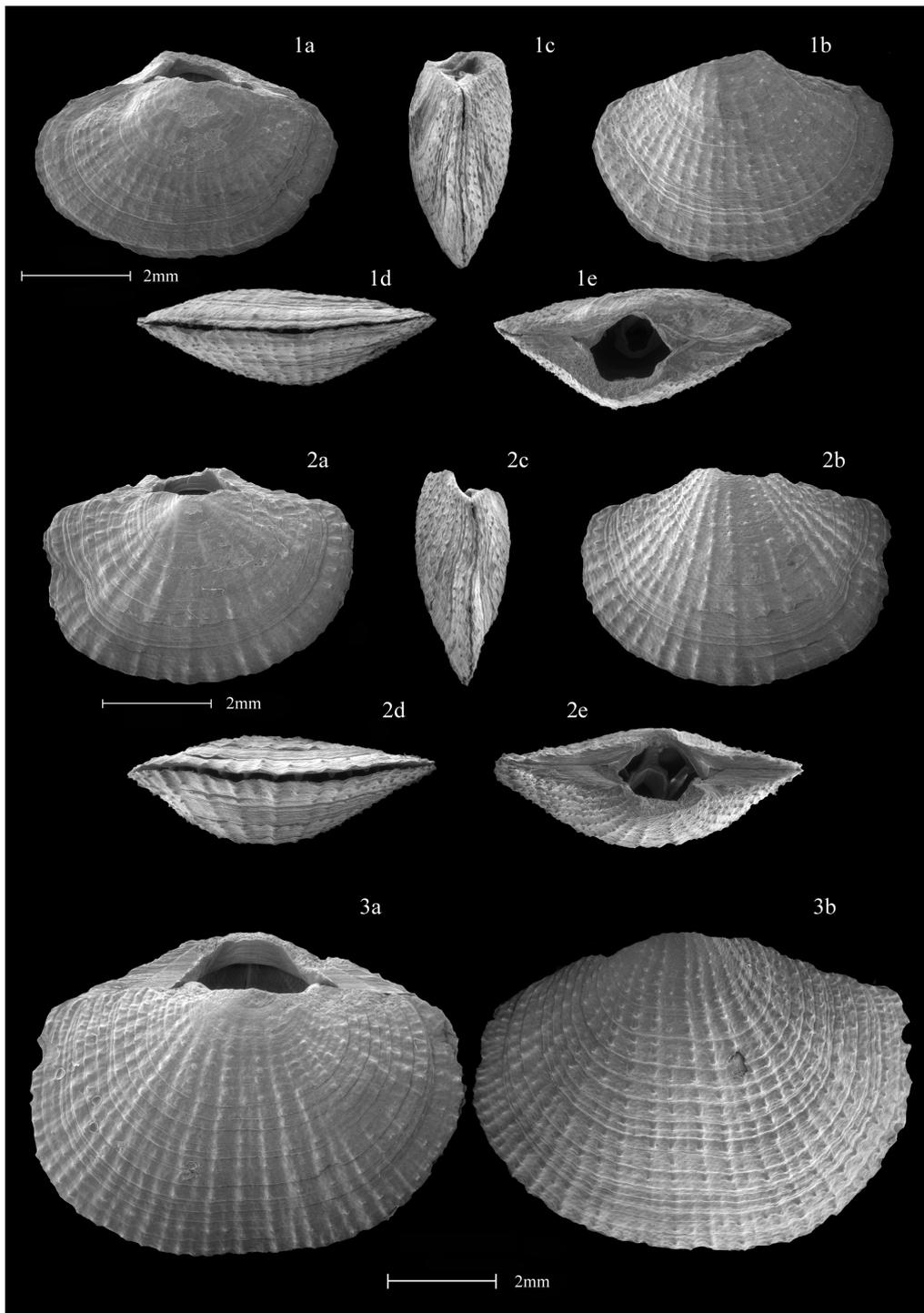


PLATE 2. Further growth stages of *Megerlia truncata* (Linné, 1767). Material collected from Anzio (Roma, Italia) at a depth of 100 m. Size of the specimens indicated with scale bars. External views of larger specimens through to adult stage of growth. The shell surface between the radial tubercles series on the ventral valve remains always smooth, without spines or scales. Material collected from Anzio (Roma, Italia) at a depth of 100 m. Size of the specimens indicated with scale bars. a: dorsal views; b: ventral views; c: lateral views; d: anterior views; e: posterior views.

Fig. 1. RBINS-INV.138507 Biconvex specimen with many radial rows of tubercles on the ventral valve. Radial tuberculation is also visible now on the dorsal valve but the tubercles are weaker. The anterior commissure is slightly sulcate, the lateral commissure is straight; The foramen seems amphithyrid due to attrition of the beak.

Fig. 2. RBINS-INV.138508 A little larger stage of growth where new radial rows of tubercles are intercalated; this specimen is ventribiconvex.

Fig. 3. RBINS-INV.138509 Adult stage of growth. For this specimen the abrasion of the beak did not occur. The foramen is submesothyrid.

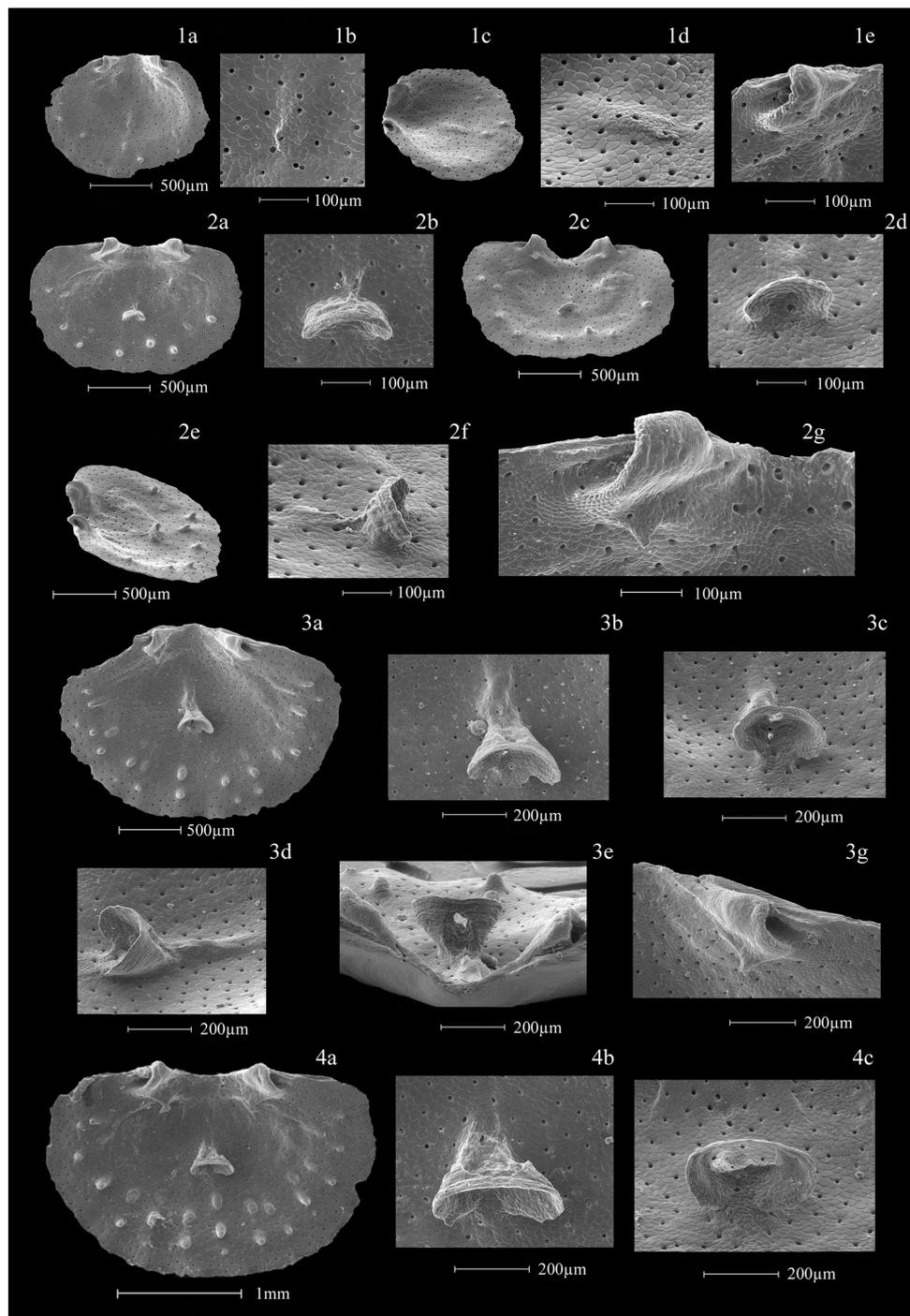


PLATE 3. Bifurcate loop development in the dorsal valve of *Megerlia truncata* (Linné, 1767). Early juvenile and juvenile specimens collected from Anzio (Roma, Italia) at a depth of 100 m. Size of the specimens indicated with scale bars.

Fig. 1. RBINS-INV.138500 The earliest stage of development. A small crest (septal pillar) appears (1a;1b ventral view). In oblique lateral view (1c; 1d) some fibers are already tracing the bifurcation of the future septum. Crura are not present (1e). A few tubercles are present on the valve floor.

Fig. 2. RBINS-INV.138501 A small concave suboval plate (a–f) is erected by the two parts of the bifurcate septal pillar (clearly visible: 2b). This plate has a slightly conical profile in lateral view (2e; 2f). Crura are emerging from the inner socket ridges (2g). A subcommissural row of tubercles are now developed on the dorsal valve floor.

Fig. 3. RBINS-INV.138504 The bifurcate septal pillar is wider (3a; 3b) and the posterior part of the conical cucullate structure begins a resorption process as a small hole is now visible posteriorly (3c, 3d; 3e). Small crura are now clearly visible (3f). There are nearly two complete concentric rows of tubercles on the dorsal valve floor.

Fig. 4. RBINS-INV.138505 The resorption process continues in direction of the anterior part of the cucullate structure. However the most ventro-anterior portion of the structure is preserved giving birth to the ring of the loop. (4b; 4c). Crura present (4a). The tubercles are stronger but generally not elongated (3a).

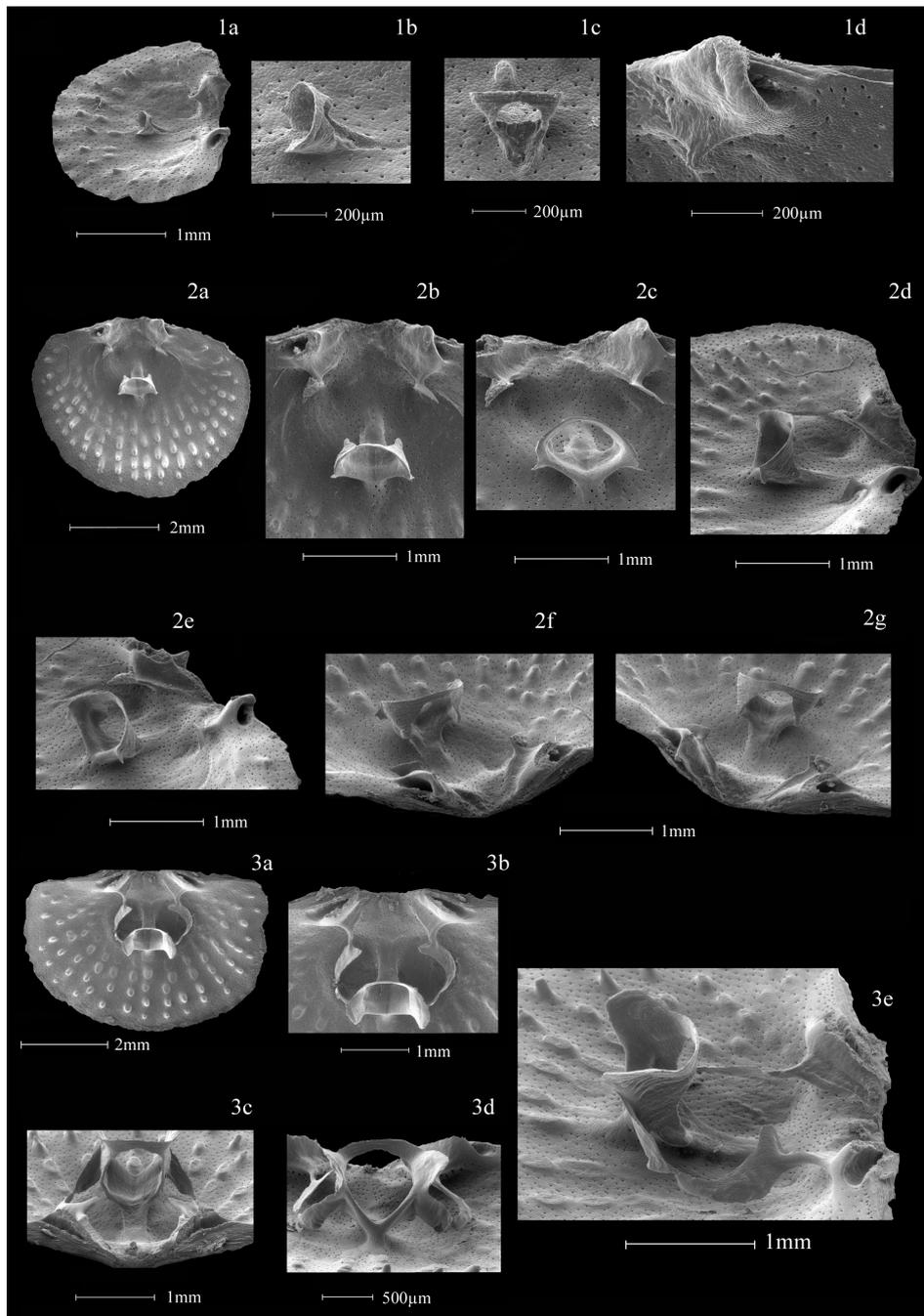


PLATE 4. Further development of the bifurcate loop development in the dorsal valve of *Megerlia truncata* (Linné, 1767). Juvenile and young specimens collected from Anzio (Roma, Italia) at a depth of 100 m. Size of the specimens indicated with scale bars.

Fig. 1. RBINS-INV.138505 A slightly larger specimen with another example of ring formation. Here the visible part of the ring is wider (1a–c).

Fig. 2. RBINS-INV.138507 At this size, the posterior parts of the descending branches begin their development (2a–d). The resorption process of cucullate phase is nearly finished and the complete thin ring is established (2a–g), the ventral side being the thinner portion. Two flanges subsist in ventro-posterior part of the ring. In the dorso-anterior part of the loop the beginning of the anterior part of the descending branches appear (2b; 2f). The tuberculation of the valve floor is made of many concentric rows. The tubercles of the posterior zone are slightly elongated while those of the anterior zone are subcircular.

Fig. 3. RBINS-INV.138508 Stage of growth showing the exact moment when the posterior and the anterior parts of the descending branches enter in contact before the fusion of the two portions. Crural processes are now developing. The anterior lateral parts of the ring are extending ahead as two thick parallel wings. In dorsal view the descending branches seem fixed to the posterior part (3a–b) of the ring but as seen in Fig. 3e they are really attached at the anterior parts of the ring. The number of concentric rows of tubercles is lower than in Fig. 2 indicating that it is a variable character.

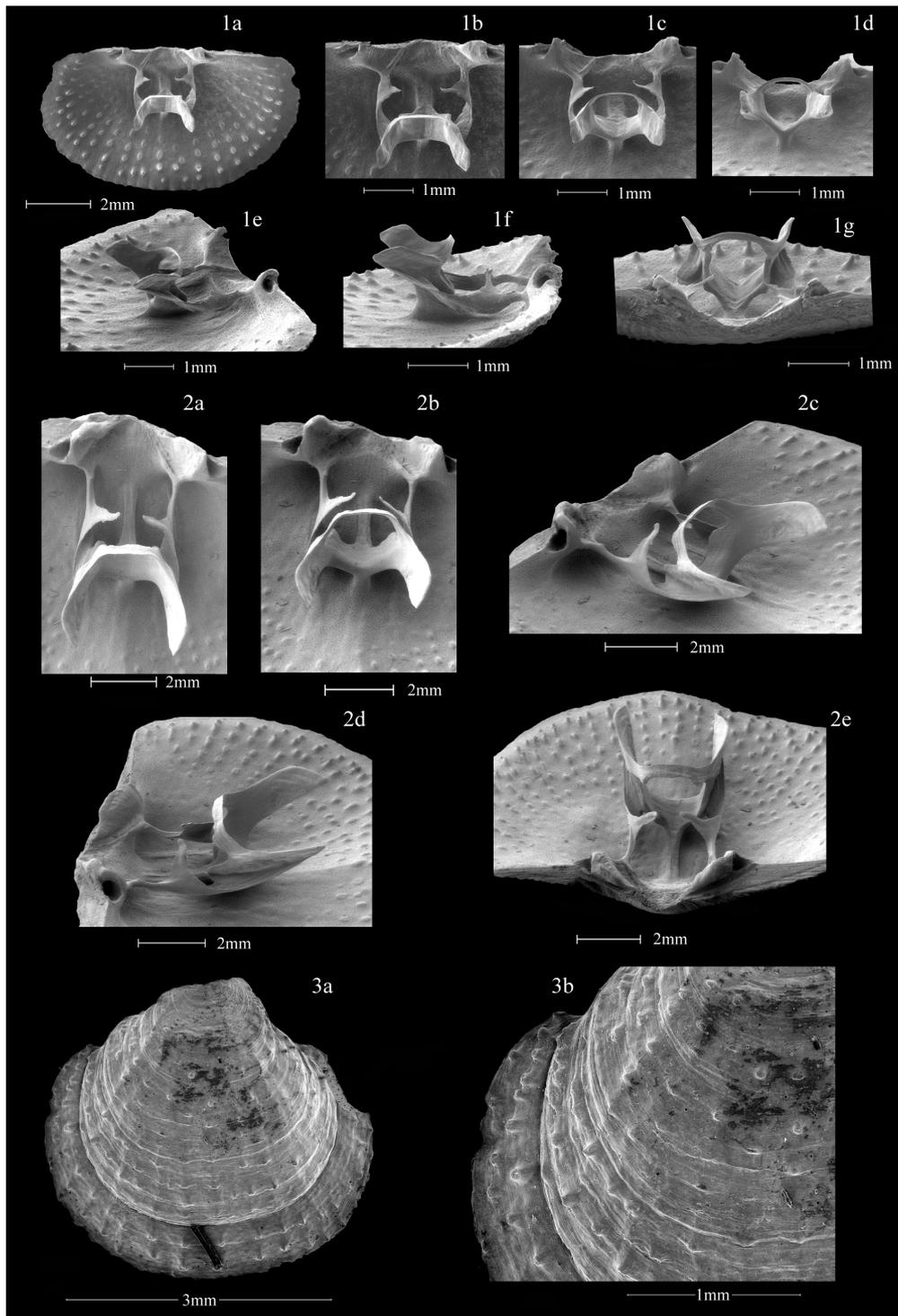


PLATE 5. End of the development of the bifurcate loop development in the dorsal valve of *Megerlia truncata* and detail of the ventral valve ornamentation in an adult specimen. Material collected from Anzio (Roma, Italia) at a depth of 100 m. Size of the specimens indicated with scale bars.

Fig. 1. RBINS-INV.138509 Enlargement of the anterior-lateral parts of the loop (1a; 1b; 1f). The ventral side of the ring is very thin (1c; 1d; 1e; 1g). Crural processes are longer and pointed and they are situated at mid-loop (1a). The two flanges of the ventro-posterior part of the ring nearly disappear by resorption (1b).

Fig. 2. RBINS-INV.138510 Adult brachidium completely developed. The crural processes are now placed more anteriorly (2a–e). Around seven rows of concentric rows of tubercles are visible (2e). Note that the ventral part of the ring is very thin but it remains relatively wide.

Fig. 3. RBINS-INV.138511 Ventral adult valve in ventral view. The tuberculate radial rows are readily visible (3a) and spaces between the tubercles are smooth without spines or scales (3b).

Taxonomy

PHYLUM BRACHIOPODA DUMERIL, 1806

SUBPHYLUM RHYNCHONELLIFORMEA WILLIAMS *ET AL.*, 1996

CLASS RHYNCHONELLATA WILLIAMS *ET AL.*, 1996

ORDER TEREBRATULIDA WAAGEN, 1883

SUPERFAMILY KRAUSSINOIDEA DALL, 1870

FAMILY KRAUSSINIDAE DALL, 1870

SUBFAMILY MEGERLIINAE HILLER, MACKINNON & NIELSEN, 2008

Genus *Lenticellaria* Simon, Logan & Mottequin, gen. nov.

Type species: *Lenticellaria gregoryi* Simon, Logan & Mottequin sp. nov.

Etymology. from the word “lenticel” a botanical term meaning a kind of pore present on the surface of the bark of trees. Lenticels may be streak-like in shape. This name is derived from the scaly ornamentation of the shell surface.

Diagnosis. Micromorphic kraussinoid slightly wider than long, with dorsal valve external surface smooth and radial tuberculate ventral valve. External surface of the ventral valve densely ornamented with very small scales disposed in concentric lines. Loop bifurcate, extremely reduced to two sharp claws. Crura present. Cardinal process, hinge plates and descending branches absent.

Lenticellaria gregoryi Simon, Logan & Mottequin, sp. nov.

Pl. 6, Figs 1–4; Pl. 7, Figs. 1–3; Pl. 8, Figs. 1–2; Pl. 9, Figs. 1–2.

Holotype. *Lenticellaria gregoryi* Simon *et al.*, Pl.6, Figs. 3a–c; Pl. 8, Figs. 1a–g, 2a–f; Pl. 9, Figs. 1a–e. It is a perfectly preserved articulated specimen which has been opened for the present study and is preserved in the collections of the Royal Belgian Institute of Natural Sciences, RBINS-BT. 4. The morphological measurements of the holotype are indicated in Table 1.

Paratypes. RBINS-BT. 5. A complete articulated specimen illustrated from Kodingareng, Makassar, Indonesia Pl. 6, Figs. 1a–b, 4a–g and Pl. 7, Fig. 1a–f. RBINS-BT. 6. A ventral valve from Kodingareng, Makassar, Indonesia illustrated Pl. 6, Fig. 2; Pl. 7, Fig. 2a–f. RBINS-BT. 8. A ventral valve from Tulamben, Bali, Indonesia illustrated Pl. 7, Fig. 3a–c. RBINS –BT. 7. Complete articulated juvenile specimen from Kodingareng, Makassar, Indonesia illustrated Pl. 9, Figs. 2a–g.

Etymology. This species is dedicated to the late Gregory Willems and his first name is used for the species name.

Locus typicus: Tanker-shipwreck near Kodingareng Island (Spermonde Archipelago), Makassar, South Sulawesi, Indonesia (5°06'17.43" S 119°17'03.92"E).

Material investigated

From Makassar (Kodingareng wreck): 15 specimens. 10 complete articulate specimens of different sizes (one was a living specimen, now preserved in ethanol), two isolated dorsal valves with brachidium and three isolated ventral valves.

From Tulamben (Bali): one articulated specimen, one ventral valve and three incomplete ventral valves.

Diagnosis of species. Micromorphic brachiopod, wider than long with a semicircular outline in dorsal view. The external surface of the dorsal valve is smooth whereas the external surface of the ventral valve has radial tuberculation. Between the radial rows of tubercles, numerous scales with typical “Gaussian curve” outline are developed in concentric lines. Foramen amphithyrid. Cardinal process and hinge plates absent. Inner dorsal valve floor tuberculate. Short crura developed. Loop, going through a cucullate phase, a “pseudo” annular phase and finally consisting of two simple claws, relatively wide, with sharp tips. Base of the bifid septum unraised. Descending branches absent. Septum on the ventral valve floor partly interrupted in its posterior portion.

Diagnose de l'espèce. Brachiopode micro-morphique, plus large que long avec un aspect semi-circulaire en vue dorsale. La surface extérieure de la valve dorsale est lisse tandis que la surface de la ventrale montre une ornementation radialement tuberculée. Entre les rangées de tubercules se développent des écailles distribuées en

lignes concentriques. Foramen amphithyride. Processus cardinal et plaques de charnière absentes. Surface dorsale interne tuberculée. Crura très courtes toujours présentes. Brachidium adulte consistant en deux pinces à extrémités pointues formées par une phase cuculée évoluant par une « pseudo » phase annulaire. Branches descendantes absentes. Septum de la valve ventrale interrompu dans sa partie postérieure.

TABLE 1. *Lenticellaria gregoryi* n. sp. Morphometric measurements were taken from the 14 measurable specimens extracted from the sieved sediments collected in the shipwrecks in Bali and in Makassar. L: length (mm); W: width (mm); T: thickness (mm); ØF: maximal width of the foramen (mm); Wbrach: maximum width of the brachidium (mm); ↔: distance between the acute tips of the brachidium (µm); L/W= ratio length to width, T/W= ratio thickness to width; ØF/W: ratio width of foramen to width. nm: value not measured. np: measure not possible (one tip is broken). “No brach”: the development of brachidium had not yet begun.

Specimens measured	L	W	T	L/W	T/W	Ø F/W	Ø F	Wbrach	↔
	mm	mm	mm				mm	mm	µm
Articulated specimens									
Holotype RBINS -BT. 4	2.43	2.92	0.95	0.83	0.30	0.25	0.74	0.66	120
Paratype RBINS -BT. 7	1.45	1.38	0.35	1.05	0.26	0.33	0.45	0.25	4
Paratype RBINS -BT. 5	2.22	2.45	0.82	0.91	0.34	0.23	0.57	0.62	np
Smallest specimen	0.89	0.88	0.23	1.01	0.26	0.26	0.23	no brach	no brach
Largest specimen	2.54	3.35	0.63	0.76	0.19	0.23	0.76	0.71	110
Specimen from Makassar	1.74	2.38	0.68	0.73	0.29	0.22	0.52	0.51	160
Specimen from Makassar	1.60	1.89	0.56	0.85	0.30	0.23	0.43	0.43	60
Specimen from Makassar	1.75	1.98	0.89	1.13	0.45	0.26	0.52	0.50	39
Ventral valves									
Paratype RBINS-BT. 6	1.87	2.43	nm	0.77		0.23	0.70		
Specimen from Makassar	1.58	1.78	nm	0.89			nm		
Specimen from Makassar	0.97	1.01	nm	0.96			nm		
Paratype RBINS-BT. 8 (Bali)	1.80	2.14	nm	0.84			nm		
Dorsal valves									
Dorsal valve Makassar	nm	2.67	nm	nm			Br	0.76	np
Dorsal valve Makassar	nm	2.59	nm	nm			0.67	0.67	110
Mean value for all specimens	1.74	2.13	0.64	0.89	0.30	0.26	0.54	0.56	86
Number of specimens measured	12	14	8	12	8	9	9	9	7
Confidence interval				0.0356	0.0266	0.0122			

Mendiagnosis. « Micromorphic » Brachiopoda, lebih lebar dari panjang dengan bentuk setengah lingkaran kelau dilihat atas katup dorsal. Permukaan luar katup dorsal halus sedangkan permukaan luar katup ventral adalah baris radial dengan duri tebal. Antara baris radial dari tuberkel ada banyak skala yang berbentuk « kurva Gaussian » dikembangkan di garis konsentris. Foramen amphithyrid. Tidak ada kardinal proses. Tidak ada engsel piring. Dalam lantai katup punggung ada tuberkel juga. Krura singkat dikembangkan. Brachidium, akan melalui fase cucullate, sebuah "pseudo" berbentuk gelang fase dan akhirnya merupakan dua cakar, relatif luas, sederhana dengan teratas tajam. Septum mendua, masih sangat datar. Cabang turun tak pernah dikembangkan. Septum di lantai katup ventral sebagian terputus di bagian posteriornya.

Description. Micromorphic kraussinid brachiopod more or less semi-circular in dorsal outline, slightly wider than long, ventribiconvex (Pl. 6, Fig. 4c) to planoconvex or sometimes concavoconvex (Pl. 9, Fig. 2a; Table 1). Cardinal area orthocline. Anterior commissure rectimarginate in juveniles to very slightly sulcate in adults. Beak

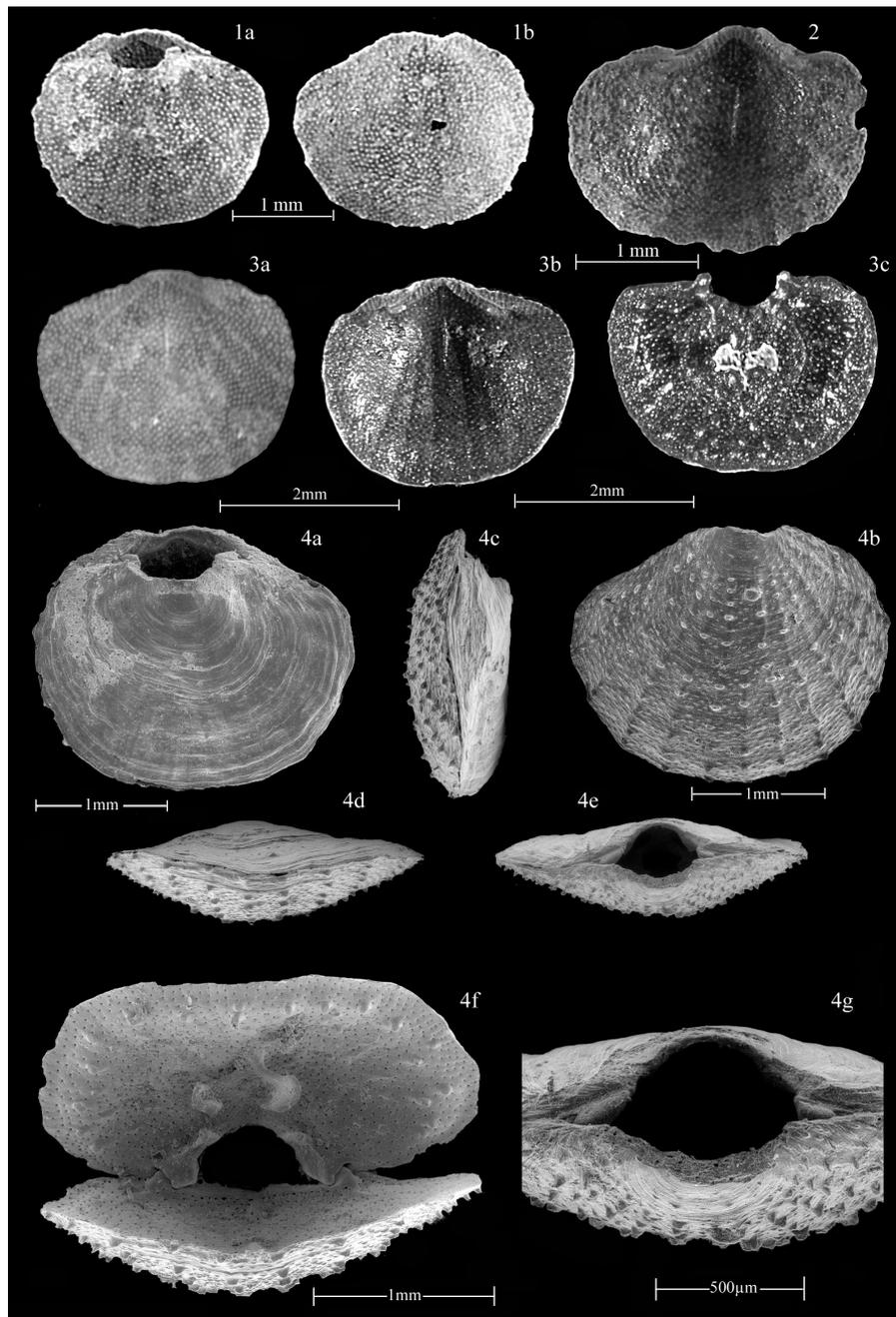


PLATE 6. *Lenticellaria gregoryi* sp. nov. Material collected by G. Willems from a tanker shipwreck at Kodingareng (Spermonde Archipelago, west of Makassar, South Sulawesi, Indonesia) at a depth of 30 m. Size of the specimens indicated with scale bars.

Fig. 1. RBINS-BT. 5. Paratype. Articulated specimen photographed with a macro-objective on a Pentax K20D. The general aspect of the shell (1a; 1b) is homeomorphic with juvenile specimens of *Megerlia* or *Annuloplatidia curiosa* Bitner, 2015. The shell surface ornamentation is unclear as it is difficult to see if the shell surface is covered with spines or scales. Under a binocular microscope there appear to be numerous punctae (depending on the type of light).

Fig. 2. RBINS-BT. 6. Paratype, a ventral valve photographed with a macro-objective on a Pentax K20D. The typical parallel disposition of the punctae in the sessile pedicle collar is clearly visible.

Fig. 3. RBINS-BT. 4. Holotype photographed with a macro-objective on a Pentax K20D. 3a: external ventral view of the ventral valve. 3b: Internal aspect of the ventral valve with the sessile pedicle collar showing parallel disposition of the punctae. 3c: Internal dorsal view showing the brachidium and the very small crura.

Fig. 4. RBINS-BT. 5. Paratype. Articulated specimen observed with SEM at low magnification. External aspect of the shell is homeomorph with *Megerlia*. The shell is slightly dorsi-biconvex (4c; 4d; 4e). The dorsal valve is smooth (4a); The anterior commissure is slightly sulcate. The foramen is not abraded and is amphithyrid (4a; 4g). The extremely reduced brachidium is made of two claws and of two small crura (4f).

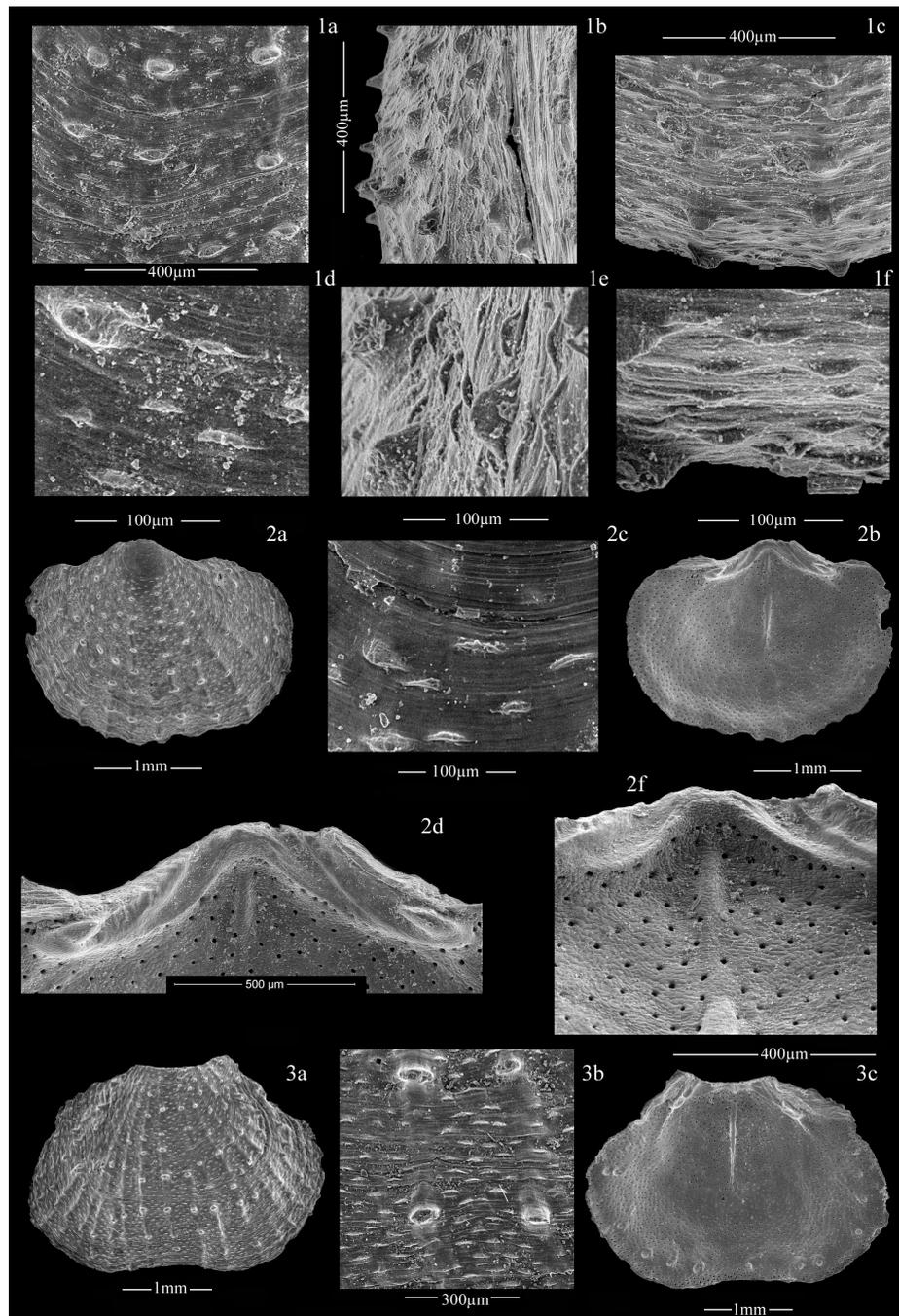


PLATE 7. *Lenticellaria gregoryi* sp. nov. Material collected by G. Willems. Figs. 1a–f and 2a–f: specimens from a shipwreck at Kodingareng (Spermonde Archipelago, west of Makassar, South Sulawesi, Indonesia) at a depth of 30 m. Figs. 3a–c: specimen from the “Liberty” shipwreck at Tulamben (Bali Sea, Bali, Indonesia) at a depth of 25 m. Size of the specimens indicated with scale bars.

Fig. 1. RBINS-BT. 5. Paratype. Articulated specimen observed with SEM at high magnification. External aspect of the shell. Radial rows of thick tubercles with shell surface between these rows of tubercles covered with small scales giving a “lenticel” aspect. At still higher magnification (1b–1f) the scales seen in anterior view appear as “Gaussian curves” (1e). a: dorsal view; b: anterior view; c: posterior view; d: dorsal view at very high magnification; e: anterior view at very high magnification; f: posterior view at very high magnification.

Fig. 2. RBINS-BT. 6. Paratype. Ventral valve. 2a : general ventral view ; 2b : general internal view with sessile pedicle collar and low median septum interrupted in its posterior part ; 2c : detail of external ornamentation with numerous small scales; 2d: detailed view of the sessile pedicle collar (with SEM the punctae are not visible); 2e: detailed view of the posterior part of the septum.

Fig. 3. RBINS-BT. 8. Paratype. Ventral valve. 3a : general ventral view ; 3b : Scales ornamentation of shell surface at high magnification; 3c: general internal view with sessile pedicle collar and low septum interrupted in its posterior part.

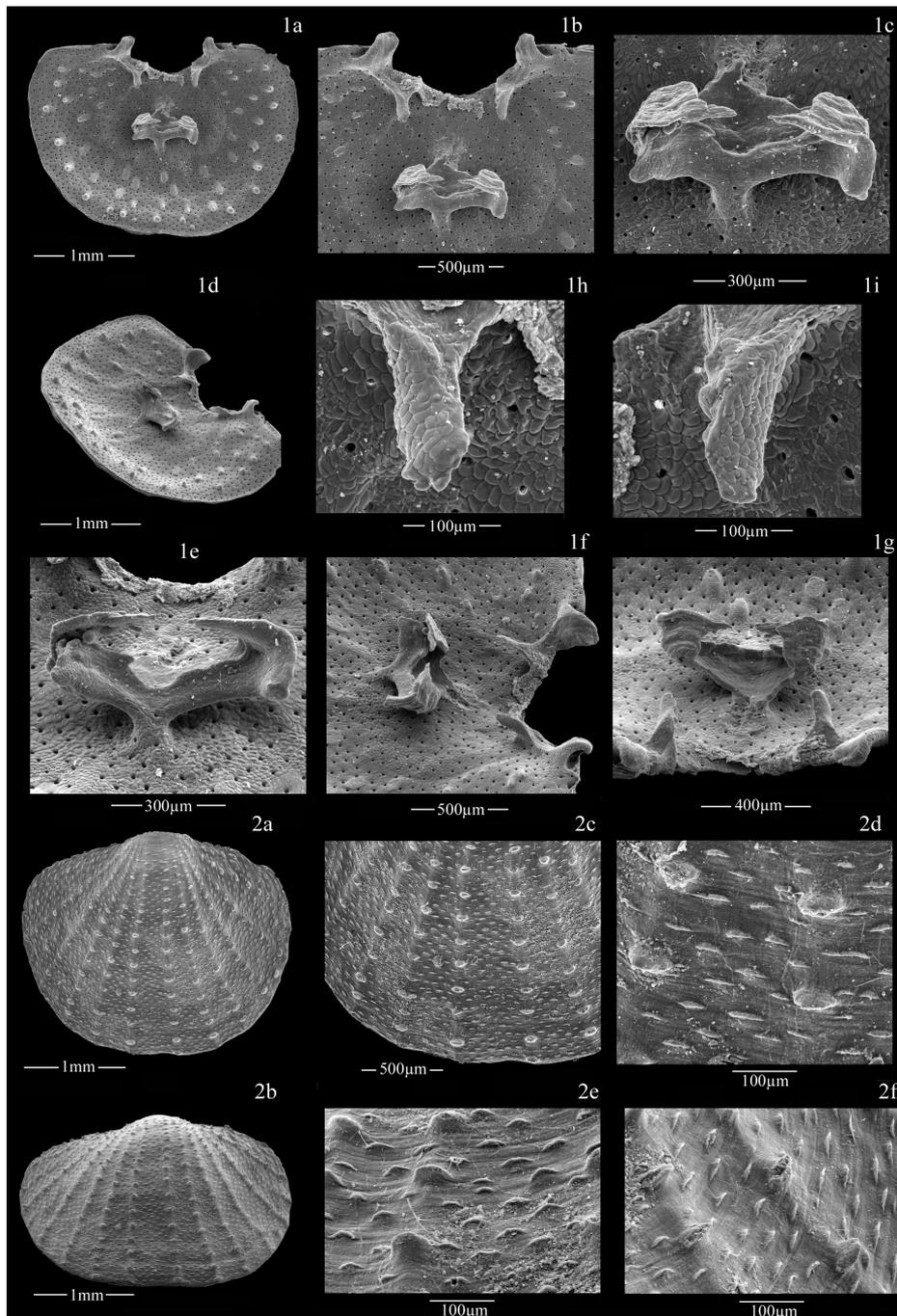


PLATE 8. RBINS-BT. 4. *Lenticellaria gregoryi* sp. nov. Holotype collected by G. Willems from sieved sediment from a tanker shipwreck at Kodingareng (Spermonde Archipelago, west of Makassar, South Sulawesi, Indonesia) at a depth of 30 m. Detailed SEM views of both separated dorsal (Figs. 1a–g) and ventral (Figs. 2 a–f) valves. Size of the specimen indicated with scale bars.

Fig. 1. 1a: Internal view of the dorsal valve showing subcircular tubercles on the valve floor, short intact crura and symmetrical sharply pointed claws; b–c: detailed view of the brachidium in ventral view. The sharp tips of the loop are clearly visible as the crura. Cardinal process absent (1b). 1c: detailed view of the loop at high magnification in ventral view. 1d: Oblique lateral view; 1e Detailed view of the loop in anterior view 1f: Detailed view of the loop in lateral view; 1g detailed posterior view of the loop. (1e;1g) show also that resorption process of cucullate structure has begun anteriorly; 1h: detailed view of the right crus; 1i: detailed view of the left crus.

Fig. 2. 2a: general view of the ventral valve in ventral view. Homeomorphy with *Megerlia* species is evident. 2b: anterior general view showing a “granulate” shell surface. 2c–f: Detailed SEM views of the external ornamentation of the shell surface. Numerous scales with Gaussian curve aspect visible together with larger tubercles. 2c–d: ventral view at moderate and higher magnification. 2e: anterior view; 2f: oblique left lateral view of left part of the shell. Low costae ornamented with tubercles are visible.

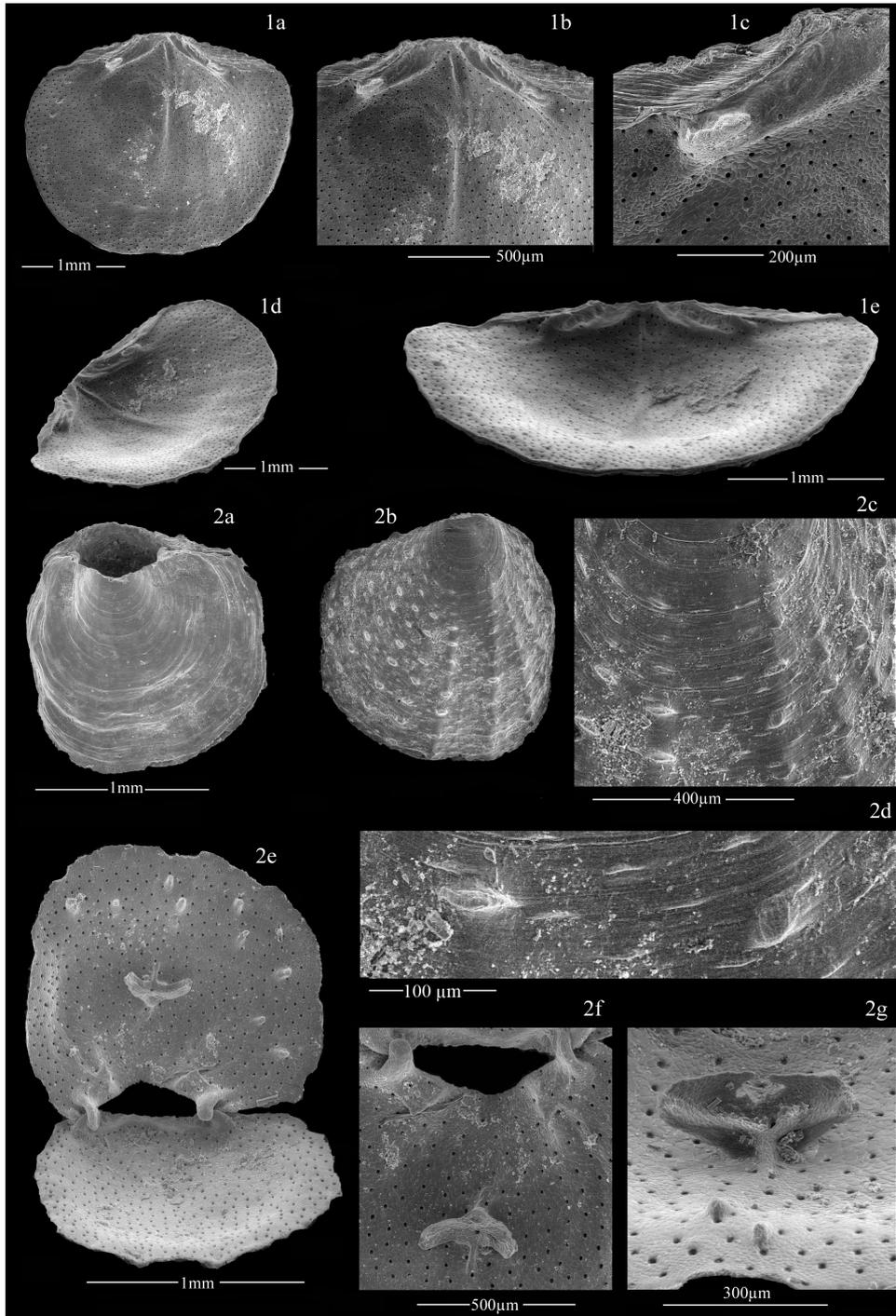


PLATE 9. *Lenticellaria gregoryi* sp. nov. Material collected by G. Willems from sieved sediment from a tanker shipwreck at Kodingareng (Spermonde Archipelago, west of Makassar, South Sulawesi, Indonesia) at a depth of 30 m. Detailed SEM views of separated ventral valve of the holotype (Figs. 1–ae) and illustration of an early juvenile articulated paratype (Figs. 2a–g).. Size of the specimen indicated with scale bars.

Figs. 1. RBINS-BT. 4. Holotype. 1a: general internal view of ventral valve in dorsal view. 1b: detailed view sessile pedicle collar and posterior interrupted portion of the ventral septum. 1c: detailed view of the cyrtomatodont tooth. 1d: general oblique lateral view illustrating the low ventral septum. 1e: anterior view of ventral valve.

Figs. 2. RBINS-BT. 7. Paratype. 2a: dorsal view of the articulated specimen. Dorsal valve smooth and foramen amphithyrid. 2b: Ventral view with rows of tubercles. 2c: detailed view of the ventral shell surface with scales between the radial rows of tubercles. 2d: high SEM magnification of the ornamentation of ventral shell surface. 2e: Opened articulated paratype showing the tuberculation of the dorsal valve floor and the brachidium . 2f: detailed view of the brachidium in dorsal view. Resorption of the anterior portion of the cucullate phase is started. Crura are appearing as very small knots. 2g: detailed anterior view of the cucullate phase showing the importance of the anterior resorption process at this stage of growth.

erect with obtuse umbo often abraded. Foramen amphithyrid, shared conspicuously by the dorsal valve in all stages of growth with convex dorsal side (Pl. 6, Figs. 4e–g). Deltidial plates poorly developed when preserved, elongate triangular, very narrow, disjunct. Dorsal valve always smooth. On the contrary, the ventral valve shows a clear radial tuberculation from the juvenile stage of growth (Pl. 6, Fig. 4b; pl. 7, Figs. 2a, 3a; Pl. 8, Figs. 2a–c; Pl. 9, Fig. 2b).

A very different aspect of the ventral valve is observed with a SEM used at a greater magnification. The structure is reminiscent of wood (Pl. 7, Fig. 3b). Spaces between the tuberculate radial rows are not smooth but ornamented with “stripes” oriented like the concentric growth lines. This is a striking distinction between this brachiopod and representatives of the genus *Megerlia* with a smooth or spiny shell surface between the tuberculate radial rows. However this morphological character is not easily seen with a binocular microscope and even with a SEM at low magnification (Pl. 7, Fig. 2a, and Pl. 7, Fig. 3a.). At still higher magnification, these “stripes” in dorsal view (Pl. 7, Figs. 1a, 1d, 2c, 3b) appear as minuscule scales with a “Gaussian curve” aspect in anterior view (Pl. 7, Fig. 1b, 1e, 1f). Scales are densely present on all specimens found even on early juvenile shells (Pl. 9, Fig. 2b). These scales with “Gaussian curve” outline are different from the tubercles which are more similar to conical relief.

Obtuse hinge angle between 120° and 130°. Cyrtomatodont teeth curved, sharply ended and with a smooth surface. (Pl. 7, Fig. 2d). Pedicle collar narrow and sessile (Pl. 7, Fig. 2f) fused with the underlying shell and appearing as a narrow thickening of the shell (Pl. 7, Fig. 2f). Shell endopunctate. Punctae of the pedicle collar parallel to the valve floor surface and perpendicular to the pores of the shell itself. This gives a characteristic striated aspect when observed with a binocular microscope (Pl. 6, Fig. 2). The number of punctae in the ventral valve varies around 294 punctae/mm².

Ventral valve with a low thin median septum always interrupted in its posterior part (Pl. 7, Fig. 2b, 2f, 3c; Pl. 9, Fig. 1b, 1e). This septum does not extend under the pedicle collar.

Inner dorsal valve floor radially tuberculate. Inner ventral valve floor not tuberculate.

Loop structure and ontogeny. The loop in the largest specimen is made of two crura and two claws only. This is always the case even in the most juvenile stage observed (Pl. 9, Figs. 2e–g). During growth, these claws widens and the space between the tip of the claws increases (Pl. 6, Fig. 4f; Pl. 8, Figs. 1b, 1e) but not regularly or linearly (Table 1). Crural bases are produced at an early stage of growth (Pl. 9, Fig. 2f) but crura do not grow significantly: they remain short. Crural processes and descending branches are never produced.

The ontogeny of this reduced brachidium begins as a typical Megerliinae process. The bifurcate septal pillar builds a posteriorly concave plate which becomes more conical. At this first stage the similarity with the ontogeny of *Megerlia* is evident. The resorption of the anterior part of this cucullate structure occurs at and just after the beginning. This resorption rapidly affects the anterior part of the cone and it continues posteriorly (Pl. 9, Fig. 2g). On the contrary, in *Megerlia* the resorption process begins posteriorly and stops before the anterior part could be dissolved (Pl. 3, Fig. 3e), building a ring. Later in *L. gregoryi* **sp. nov.** when the resorption process is finished it remains two claws which increase in size progressively through growth but which never conjoin to form a ring (Table 1).

This is one of the most reduced loop developments observed in Kraussinoidea. There are no ring and descending branches like in *Megerlia*. Crural bases are developed but “*pro partim*” descending branches extending from the septum like flanges, as seen in *Megerlina*, are not produced. The wide Y-shaped septum of *Kraussina* is quite different. The loop of *Pumilus antiquatus* Atkins, 1958 is the nearest more or less comparable structure. However, all other morphological features in *P. antiquatus* are markedly different (Lee and MacKinnon, 2006).

***Lenticellaria marerubris* Simon, Logan & Mottequin sp. nov.**

Pl. 11, Figs. 1–6.

1921 *Megerlia truncata* var. *paucistriata*: Jackson, p. 48.

1973 *Megerlia echinata* (Fischer & Oehlert): Cooper, p. 18–19, pl. 3, figs. 27–31).

2008 *Megerlia truncata* var. *paucistriata*, Jackson: Bitner, Logan & Gischler, p. 279.

pp 2008 *Megerlia truncata*: Bitner, Logan & Gischler, pp. 279, 284.

pp v 2008 *Megerlia echinata* (Fischer & Oehlert, 1890): Logan, Tomašových, Zuschin & Grill, p. 395; fig. Q non figs. 2, P, R, S, T.

pp v 2013 *Megerlia echinata* (Fischer & Oehlert): Logan & Bitner, pp. 161, 171.

Holotype. *Lenticellaria marerubris* sp. nov. Pl.11, Figs.1a–1o. Well preserved articulated specimen that has been opened for the present study. It is preserved in the collections of the Natural History Museum of Vienna, Austria (NHMW 87192/GP 247). The morphological measurements of the holotype are indicated in Table 2.

Paratypes: NHMW 87192/GP 248: small articulated adult (Pl. 11, Figs.2a–e; Table 2) with a dorso-biconvex structure.

NHMW 87192/GP 249: large articulated adult with a quite distorted outline (Pl. 11, Figs. 3a–e; Table 2).

NHMW 87192/GP 250: medium sized adult specimen used for illustrating the ventral external ornamentation (Pl. 11, Fig. 4a; Table 2).

NHMW 87192/GP 251: early juvenile articulated specimen with a loop at the early cucullate stage of development (Pl. 11, Figs. 5a–f; Table 2).

NHMW 87192/GP 252: young articulated specimen showing the two claws of the loop at earliest stage of growth (Pl. 11, Figs. 6a–d).

Etymology. the specific name “*marerubris*” is the latin translation of “from the Red Sea”.

Locus typicus: Dahab, Egypt, Gulf of Aqaba at a depth of 12 m.

Material investigated. Most of the specimens studied were collected by M. Zuschin (Fig. 4) in Dahab, Gulf of Aqaba, Egypt in very shallow water (12 m) and a few specimens more were collected at Port Sudan (see also Logan et al., 2008, fig. 1, p. 300 and Table 1, p. 301). For this study 38 complete articulated shells, 26 dorsal valves (sometimes fragmented) and 48 ventral valves (sometimes fragmented) were observed.

Diagnosis of species. Micromorphic brachiopod with a very variable outline in dorsal view depending on the topography of the substrate to which the specimen is attached. Shell often distorted but sometimes semicircular in outline. External surface of dorsal valve smooth. Ventral valve with radial tuberculation. Between the radial rows very small scales are regularly developed in concentric lines. Foramen amphithyrid. Cardinal process and hinge plates absent. Inner dorsal valve floor tuberculate. Short crura developed. Loop made of two claws relatively narrow and thin with sharp tip and with a clearly raised pedestal. Descending branches absent. Septum on the ventral valve floor partly interrupted in its posterior portion.

TABLE 2. *Lenticellaria marerubris* sp. nov. Morphometric measurements were taken from holotype, paratypes and other measurable articulated specimens collected in Dahab (at -12 m), Gulf of Aqaba, Red Sea by M. Zuschin (NHMW). L: length (mm); LDV: length of dorsal valve; W: width (mm); T: thickness (mm); ØF: maximal width of the foramen (mm); Wbrach: maximum width of the brachidium (mm); ↔: distance between the acute tips of the brachidium (µm); L/W= ratio length to width, T/W= ratio thickness to width; ØF/W: ratio width of foramen to width. Mean values, standard deviations and confidence intervals are indicated.

Specimens	L	W	T	Ø F	L/W	T/W	Ø F/W	Wbrach	↔
	mm	mm	mm	mm				mm	µm
all from Dahab, Gulf of Aqaba	1.95	2.21	0.74	0.66	0.88	0.34	0.30	0.62	170
Holotype NHMW 87192/GP 247	1.34	1.83	0.64	0.47	0.73	0.35	0.26	0.30	75
Paratype NHMW 87192/GP 248	2.10	2.71	0.82	0.72	0.75	0.30	0.27	0.75	262
Paratype NHMW 87192/GP 249	1.99	1.41	0.85	0.70	0.77	0.60	0.50	0.60	3
Paratype NHMW 87192/GP 250	0.99	1.00	0.41	0.30	0.99	0.41	0.30	0.06	0
Paratype NHMW 87192/GP 251	2.81	3.13	1.31	0.94	0.90	0.42	0.30	0.85	230
Paratype NHMW 87192/GP 252									
Mean value for all specimens	1.68	2.01	0.58	0.62	0.84	0.47	0.31	0.46	98.55
Number of specimens measured (N)	29	29	29	29	29	29	29	23	20
σ	0.4437	0.4418	0.1621	0.1434	0.1734	0.0730	0.0568	0.1841	77.744
σ/√N [Confidence interval (±)]	0.0824	0.0820	0.0301	0.0266	0.0322	0.0147	0.0105	0.0384	17.384

Diagnose de l'espèce. Brachiopode micro-morphique de forme très variable en vue dorsale dépendant de la structure du substrat sur laquelle le spécimen vit fixé. La coquille est souvent fortement déformée mais parfois elle peut apparaître semi-circulaire et plus régulière. La surface externe de la valve dorsale est lisse. La valve ventrale est radialement tuberculée. Entre les rangées de tubercules se développent de très petites écailles disposées

concentriquement. Foramen amphithyride. Processus cardinal et plaques de charnières absentes. Surface interne de la valve dorsale tuberculée. Crura très courtes clairement développées. Le brachidium se compose de deux pinces plutôt étroites et minces avec des pointes aigües. Le septum bifide est nettement surélevé. Branches descendantes absentes. Septum de la valve ventrale interrompu dans sa partie postérieure.

Mendiagnosia. « Micromorphic » Brachiopoda dengan bentuk yang sangat bervariasi dilihat atas katup dorsal. Kadang-kadang bentuk juga setengah lingkaran tergantung pada substrat dimana spesimen hidup dilampirkan. Shell sering sangat terdistorsi tapi kadang-kadang bisa muncul berbentuk setengah lingkaran dan lebih teratur. Permukaan luar katup dorsal halus sedangkan permukaan luar katup ventral adalah baris radial dengan tuberkel terucut yang kecil. Antara baris radial dari tuberkel ada banyak skala yang sangat kecil dikembangkan di garis konsentris. Amphithyrid foramen. Proses kardinal dan engsel piring tidak ada. Dalam lantai katup punggung ada tuberkel juga. Krura singkat dikembangkan. Brachidium merupakan dua cakar, sempit dan tipis sederhana dengan teratas tajam. Septum bercabang secara signifikan meningkat. Cabang turun tidak ada. Septum dari katup ventral terputus di bagian posteriornya.

Description. Micromorphic kraussinid brachiopod (Table 2) with a very variable outline in dorsal view depending on the topography of the substrate to which the shell is attached. This species probably lives with its dorsal valve applied tightly to the substrate. The shell is plano-convex or concavo-convex, ventri-biconvex (Pl. 11, Fig. 1d), sometimes biconvex and rarely dorso-biconvex (Pl. 11, Fig. 2c–2d). Cardinal area orthocone. Anterior commissure rectimarginate, slightly sulcate to sulcate. Lateral commissure sinuous. Beak erect, often with intact obtuse umbo, sometimes slightly abraded. Amphithyrid foramen shared conspicuously by the dorsal valve. The dorsal side of the foramen is very convex (Pl. 11, Figs. 1g, 2c, 2e). Deltoidal plates, very small, triangular, disjunct. Dorsal valve with external surface smooth except for several distinct growth lines. Ventral valve external surface with radial tuberculation and many very small scales disposed concentrically on the surface between the radial rows of tubercles (Pl. 11, Figs. 3b, 4a, 5b, 6b). The tubercles in this species are quite spiny in lateral view (Pl. 11, Figs. 1d–e, 2c).

Obtuse hinge angle quite variable depending of the peculiar outline of each specimen. Cyrtomatodont teeth smooth, robust, short, flat dorsally and obtusely pointed. Pedicle collar thickened, sessile (Pl. 11, Fig. 1n) with numerous punctae parallel to the external surface (visible with a binocular microscope, not with the SEM).

Socket ridges thick, mainly the inner socket ridge that is also higher. The sockets are not deep. Cardinal process absent.

Ventral valve with a low thick septum interrupted in its posterior part. The septum reaches the pedicle collar but does not join it. The commissural dorsal valve floor is heavily tuberculate. The commissural ventral valve floor is not tuberculate but hollow traces of the tips of dorsal tubercles are clearly visible.

The brachidium consists of two pointed relatively slender claws attached to the dorsal valve floor by a relatively high pedestal. The distance between the tips of the claws is highly variable (Table 2) and depends partly on the general size of the specimen but also on the stage of ontogeny reached. Short crura are clearly developed but descending branches are never produced.

Comparison between the two *Lenticellaria* species

Both species offer all the generic characters given in the genus diagnosis, including the small size, the smooth dorsal valve, the radially tuberculate ventral valve with concentric small scales between the radial rows of tubercles, an amphithyrid foramen and most significantly a brachidium made of two short crura and two pointed symmetrical claws (absence of complete ring), and an interrupted septum in the ventral valve. Both species have also the same ontogeny.

However the two species differ in the general outline that is much more variable in *L. marerubris* **sp. nov.** than in the semi-circular *L. gregoryi* **sp. nov.** The scales ornamenting the surface of the ventral valve are smaller in *L. marerubris* **sp. nov.** than in *L. gregoryi* **sp. nov.** The teeth of *L. gregoryi* **sp. nov.** are relatively thin, curved and pointed while those of *L. marerubris* **sp. nov.** are short and more robust, flat dorsally and obtusely pointed. The claws of the brachidium and the septum supporting them are different in these species. In *L. gregoryi* **sp. nov.** the septum is not elevated: the pedestal is reduced to a secondary shell secretion covering the valve floor and the two claws are relatively wider. In *L. marerubris* **sp. nov.** the septum is elevated above the dorsal valve floor forming a pedestal and the two branches of the claws are slender.

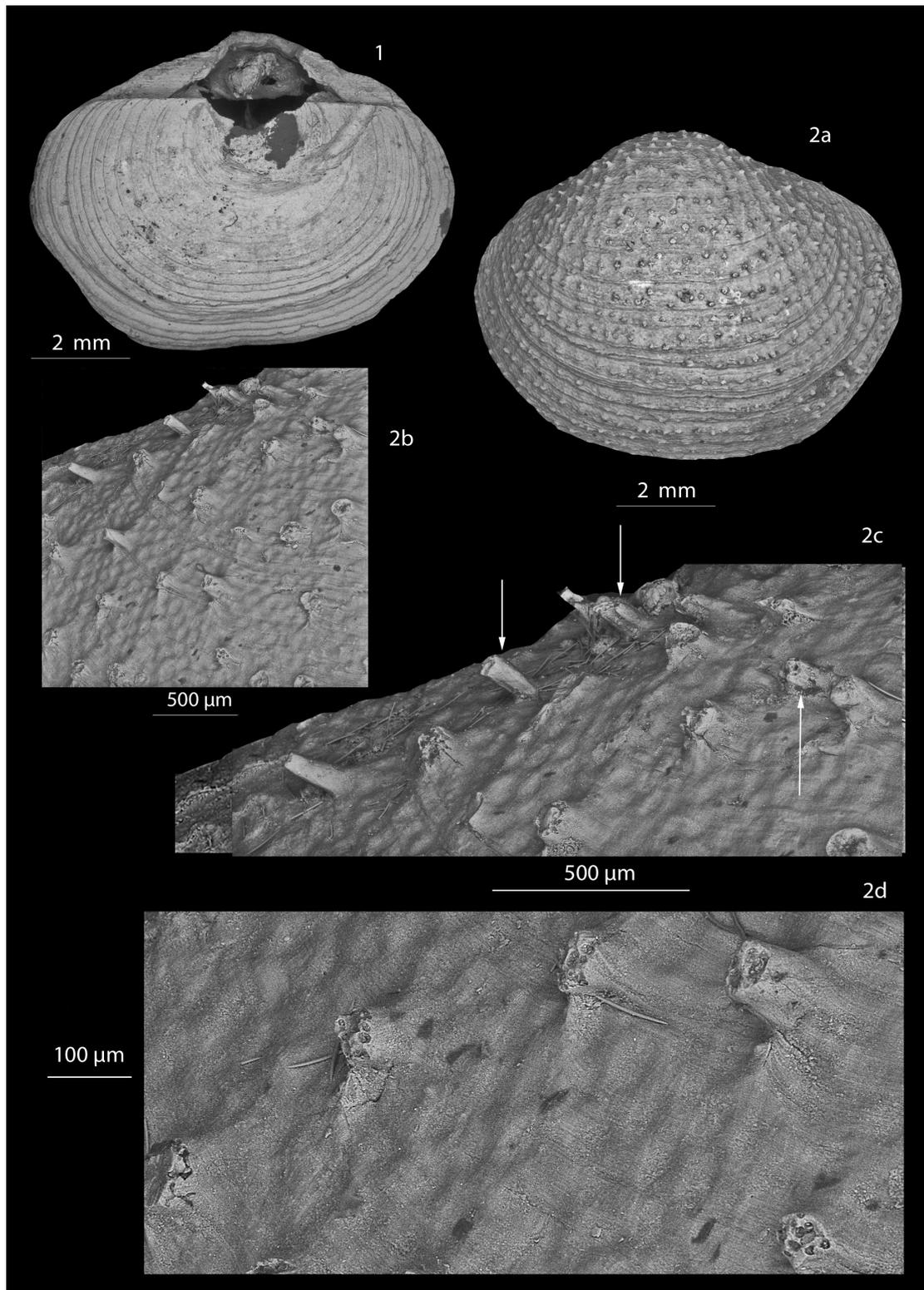
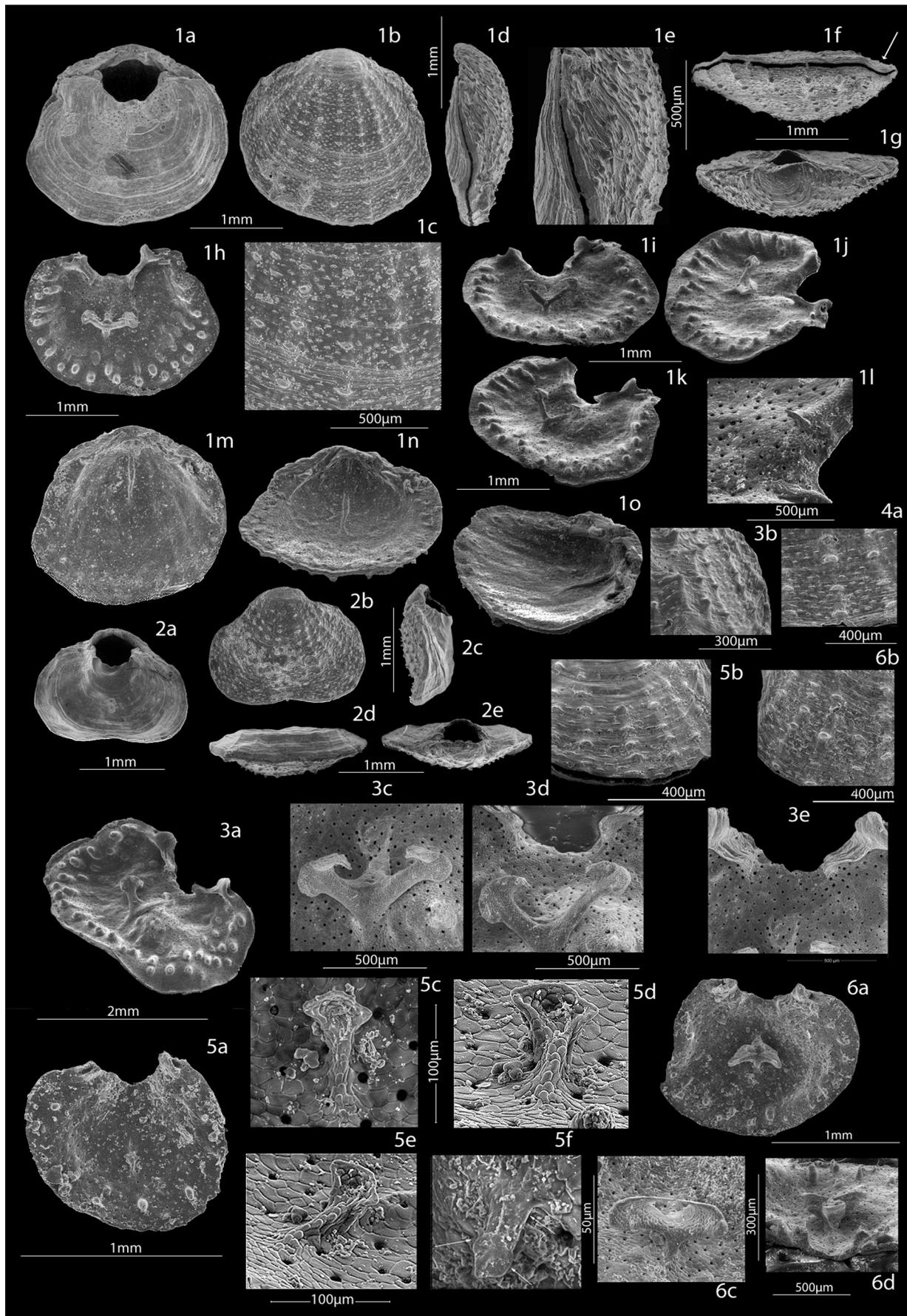


PLATE 10. Material type of *Megerlia echinata* (Fischer & Oehlert, 1890), collected off Cape Bojador, Sudan between 640–782 m during the expedition of the “Travailleur”. Specimen preserved in Paris at the Muséum National d’Histoire Naturelle (MNHN-IB-2013-317). Detailed SEM views of the articulated specimen. Size of the specimen indicated with scale bars.

Fig. 1: General dorsal view showing the smooth dorsal valve with its concentric growth lines and a relatively wide amphithyrid foramen.

Figs 2: Ventral views. 2a: general view of the ventral valve with its spiny ornamentation. 2b: detailed observation of the spiny ornamentation that is quite different of the tubercles observed on the specimens of *M. truncata*. 2c: Higher magnification of the spiny ornamentation showing that spines are not only on the radial costae but also on the whole surface of the valve (arrows). 2d: very high magnification showing the alveolar structure of the spines.



Genus *Hillerella* Simon, Logan & Mottequin gen. nov.

Type species *Hillerella bisepta* Simon, Logan & Mottequin sp. nov.

Etymology. Named for Norton Hiller in recognition of his important studies on Recent kraussinoid brachiopods.

Diagnosis. Micromorphic kraussinoid, wider than long, biconvex, tuberculate radial costae mainly on ventral valve; dorsal valve with less prominent costae; ventral valve interior with single central septum, dorsal valve without cardinal process or crura; floor of dorsal valve interior with two prominent subparallel septa directed posteriorly from loop towards the hinge line; loop consisting of an arch supported by two slightly divergent plates attached to valve floor.

Diagnose. Brachiopode kraussinoïde micro-morphique, plus large que long, biconvexe; valve ventrale avec côtes radiales tuberculées; valve dorsale avec côtes moins proéminentes; valve ventrale avec septum central; valve dorsale sans processus cardinal ni crura; surface interne de la valve dorsale avec deux septa subparallèles proéminents dirigés postérieurement du brachidium jusqu'à la charnière; brachidium consistant en une arche supportée par deux plaques divergentes attachées à la surface interne de la valve.



PLATE 11. *Lenticellaria marerubris* sp. nov. Material collected from the Red Sea, Gulf of Akaba, Dahab, by Martin Zuschin (NHMW) at a depth of 12 m. Size of the specimens indicated with scale bars.

Fig. 1. Holotype. Articulated fully adult specimen opened for this study in order to illustrate the brachidium (NHMW 87192/GP 247). 1a: dorsal view showing the smooth dorsal valve with concentric growth lines and the wide amphithyrid foramen. This specimen is not distorted and has a nearly semicircular outline. 1b: ventral view showing the tuberculated surface of the ventral valve. Radial rows of tubercles are clearly visible and between these rows an ornamentation made of many concentric lines of very small scales. 1c: detailed view of the tubercles and scales of the same ventral valve. 1d: lateral view. The beak is erect. The lateral commissure is sinuous. In this position the pointed tubercles and the scaly surface of the ventral valve are clearly visible. 1e: detailed view of the lateral view. 1f: anterior view. Anterior commissure is rectimarginate in this specimen. 1g: posterior view. The strong convexity of the dorsal side of the foramen is typical for all specimens investigated. 1h: ventral view of the tuberculate dorsal valve showing the brachidium developing two claws supported by a pedestal. Short crura are visible. 1i: internal anterior view of the dorsal valve showing the high pedestal, the two slender claws and the short crura. The crura are not supported by crural plates or thick crural ridges. 1j: oblique lateral view. 1k: oblique antero-lateral view. 1l: detailed view of the short crura.

Fig. 2. Paratype. Articulated fully adult specimen presented for illustrating the possibility of dorso-biconvex shell and distortion. (NHMW 87192/GP 248). 2a: dorsal view showing smooth dorsal valve and large amphithyrid foramen. Note the cordate outline for this specimen. 2b: ventral view showing the radial rows of tubercles and the scaly surface of the valve. 2c: lateral view showing the sinuous lateral commissure, the convex dorsal of the foramen and the spiny surface of the ventral valve. 2d: anterior view. 2e: posterior view.

Fig. 3. Paratype. Articulated fully adult specimen used for illustrating a strongly distorted shell (NHMW 87192/GP 249). 3a: internal view of the tuberculate dorsal valve with brachidium. 3b: detailed view of the external ventral valve ornamentation. 3c: detail ventral view of the brachidium with its pedestal. 3d: anterior view of the two claws of the brachidium. 3e: detailed view of crura.

Fig. 4. Paratype. Articulated fully adult specimen used for illustrating the details of the ventral valve ornamentation. (NHMW 87192/GP 250). 4a: detailed view of the spiny tubercles and of the very small scales on the surface.

Fig. 5. Paratype (NHMW 87192/GP 251). Articulated early juvenile specimen illustrating the ontogeny for this species. 5a: internal view of the dorsal valve with the brachidium at early cucullate phase of development. The crura are just beginning to emerge. The commissural tuberculation of the valve is still reduced. 5b: detailed view of the ventral valve ornamentation. The rows of tubercles and the scaly surface are already developed. 5c: detailed ventral view of the brachidium. Note that the pedestal is already developed. 5d: anterior view of the brachidium. 5e: oblique lateral view of the brachidium. 5f: detailed view of a crus in development (arrows).

Fig. 6. Paratype. Articulated juvenile specimen illustrating later stage of the ontogeny (NHMW 87192/GP 252). 6a: internal view of the dorsal valve with the brachidium at a second stage of development. The resorption process of the posterior part of the cucullate structure is completed and claws in their first appearance are produced. 6b: detailed view of the ventral ornamentation. 6c: detailed anterior view of the brachidium. 6d: detailed posterior view of the brachidium showing the resorption process when completed.

***Hillerella bisepta* Simon, Logan & Mottequin, sp. nov.**

(Pl. 12. Figs. 1–7)

Megerlia echinata (Fischer & Oehlert, 1890)—Logan, Tomašových, Zuschin & Grill, 2008, p. 305, Figs. 2P, R, S, T (not Q).

Diagnosis. Micromorphic kraussinoid, wider than long, biconvex, ventral valve with tuberculate radial costae; dorsal valve with less prominent radial ornamentation; ventral valve interior with single central septum not interrupted in its posterior part, hinge line with prominent teeth; dorsal valve hinge line with sockets but without cardinal process or crura; dorsal valve floor with usually a single commissural row of tubercles, dorsal valve interior with two prominent subparallel septa directed posteriorly from loop and slightly converging towards the hinge line, loop consisting of an arch supported by two slightly outwardly-inclined plates attached to valve floor, with a thin ventral bridge and with ventro-anterior expansions not strongly developed.

Diagnose. Brachiopode kraussinoïde micro-morphique, plus large que long, biconvexe; valve ventrale avec côtes radiales tuberculées; valve dorsale avec côtes moins proéminentes; valve ventrale avec septum central non interrompu dans sa partie postérieure; ligne de charnière avec des dents proéminentes; ligne de charnière de la valve dorsale avec sockets mais sans processus cardinal ni crura; surface interne de la valve dorsale avec deux septa subparallèles proéminents dirigés postérieurement du brachidium jusqu'à la charnière; brachidium consistant en une arche supportée par deux plaques divergentes attachées à la surface interne de la valve avec une partie ventrale extrêmement fine et avec des expansions ventro-antérieures peu développées.

Etymology. Specific epithet describes the diagnostic subparallel septa in the interior of the dorsal valve.

Type locality (locus typicus). Station 100/8 at 90m depth off Port Sudan, Red Sea (18° 57.5' N, 38° 15.8' E) (Grill & Zuschin 2001; Logan *et al.*, 2008, Fig. 1).

Holotype. Ventral and dorsal valves of an articulated specimen, Pl.12, Figs.1a–f from type locality, with dimensions indicated in Table 3 (NHMW 87192/GP 253).

Paratypes. (Pl. 12, Figs. 2–6) all from the type locality except Pl. 12, Fig. 7 which has been collected from Toliara (SW. of Madagascar). Measurements are indicated in Table 3. (NHMW 87192/GP 254–255 and NBM—010321, NBM—008251).

Material. Seven articulated specimens, 90 dorsal valves often fragmented and rarely intact, 88 ventral valves often fragmented too, all from the type locality 100/8 at 90 m depth off Port Sudan, Red Sea (Fig. 3 and see Grill & Zuschin 2001 and Logan *et al.*, 2008 for details of exact location, substrate type and depth).

Also a single bivalved specimen collected by Jacques Picard c.1965 from dredged sediments in the vicinity of shallow coral reefs (to which the specimen was presumably attached) at Toliara, south-western Madagascar.

Description. Shell small, wider than long, maximum width about 3 mm at mid-line, usually biconvex, but occasionally verging on plano-convex; shell surface of ventral valve costate (Pl. 12, Figs.1a,c), with between 10–14 radiating ribs, shallow, furnished with strong tubercles, some with spinose tips (Pl. 12, Fig.1c,d). Anterior commissure rectimarginate, occasionally sulcate. Hinge line orthocline, with prominent abraded beak (Pl. 12, Fig. 2a) with large amphithyrid foramen. Shell surface of dorsal valve with less prominent radial costae, and with fewer tubercles (Pl. 12, Fig.1b).

Ventral valve interior with prominent pedicle collar, strongly folded laterally when seen in anterior view (Pl. 12, Fig. 2a). Narrow striated interarea, very small triangular disjunct deltidial plates and prominent teeth (Pl. 12, Fig. 2b). Median septum extending anteriorly to about half length of valve (Pl. 12, Fig. 2a). No tubercles. Shell endopunctate.

Dorsal valve interior without cardinal process, outer socket ridges very low, much higher inner socket ridges excavate below but without crura, dental sockets deep. Strong divergent ridges sustain the sockets in the bottom of the valve (Pl. 12, Figs. 4, 5a–b). Two prominent parallel septa extend posteriorly on valve floor from about the mid-point, lengthening with age but present in even the smallest specimens (Pl, 12, fig.3). Anterior ends of septa attached to two slightly outwardly-inclined narrow plates anchored to, and emerging upwards from, the valve floor (Pl. 12, Fig. 5c).

An ontogenetic sequence shows the gradual development of the loop from a very early stage (Pl. 12, Figs. 1e–f) to later mature stages (Pl. 12, Figs. 4, 5a–d, 6, 7a–b). Plates support an arch or cross-bar which, with ontogeny, gradually builds inward from the top of either plate to eventually join, completing the cross-bar, which bridges the gap and acts as a support for the lophophore. The lateral terminations of the cross-bar may be bulbous (Pl. 12, Figs. 6, 7a–b). Anterior margin of dorsal valve with a single row of tubercles (Pl. 12, Figs. 1e, 5a, b, 7a), with excavated tips (Pl. 12, Fig. 1e, 5a, 7a). Shell endopunctate (Pl. 12, Fig. 5c).

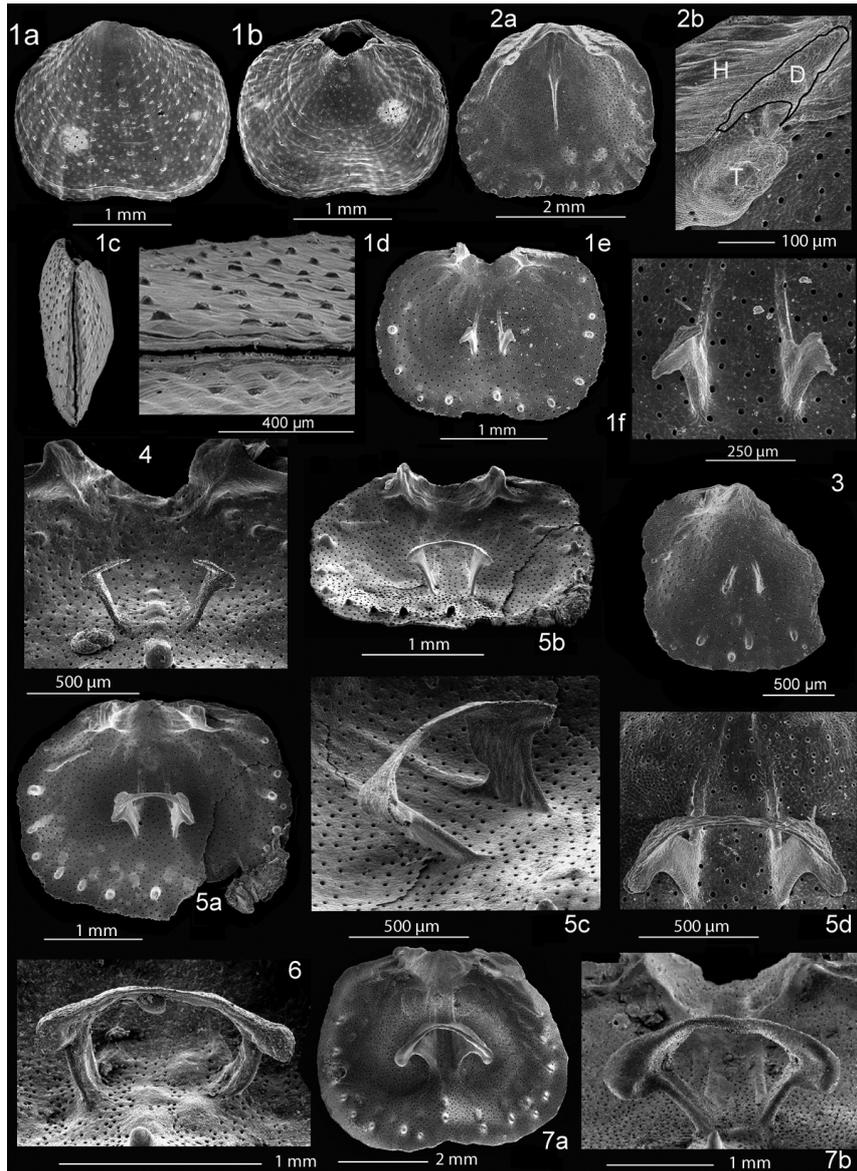


PLATE 12. *Hillerella bisepta* sp. nov. all collected from Port Sudan at 90 m. Station 100, Fig. 3, except specimen figured in fig. 7, which comes from Toleara, Madagascar.

Fig.1. *Hillerella bisepta* sp. nov. Holotype (NHMW 87192/GP 253). 1a: External view of ventral valve showing radial ornament of costae, tubercles and small spines. 1b: External view of dorsal valve showing radial ornament of faint ribbing, no tubercles or spines. 1c–d: Profile view of both valves attached, showing differences in ornament between the two valves. 1e–f. Interior of dorsal valve. 1e: early stage development of septal ridges and arch of loop of brachial skeleton. Note single row of marginal tubercles with excavated tips. 1f: enlargement of brachial skeleton and septal ridges shown in previous figure.

Fig.2. Paratype 1. (NHMW 87192/GP 254). 2a: Interior of ventral valve, with pedicle collar, hinge area, teeth, median septum and tuberculate margin. 2b: enlargement of part of hinge area (H) of previous specimen, showing tooth (T) and disjunct deltidial plate (D) outlined in black.

Fig. 3. Paratype 2. (NHMW 103331-5). Interior of early juvenile stage in ontogeny of dorsal valve, showing biseptal development preceding loop.

Fig. 4. Paratype NBM-010321. Interior of juvenile dorsal valve, anterior view of loop of immature form showing progressive development of arch of loop towards fusion.

Fig.5. Paratype 4. (NHMW 87192/GP 255). 5a: ventral view. 5b: anterior view. 5c: oblique lateral view. 5d: detail of the ventral bridge. Note marginal tubercles with excavated tips in 5a.

Fig. 6. Paratype NHMW 103335. Detailed view of a mature loop with bulbous extremities.

Hillerella bisepta sp. nov. Specimen collected from Toliara (SW Madagascar), c1965, dredged by J. Picard (no depth data).

Fig.7. Paratype NBM-008251. Interior of a dorsal valve. 7a: general ventral view showing brachidium and marginal tubercles with excavated tips. 7b: thickened mature loop and bulbous extremities.

Remarks. This species was briefly described and illustrated by Logan *et al.* (2008) from specimens collected by Zuschin and others from a wide variety of localities in the northern and central areas of the Red Sea, including the Port Sudan area. It was misidentified as *Megerlia echinata* (Fischer & Oehlert 1890) at that time. Consequently we have now established the new genus *Hillerella*. While this genus has some of the attributes of the other members of the family Kraussinidae (*Kraussina*, *Megerlia*, *Megerlina* and *Pumilus* (Lee & MacKinnon, 2006) it differs from other members of this family mainly in its small size typical of Red Sea brachiopods in general (Zuschin & Mayrhofer, 2009), the possession of subparallel septal ridges on the floor of the dorsal valve and the unique structure of the loop. Unlike *Hillerella*, *Lenticellaria* has a single central pillar with a bifurcate loop on either side to support the lophophore, while the separate claws never conjoin. The single example from Toliara, Madagascar (Pl. 12, Fig. 7a, b) shows a thicker crossbar than typical Red Sea specimens, with more bulbous lateral terminations and the space between the underlying supports is narrower at the base, but nevertheless has the diagnostic subparallel septal ridges and loop structure to justify being assigned to *H. bisepta*.

TABLE 3. *Hillerella bisepta* sp. nov. Morphometric measurements made on holotype and paratypes all collected from Port Sudan, Red Sea at a depth of 90 m except specimen NBM-008251 which was dredged by J. Picard, c. 1965, at Toleara, SW of Madagascar (no depth indicated). L: length (mm); LDV: length of dorsal valve; W: width (mm); T: thickness (mm); ØF: maximal width of the foramen (mm); Wbrach: maximum width of the brachidium (mm); L/W= ratio length to width, T/W= ratio thickness to width; ØF/W: ratio width of foramen to width.

	L or (LDV)	W	T	ØF	L/W	T/W	ØF/W	Wbrach
Specimens from Port Sudan, 90m.								
Holotype NHMV 87192/GP 253	1.78	2.15	0.75	0.56	0.83	0.35	0.26	0.52
Paratype NHMV 87192/GP 254	2.70	3.08	n.m.	n.m.	0.88	n.m.	n.m.	n.m.
Paratype NHMW 103331-5	(1.18)	1.25	n.m.	n.m.	n.m.	n.m.	n.m.	0;28
Paratype NBM-010321.	(1.65)	2.60	n.m.	n.m.	n.m.	n.m.	n.m.	0.50
Paratype NHMW 87192/GP 255	2.38	2.67	1.10	0.64	0.89	0;41	0.24	0.89
Paratype NHMW 103335	2.64	2.65	n.m.	0.55	0.99	n.m.	0.21	1.30
Specimen from Toleara SW of Magascar (dorsal valve)								
Paratype NBM-008251.	n.m.	5.65	n.m.	n.m.	n.m.	n.m.	n.m.	2.16

Homeomorphy and comparison with other kraussinid brachiopods. Homeomorphy is common among brachiopods and is often an important cause of misinterpretation. The most striking homeomorphy for *Lenticellaria gregoryi* sp. nov. is observed with the recently erected *Annuloplatidia curiosa* Bitner, 2014 (see Bitner, 2014, Fig. 9 A–H, p. 257). This micromorphic species is easily confused with a young *Megerlia* or with our new species. The brachidium is however typical of the genus *Annuloplatidia* Zezina, 1981.

The homeomorphy between *L. gregoryi* sp. nov. and young different species of *Megerlia* (Pls. 1–5) is clearly visible.

Controversies concerning the validity of certain *Megerlia* species are still discussed in the literature and most are due to homeomorphy.

M. echinata (Fischer & Oehlert, 1890), for instance, is considered as an ecological variant of *M. truncata* by Logan (1979) and Logan *et al.* (2004). For Miocene specimens Bitner (1990, 1993) has the same opinion. For Emig *et al.* (2015) this species is a synonym of *M. truncata*. On the contrary *M. echinata* was regarded as a separate species by Brunton & Curry (1979), Cooper (1973b, 1981a, 1981b), Brunton (1989) and Anadón (1994). It is reconsidered again as a valid species by Logan *et al.* (2007, 2008).

Detailed morphological observations of the type specimen and SEM illustrations have not been published until now (Plate 10). The type specimen shows all the characters proposed independently by Atkins (1961a, p. 89) for her *M. echinata* material collected by the R.V. *Sarsia* (1958 & 1959) at depths between 556–882 m. The flat dorsal valve is smooth (without any radial costae) with numerous concentric growth lines (Pl.10, Fig. 1) whereas the ventral valve is ornamented by long spines (Pl.10, Figs.2a–b). All these spines are not only placed on radial costae

but they can be developed on the whole surface of valve (Pl.10, Fig. 2c). Broken spines show a typical alveolar structure (Pl.10, Fig. 2d). The differences between the lophophore of *M. echinata* and *M. truncata* were discussed by Atkins (1961b).

A problem of zoogeographical order remains. The original specimen of *M. echinata* collected by “Le Travailleur” has been trawled off Cape Bojador (Sudan) between 640–782 m deep. The material studied by Atkins came from the western Atlantic. Phylogenetic analyses should establish definitively the taxonomic status of *M. echinata* and its relationship with other megerlinid species and also will confirm if the material from Cape Bojador and from the western Atlantic are the same species.

Similar problems in regard to *Megerlia gigantea* (Deshayes, 1863) were discussed by Cooper (1981) and still no definitive solution has been found. For Bitner (2007, 2008) and Emig *et al.* (2015) *M. gigantea* is regarded as a synonym of *M. truncata* whereas it is a distinct species for Laurin (1997), Cooper (1981) and Gaspard (2003).

The specimen illustrated by Laurin as *M. echinata* (1997, fig. 38, p. 452 and fig. 39, p. 453) is quite unusual. No complete description of this material is given and the illustrations consist of two drawings. His fig.38 may be “synthetic” as no details of the tuberculation and of the ventral ornamentation are provided. The loop represented in fig. 39 is quite different from the loop seen in *Megerlia* at the same stage of growth (Pl. 4, Figs. 3a–e and Pl. 5, Figs. 1a–g). These drawings probably represent another genus. Recently, Bitner (2014, p. 258) placed these specimens in synonymy with her newly-erected species *Annuloplatida curiosa* from French Polynesia. She suggests that Laurin made a wrong interpretation of his material. However, this material should be re-studied again in regard to its taxonomic position.

The specimen reported by D’Hondt (1987) is more problematic and this material should be revised because his determination is based only on Cooper’s description (1981) and no description and illustration of this single specimen was provided. Note that among the morphological characters drawn on the original figure of Deshayes (1863, p. 37, pl. 2, figs. 10, 11) no “ring” is visible. Only a bifurcate septum producing a fork is apparent which is joined by descending branches. The ring is probably broken.

The specimen of *Megerlia echinata* illustrated by Cooper (1973, pl. 1, figs. 1–3) collected from southwest Cape of Good Hope has a width of 10 mm and is much larger than *L. gregoryi* **sp. nov.** The dorsal valve is smooth and the ventral valve has radial tuberculation. The surface between the radial rows of tubercles is covered with straight small spines which differ from the scales observed in *L. gregoryi* **sp. nov.**

Megerlia representatives and also *M. truncata* appear to have an almost global distribution (Logan, 2007; Bitner, 2007, 2008). This species is common in the Mediterranean Sea and seems to be widely distributed in the Caribbean Sea, along the West African coast (though not as far south as Cape Verde as indicated in Logan, 1988), Canary Islands and Madeira (Logan, 1983 & Logan, 1988) and as far as Japan, Philippines, Hawaii and other Pacific zones (see references in Logan, 2007, p. H3114). Such a wide distribution, interrupted by vast gaps, is difficult to explain, and is in need of revision.

Specimens from the Persian Gulf were assigned to this species by Jackson (1921) under the name *Megerlia truncata* var. *paucistriata* (see also Bitner, 2008, p. 279 and Bitner *et al.*, 2008). They are not illustrated but the description fits perfectly with *L. marerubris* **sp. nov.** We put *M. truncata* var. *paucistriata* in synonymy with *L. marerubris* **sp. nov.**

Some specimens of *M. truncata* should be revisited, for instance the specimen from French Polynesia described by Bitner (2007, fig. 3, I–J). This is a small specimen but its loop is unknown as dried soft parts are present. Bleaching this material should be useful for knowing the brachidium structure to aid in the generic identification. A similar question concerns the specimen illustrated in Bitner (2008, fig. 19, D–E) as it is very small. Its attribution to *Megerlia* or *Annuloplatidia* should be reconsidered. Recently, Bitner (2014) suggested that all her described *Megerlia* specimens from Pacific waters are in fact *Annuloplatidia curiosa* Bitner, 2014 and she placed these *Megerlia* specimens in synonymy with this platidiid brachiopod. However, as *Lenticellaria gregoriae* sp. nov is also quite similar to *Annuloplatidia* externally, bleaching this material is necessary for knowing the real brachidium structure and to aid in the generic identification.

Megerlia acrua Hiller, 1986 may be another problematic species from the eastern coast of South Africa. The external outline is similar to *Megerlia* species but the brachidium which develops a complete ring does not possess crura and descending branches. Studying the brachiopods collected from the BENTHEDI– cruise in the Mozambique, Zezina (1987) suggested the name *Megerlina gigantea* (Deshayes, 1863) for a kraussinid specimen devoid of crura. She did not give any comments concerning the presence of a ring (or the presence of a broken

ring?). Her description is quite short and no illustration is available for this material. Bitner (2007) suggested that this kraussinid brachiopod could be an *M. acrura*. This opinion has been adopted again by Hiller *et al.* (2008).

To know if *M. acrura* should be placed in a new genus was considered "a moot point" by Hiller *et al.* (2008, p. 381).

Discussion and conclusions

This paper, as suggested in many others previously published, shows that it is easy to recognize a kraussinoid brachiopod but it is much more difficult to identify clearly the limits between species and genera. However, pending a detailed molecular phylogenetic study based on large amounts of material collected from around the world, we must highlight for all species the morphologically-distinctive characters which could enable us to try to understand the radiative evolution within the Megerliinae. What is clearly visible is the plasticity of the brachidium in this subfamily. The most complete brachidium structure is the *Megerlia* loop with crura, crural process, complete descending branches and presence of a complete ring. The wide distribution of the Kraussinidae through the Atlantic, Indian and Pacific oceans has promoted various possibilities of evolution. The part of the world where the most numerous distinct genera are present are the South African waters including the western region of Madagascar (*Megerlia*, *Kraussina*, *Megerlina* and *Hillerella* **gen. nov.**). An evolution occurred in many different directions: to the west through the Atlantic, to the east through the Indian and then the Pacific waters, to the north-east along the eastern African coast to the Red Sea, the Gulf of Aqaba, and inside the Mediterranean Sea. The Persian Gulf, Red Sea and Mediterranean Sea are also from a paratethyan origin.

A general consideration is that this evolutionary process follows the reduction of the brachidium structure. This is successful as the individuals become adult more rapidly and their reproduction is accelerated. Size is also generally reduced and even micromorphic forms appeared in different regions. Representatives of *L. gregoryi* **sp. nov.** and *L. marerubris* **sp. nov.** and *Hillerella bisepta* **sp. nov.** are paedomorphic. This reduction of size and loop structure could be interpreted as an advantageous heterochrony. It is noteworthy that brachidia reduction structures observed are made in varied directions and different parts of the loop are affected. In *L. gregoryi* **sp. nov.** and *L. marerubris* **sp. nov.** crura appear but descending branches are not developed and no ring is maintained. In contrast, in *Hillerella bisepta* **sp. nov.** the ring is maintained but no crura are developed. The bifid septum is extremely wide forming a biseptal outline.

In *M. acrura* the shell size is not reduced, crura and descending branches are not developed but a complete ring loop is observed. This species is a kind of very large "*Hillerella*" and it indicates that in the source area of kraussinid brachiopods such a reduction of the brachidium occurred probably much earlier.

All these "variants" are stable for their morphological characters in the area where they are found. Moreover these areas are isolated from each other and separated by vast distances that increase the possibilities for an allopatric speciation and special adaptations. For *L. gregoryi* **sp. nov.** a cryptic speciation can also be indicated (Lüter *et al.*, 2008).

In the subfamily Kraussininae the brachidium is also strongly reduced and the species and genera are distinguished with variations which are of the same level than the variations commented here for the Megerliinae species (presence or absence of crura, presence or absence of partial descending branches, etc.). In the Kraussininae the different species of *Megerlina* for instance are still a difficult question as pointed out by Hiller (1986).

So, this paper considers that the widely isolated megerlinid brachiopods are distinct species representative of different new genera. If all these different species were retained in a unique genus, namely *Megerlia*, a diagnosis such as "loop with or without ring, crura present or absent, descending branches present or absent, numerous concentric or only one commissural tubercles rows on the inner valve floor, pedicle collar excavate or sessile, etc." would be imprecise and pointless.

For these reasons the erection of the genus *Lenticellaria* **gen. nov.** and *Hillerella* **gen. nov.** with their new species *L. gregoryi* **sp. nov.** *L. marerubris* **sp. nov.** and *H. bisepta* **sp. nov.** are justified. If the diagnosis of the genus *Megerlia* is accepted as described here, *Megerlia acrura* Hiller, 1986 should be placed in a separate genus. The taxonomic status of the subfamilies Megerliinae and Kraussininae need to be revised as follows:

-Subfamily Megerliinae Hiller *et al.*, 2008.

Diagnosis (emended): Kraussinoidea often with crura but not always, uniting sometimes with descending branches to form a diploform or bilacunar adult brachidium or without descending branches in paedomorphic genera. Brachidium with a complete ring obtained by resorption of the cucullate phase.

Genera: *Megerlia*, *Lenticellaria* **gen. nov.** and *Hillerella* **gen. nov.**

Additional taxonomic note. *Hillerella* **gen. nov.** is placed in this subfamily on the basis of the general outline of the shell and the presence of a complete ring. However, the biseptal development in the dorsal valve and the loop consisting of an arch supported by two slightly outwardly-inclined plates attached to valve floor is a major difference and further phylogenetic studies could lead to the erection of a third subfamily.

-Subfamily Kraussininae Dall, 1870.

Diagnosis (emended): Kraussinoidea without crura. Bifurcate septum with or without accessory distal processes. Brachidium without complete ring.

Genera: *Kraussina*, *Megerlina* and *Pumilus*.

The distribution of *M. truncata sensu stricto* should be carefully and phylogenetically re-studied. This species is essentially present in the Mediterranean Sea and in the Lusitanian Province of the western Atlantic. Many specimens from the Mediterranean Sea have been reviewed for this paper and all the specimens observed have a radial ornamentation on the both valves which is often less prominent on the dorsal valve. Smooth dorsal valves as seen in *M. echinata* have never been observed. Its presence in the Caribbean Sea is possible. However its presence in South Africa, Indian Ocean and Pacific Ocean is highly improbable.

M. echinata is a deep water species with smooth dorsal valve and spiny ventral valve. The spines are alveolar in structure which is not observed in *M. truncata*. It is present in South African waters and along the Sudan coast. It may also be present in deep waters of the eastern Atlantic but this needs to be demonstrated phylogenetically.

This paper emphasizes the importance of homeomorphy in megerlinid brachiopods and shows that identifications of material without knowing the exact structure of the loop is a risky exercise as indicated by the possible confusion between *Megerlia*, *Lenticellaria* and *Annuloplatida curiosa* Bitner, 2014

The precise limit of a genus is always a moot question. Species level only is an indisputable taxonomic reality. Genera are human concepts which should help to reveal relationships between species. Morphological distinctions are useful in this taxonomic process but they are not sufficient to obtain indisputable results. A molecular phylogenetic analysis is, of course, the best way to understand the affiliation between species and it is urgently needed for the newly-described species in this paper.

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