# About the mitromorphid species group *Anarithma lachryma* (Reeve, 1845) (Conoidea Mitromorpha) at reef levels of Balicasag Island (Central Philippines)

#### Franck Boyer

4, impasse Pasquier, 30190 - Garrigues Sainte Eulalie, France; e-mail: franck.boyer7@orange.fr

#### **ABSTRACT**

Mitra lachryma (Reeve, 1845) (Conoidea Mitromorpha) is restored as type species of the genus Anarithma Iredale, 1916, and a series of eleven species ranging in Balicasag (Central Philippines) is proposed to belong to a restricted A. lachryma species group, composed of both planktotrophic and lecithotrophic species, all kind of intergrading situations being reported. Two new species are described in this species group, as A. bulbosa n. sp. and A. melvilli n. sp. The protoconch morphologies examined in the Anarithma complex are considered to reflect high plasticity and to support the hypothesis of a continuum in larval strategies, which contradicts binary taxonomies based on planktotrophic versus lecithotrophic protoconchs. The chromatic features of the teleoconch are considered to be more heritable and playing as better clue of the phyletic distances occurring in this group. Both competitors groups within the Anarithma complex and specific transitions to other mitromorphid genera are discussed.

#### KEY WORDS

Mitromorphidae; *Anarithma*; *Mitromorpha*; *Lovellona*; reef levels; Central Philippines; shell morphology; shell chromatic pattern; phenetic variability; characters heritability.

Received 22.10.2021; accepted 08.01.2022; published online 04.03.2022

#### INTRODUCTION

Until recent years, the mitromorphid fauna of the Indo-Pacific Province has been subject to very few and scattered specific descriptions and to a limited number of revision works, principally from Kilburn (1986) about the subfamily Borsoninae Bellardi, 1875 in South Africa and Southern Mozambique, and from Cernohorsky (1988) who focused more specially on the revision of four species of the Central and Western Pacific, attributed to the "sub-genus" *Anarithma* Iredale, 1916. In his article, Kilburn did recognize the mitromorphid species as distributed in four genera: *Mitromorpha* Carpenter, 1865 (with all the revised species placed in the subgenus

Mitrolumna Bucquoy, Dautzenberg et Dollfus, 1883), Maorimorpha Powell, 1939, Lovellona Iredale, 1917 and Anarithma Iredale, 1916. From his side, Cernohorsky (1988) did unite the mitromorphid fauna within a single genus Mitromorpha among the Borsoniinae, this genus Mitromorpha being divided in the three subgenera Lovellona, Mitrolumna and Anarithma.

The description of a great number of new mitromorphid species from Western Pacific by Chino & Stahlschmidt on 2009 and 2014, mostly collected in the Philippines and placed by them in the genera *Mitromorpha* and *Lovellona*, did renew deeply the topic, demonstrating not only an unsuspected high specific diversity in this area, but suggesting also a high morphologic disparity with various transitional

forms asking for a reassessment of the taxonomic classification in this group.

A recent study by Bouchet et al. (2011), mainly based on previous molecular analysis, proposed a new classification of the superfamily Conoidea Fleming, 1822 recognizing Borsoniidae Bellardi, 1875 and Mitromorphidae Casey, 1904 as distinct families, with *Anarithma*, *Mitromorpha*, *Lovellona* and *Maorimorpha* recognized as operational mitromorphid genera besides three more confidential ones.

Numerous new species described by Chino & Stahlschmidt (2009) are matching the features commonly attributed to Anarithma, but they were placed by the authors in the genus Mitromorpha, without explicit argumentation. This situation seems to come from the fact that most of these species do show morphological features intergrading between the standard keys defining usually the genera Anarithma and Mitromorpha. So lumpering all these species under the older name Mitromorpha did play apparently as a provisional arrangement avoiding the problem of a revision of the generic keys. The point is especially evident about the characters of the protoconch, both multispiral and paucispiral protoconchs being found in this set of "Mitromorpha species", quite similar teleoconchs often occurring despite contrasted protoconchs, whereas multispiral protoconchs were until now considered as diagnostic feature for Anarithma species, versus paucispiral protoconchs for Mitromorpha species.

As a matter of fact, the discovery of a highly diversified and disparate mitromorphid fauna in Western Pacific does play as new fact leading to the change of the extant paradigm. As a first step towards an advanced reassessment of the internal taxonomy of the Mitromorphidae, we propose to focus on a revision of *Anarithma lachryma* (Reeve, 1845), herein restored as type species of the genus *Anarithma*, and on its species group composed of its most evident close relatives. By necessity, this inquiry will lead to check most of the species attributable to *Anarithma* in the Philippines, including several species originally described in the genus *Mitromorpha*.

This study is based on the morphological comparison of a vast amount of shell material collected at reef levels off Balicasag (Central Philippines), allowing to check at large escale the phenetic variability occurring in most of the considered forms.

The comparison between the sympatric mitromorphid phenae did allow to recognize two undescribed *Anarithma* species, and to suggest the outline of competitor groups as well as intergrades linking taxonomic categories.

#### **MATERIAL AND METHODS**

### Relevance of a phenetic study of the shell characters

The point is to verify if the study of the shell characters can valuably support a taxonomic inquiry, and what are the conditions of such a validity. The material under study is principally composed of mitromorphid shells selected from lumun-lumun samplings (nets trapping) performed off Balicasag Island (Panglao) at 50–150 m by Emmanuel Guillot de Suduiraut in the years 1998–2000, now in the collection of the author. Some additional material was used for comparison: Balicasag, Panglao, 50–150 m and 100–200 m, Sandro Gori collection; Aliguay Island, Mindanao, 100–150 m, Sandro Gori collection; Punta Engano, Mactan, 80 m, Walter Renda collection.

This material was collected in live condition and it looks to be in a fresh state, but it was generally washed in a dilute solution of sodium hypochlorite, so in most cases the animal parts were dissolved or dammaged. Only in the case of the recent material from Mactan, most of the animals are conserved in dry conditions, the details of the sculpture and of the microsculptures of the shell (protoconch and teleoconch) being well-conserved and the colour shades saved in vivid and shining conditions. In these conditions the study of the material will be limited to the morphology and to the decoration pattern of the shells, generally in correct state of conservation in our material from Balicasag.

For several species or forms, a documentation was found on Internet and in the grey literature about the animal chromatism. However in most cases this documentation is not linked to evident shell morphologies, the locality data are unprecise, dubious or absent, the pictures are poorly descriptive, and overall the variability occurring in the population is not reported. So we considered that this documentation was not reliable in the frame of our

phenetic study and the chromatism of the animal was not used as key feature.

As far as the Indo-Pacific mitromorphids are concerned, the documentation about the radula remains very poor. The most prominent data are found in Bouchet et al. (2011: figs. 6A-C), where are illustrated the radulae of Lovellona atramentosa (Reeve, 1849), "Mitromorpha" metula (Hinds, 1843), and Anarithma sp., all specimens collected from Panglao in shallow water. The tooth of L. atramentosa looks to be very slender and tapered, whereas the teeth of "M." metula and of Anarithma sp. look to be shorter, stouter and very similar altogether. However this documentation cannot be of any help in the frame of our study, as the data do not reflect neither the specific diversity nor typify the main groups (for instance the shell of "Mitromorpha" metula clearly belongs to Anarithma: see in Systematics), the morphological variability is not documented at the specific scale, and overall these three radular teeth are not differing from teeth found in various Conus groups (pers. obs.).

On the other hand, no operational documentation is available about the internal anatomy and molecular data (genetic distances estimated for some genes) of the mitromorphids.

From the lack of documentation about the animal chromatism, the radular morphology, the internal anatomy and the biochemistry of the mitromorphids, one could infer that any valuable taxonomic study cannot be carried out looking for the species limits, the degrees of interspecific relationship and the taxonomic organization of the group. Such a maximalist point of view must be however tempered, as suggested for instance by the study of Kantor et al. (2008) about the "morphological proxies for taxonomic decision in turrids", testing the value of shell and radula characters through a calibration by molecular data. As a matter of fact, their results show to be pretty equivocal: on the ground of their limited experiment and of the absence of alternative hypothesis, the radula does not prove to be clearly "a more adequate proxy" than the shell morphology for genus or (sub)family allocation, and furthermore no demonstration is made about the relevance of the molecular calibration for validation of the efficiency of shell morphology or of radular features as taxonomic tools.

This sends us back to the basic principles of the Integrative Taxonomy, which are to document, to

cross and to arrange as many characters as possible, reflecting the variability of the populations and ensuring the reliability, the relevance and the comparability of the clues. In the present case, we have at hand a big amount of shells in good condition, collected in sympatry, and allowing to observe and to compare a great number of morphological and chromatic characters, to cross many features combinations and to verify the variability of the characters in an extensive way. The intensity of the observations and the great number of variables under study are by themselves the guarantee of reliable results in a populational approach, even if not exhausting all the fields of the taxonomic investigation. So we propose to apply this methodologic approach to our material, through a phenetic study restricted to the shell morphology and to the shell chromatism.

#### About the protoconch typology

Kilburn (1986, figs. 15–20) illustrated the protoconchs of few mitromorphid species, but he did not pay a special attention to the protoconch morphology as key feature for determination at supraspecific levels. Cernohorsky (1988, figs. 1, 2) illustrated the protoconch of Mitromorpha peaseana (Finlay, 1927) (Fig. 1) and the protoconch of Anarithma metula (Hinds, 1843) (Fig. 2), both from specimens of the Hawaiian Archipelago, but in his comments he is speaking about "embryonic whorls" for the whole protoconch, whether paucispiral with less than 2 whorls or multispiral with more than 4 whorls. From the records given by Kilburn (1986) and other authors, Cernohorsky (1988) came to the conclusion that there is "clearly an overlap in the number of embryonic whorls between the Mitrolumna group (1.5–3.25) and the Anarithma group (2.75-4.5) of species", and that "a generic placement on features of protoconch characters would result in nomenclatural chaos".

The use of the protoconch morphology as determination tool at the specific, generic or even family scales remains controversial in several aspects, and it was the subject to important questioning in the field of some turrid groups along the recent years, for instance in Fedosov & Puillandre (2012) and in Giannuzzi-Savelli et al. (2018). The issue seems to come at least partially from common prejudices re-

produced by the technical vocabulary used in different ways and from the strict dichotomy generally accepted about "planktotrophic" versus "lecithotrophic" patterns.

Even the simple recognition of planktotrophic multispiral protoconchs versus non-planktotrophic paucispiral protoconchs is not stabilized, some authors considering for instance that a planktotrophic stage is occurring over 1 or 1.5 whorls for the "embryonic shell", whereas other authors are considering that a planktotrophic stage is only evidenced over 2.5 "embryonic whorls". As precursor in the study of the larval development of the marine invertebrates, Thorson (1950) did recognize three types of pelagic larvae beside embryonic development without pelagic stage: lecithotrophic larvae originating from large yolkly eggs, not feeding from plankton during their short pelagic life but growing during this stage; planktotrophic larvae originating from small eggs and feeding from plankton during their long pelagic stage; and planktotrophic larvae with a short pelagic life and no visible development during this stage, thus not feeding from plankton or from egg reserves.

Bouchet & Warén (1979) were typifying the larval development in marine mollucs through a binary conception and they were sanctioning new vocabulary acceptances: "direct development", with larval growth occurring in the egg capsule and the young adopting benthic life immediately after hatching; "lecithotrophic development", with the young spending short time as veliger, without feeding and growing; "planktotrophic development", with the young spending longer time feeding and growing as veliger. Bouchet & Warén (1979) were naming as "embryonic shell or protoconch" the "primary shell" formed in the egg capsule and said to have less than one whorl, whereas in planktotrophic species the "larval shell" is said to be formed at the veliger (post-embryonic) stage and to have 1 to 5 whorls.

Lieberman & Vrba (1995) did adopt a noticeably different vocabulary applied to the study of two turritellid species in the frame of their article about the "Hierarchy Theory". They spoke about «larval shell or protoconch » instead of "embryonic shell", and the post-embryonic stage is said to represent "the transition to the juvenile stage". Their figures did not clearly evidence the transitional steps, but the authors did precise that "in non-planktonic species the transition from larva to juvenile is occurring after approximatively 2.5 whorls", whereas "in planktonic species the transition occurs after approximatively 0.5 whorls".

McEdward (1997) did renew the current paradigm of two contrasted larval types in marine invertebrates (feeding and non-feeding), reporting documented cases of "planktotrophs with intermediate egg sizes, differing degrees of dependence on exogenous food, and differing capacities for facultative feeding". From these observations, McEdward infered that "a continuum of larval strategies is predicted".

In view to avoid any ambiguous meanings, we shall use the terms of "protoconch" for the pre-juvenile stage of the shell in its whole, distinguishing the embryonic shell (or nucleus) from the larval shell (post-embryonic stage), and we shall report the number of protoconch whorls in each form, based on a large scale verification of the protoconch variability. In the whole, the transition from the embryonic shell to the larval shell proved to be practically undiscernible, even in the multispiral protoconchs with most numerous number of whorls. Following the implicit classification of Lieberman & Vrba (1995), we shall define as "paucispiral" the protoconch wrapping up to 2.5 whorls, versus "multispiral" for the protoconchs wrapping over 2.5 whorls. The arbitrary aspects of such a classification will be tackled in the Discussion.

#### Relative rarity and sampling bias

Some species are represented in great number in our samplings, whereas others are represented by very few specimens, due to respective natural abundance of the species in the nature, but also from local environmental conditions (including marginal distribution of some species) and overall from sampling bias introduced by the lumun-lumun fishing. Lumun-lumun nets (very long rolls of nets dropped in the sea as mollusca traps) are used in two principal ways: at upper reef levels (30-60 m) and frequently at mid-level depths (80–100 m). Lumun-lumun nets are suspended some meters off the ground, in view to avoid to be caught in the coral formation; at deeper levels (sometimes at 100–150 m, and always at 150-200 m and deeper) lumunlumun nets are sticked to the bottom, as not to be hampered by possibly hooking up with coral formations. As a result, the kind of fauna found in each case is pretty different: in suspended nets; there are overall found species with a free-swinning larval stage (planktotrophic species with long drifting stage as well as lecithotrophic species with more paucispiral protoconchs but however with a short drifting stage), whereas in nets sticked to the bottom at deeper levels can also be found sand dwellers with direct development. In the whole, lumun-lumun nets are giving few species (or individuals) with direct development and devoting to the hard bottoms. As a matter of fact, the gastropod groups known to have globally a direct development (such as the marginelliforms, for instance) are very poorly represented in our samplings, and sand dwellers look to be quite absent. From these elements, we can infer that most of our material is coming from suspended nets, the result being a severe sampling bias in favor of planktotrophic species and of lecithotrophic species with a more or less short drifting stage.

#### Method

As far as the *Anarithma lachryma* complex is concerned and for convenience of demonstration, we are provisionally grouping the considered species in six main phenetic assemblages, principally based on

similarities in the protoconch type, in the general shell shape and in the decoration pattern, and secondarily on similarities in the shell sculpture:

as A series: the "A. lachryma planktotrophic species group" is composed of species having a pyramidal multispiral protoconch and presenting a decoration pattern resembling closely the pattern found in A. lachryma;

as B series: the "A. lachryma lecithotrophic species group" is composed of species presenting a decoration pattern resembling closely features found in the A series, but having a lecithotrophic larval shell;

as C series: the "lecithotrophic diverging series" is composed of lecithotrophic species diverging more deeply from the decoration pattern found in the A series;

as D series: the "planktotrophic polychromatic species group", brother group composed of species having the same pyramidal multispiral protoconch found in the A series, but presenting a distinctive polychromatic decoration pattern;

as E series: *A. thalaoides* (Chino et Stahlschmidt, 2014) is a lecithotrophic species from a distinctive lineage with strong inflated protoconch, narrow slender outline and heavily goffered shell structure;

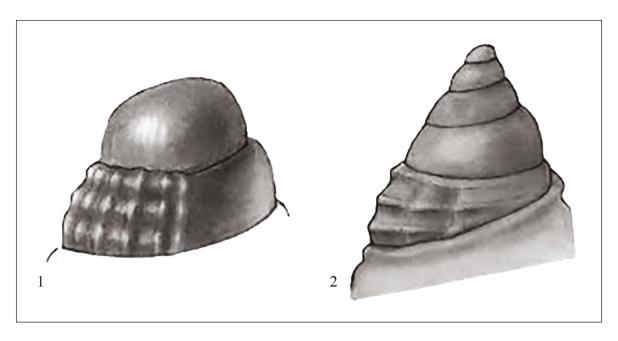


Figure 1. Protoconch of *Mitromorpha* (*Mitromorpha*) peaseana Finlay, Hawaiian Is., in Cernohorsky, 1988, fig. 1. Figure 2. Protoconch of *Mitromorpha* (*Anarithma*) metula Hinds, Hawaiian Is., in Cernohorsky, 1988, fig. 2.

as F series: *A. fischeri* (Hervier, 1900) is a plankthotrophic species matching closely the A series for the protoconch shape and for the shell sculpture, but diverging deeply for the black and white decoration matching the pattern found in several *Lovellona* species.

This presentation method based on phenetic proxies does not imply by itself taxonomic evidences, as it will be explained in the Discussion.

**ABBREVIATIONS** AND ACRONYMS. BPBM: Bernice Pauahi Bishop Museum, Honolulu, Hawaii; MM: Manchester Museum, Manchester, England, Great Britain; MNHN: Muséum national d'Histoire naturelle, Paris, France; NHM: Natural History Museum, London, England, Great Britain; NMST: National Museum of Science and Nature, Tokyo, Japan; NMW: National Museum of Wales, Cardiff, Wales, Great Britain; UCB: University of California, Berkeley, U.S.A.; UFL: University of Florida, Gainesville, U.S.A.; WORMS: World Register of Marine Species (http://www.marine species.org); FBC: collection of Franck Boyer, Garrigues Sainte Eulalie, France; SGC: collection of Sandro Gori, Livorno, Italy; GPC: collection of Guido Poppe, Cebu, Philippines; id.: idem; ib.: ibidem; spm: specimen; L: length size.

#### **RESULTS**

#### Systematics

Superfamilia CONOIDEA Fleming, 1822
 Familia MITROMORPHIDAE Casey, 1904

 (erected by Bouchet, Kantor, Sysoev & Puillandre, 2011)

Genus Anarithma Iredale, 1916

Type species. Usually considered as *Clavatula metula* Hinds, 1843, (i.a.: Kilburn, 1986: 711; Cernohorsky, 1988: 65–66; WORMS taxname 432393), but restored here as *Mitra lachryma* Reeve, 1845, by monotypy, as explained below.

As reported by Cernohorsky (1988), Iredale (1916: 27) formally appointed by simple indication (i.e., by monotypy) "Columbella lachryma Gaskoin" as type species of his new genus Anarithma, despite considering in the next page (ib: 28) that Columbella lachryma is in fact a ju-

nior synonym of *Clavatula metula* Hinds. "*Columbella lachryma* Gaskoin" is in fact an unpublished name and it must be considered here as simple incident substitution to "*Mitra lachryma* Reeve", a taxon clearly belonging to the mitromorphid fauna.

Mitra lachryma Reeve being considered as junior synonym of Clavatula metula Hinds by subsequent reviewers, the latter was commonly adopted as type species of Anarithma. In the course of the present article, we shall demonstrate that Mitra lachryma is in fact a distinct species and not a synonym of Clavatula metula, so Mitra lachryma Reeve is here restored as type species of the genus Anarithma.

# A series: the A. lachryma planktotrophic species group

Anarithma metula (Hinds, 1843) (Figs. 3–26)

Clavatula metula Hinds, 1843: p. 44; no type figure; no locality.

Columbella (Seminella) pacei Melvill & Standen, 1896: p. 274–275, pl. IX, fig. 5; Lifu.

Columbella (Seminella) stepheni Melvill & Standen, 1897: 407 (replacement name of *C. pacei*).

Columbella dibolos Barnard, 1964: p. 17, fig. 1f; Natal, 40 fms.

Type material. Holotype NHM Reg. Nb. 1879.2.26.81 (Figs. 3–4), L = 3.85 mm, no locality.

Other Material Examined. MM: 1 syntype de *Columbella (Seminella) stepheni* Melvill & Standen, 1897 Reg. Nb. MANCH.EE.3765 (Figs. 5, 6), Lifu. NMW: 10 syntypes de *C. stepheni* Reg. Nb. 1955.158.00374–00375 (Figs. 7–18). The syntype pictured in Fig. 18 will be proved to belong to another species, described below as new. MNHN: Collection Maurice Jay, La Réunion, 0–40 m, numerous spm. FBC: Central Philippines (Balicasag Island, Mactan Island, Aliguay Island), 50–150 m, numerous spm (Figs. 19–26). SGC: Mirissa, Sri Lanka, 20–40 m, several spm.

DESCRIPTION. Hinds, 1843, p. 44: "Clav. testá ovatá, acuminatá; anfractibus quinis planulatis, obsoletè costulatis, transversim striatis, pallidè rufo fasciatis; suturâ lineâ elevatâinstructâ; apertura li-

neari; labro subinflexo ; canali subnullo. Axis 2 lin. Hab. - ? ".

TYPE LOCALITY. Here designated as Balicasag Island, 50–150 m, Central Philippines.

DISTRIBUTION. Anarithma metula proves to have a wide distribution in the Indo-Pacific Province, but it is possibly not general. In the Pacific field, morphs attributable to the species can be confirmed for most of the northern tropical latitudes, from the Philippines (Guido Poppe and pers. obs.), Papua New Guinea (MNHN collections), New Caledonia (type material of C. stepheni Melvill et Standen, 1897), Kwajalein in the Marshall Islands (Scott Johnson, pers. comm.) and the Hawaiian Archipelago (Dan Polhemus, pers. comm.). But the occurrence of the species remains to be verified for most of the Pacific southern latitudes, from eastern Australia and New Zealand, up to Polynesia where contrasting decoration patterns were documented and possibly belong to closely related species (i.a.: photos of a specimen from Moorea by Gustav Paulay, UCB). In the Indian Ocean, morphotypes attributable to A. metula were verified from the Dhofar, southern Oman (Horro & ali, 2021), from southern Sri Lanka (SGC) and from Phuket, southwestern Thaïland (G. Poppe, pers. comm.), but it seems to be absent from the upper Arabian Sea (i.a. absent from Masirah Island, pers. obs.) and it remains to be confirmed from the Red Sea and the rest of northwest Indian Ocean. At southern latitudes of Indian Ocean, the species is confirmed from South Africa (Kilburn, 1986: figs 155–157), from Mozambique (Juan Horro, pers. comm.) and from La Réunion (MNHN, pers. obs.).

In the Central Philippines, the species was mostly collected in lumun-lumun trapping at 30–80 m, but findings were sometimes reported from the shallow waters (G. Poppe, pers. comm) down to 150 or 200 m (Sandro Gori, pers. comm.).

REMARKS. Even if presenting quite uncommon features such as a narrow subcylindric outline and a general light-tan subhyalinous colour ground, the holotype of *A. metula* (Figs. 3, 4) belongs to the range of shell variability observed at large scale for the species. The series of 10 conspecific syntypes of *A. stepheni* (Figs. 5–17) is displaying the variation in shape and color most commonly found in *A. metula*. In our live collected specimens from Balicasag, extreme phenic variations of the species are ranging from slender oval outline (Figs. 19–21) to

biconic outline (Figs. 25, 26), and from light-honey ground for the part of the upper two thirds (Figs 19-21) to general subhyalinous greyish-white (Figs. 25, 26). The most usual form is pictured in Figs. 23, 24. The length size is ranging from 3.0 mm to 4.5 mm. Beyond its rather important phenetic variability, the most distinctive features of A. metula are a high multispiral white protoconch of 4 to 4.75 whorls (average length: 4.4 whorls) with a tiny sharp nucleus (Fig. 22), rather strong knobs on the two upper spiral cords at the level of the axial ribs, frequent thin mustard-yellow lines in the interspace of the cords on the lower third of the shell, on the ventral side the upper part of the axial ribs is showing alternatively either a light orangebrown vertical mark or a whitish ground, whereas on the dorsal side a darker large brown-orange is spreading over most of the body whorl, forming a crenulate pattern at the level of the upper part of the axial ribs, alternatively recovering them either fully or partially.

The three syntypes of *Columbella dibolos* Barnard were consulted by Kilburn (1986: 714) and despite their strongly worned state, they were formally recognized by him as conspecific with *A. metula*. The species is proved by Kilburn to range off South Africa through pictures of a specimen (1986: figs. 155–157) matching perfectly the type material from MM and NHM.

The other synonymies proposed by Cernohorsky (1988: 66) are contested here: Mitra lachryma Reeve, 1845 is demonstrated below to clearly correspond to another species; Columbella pamila Duclos, 1848 is demonstrated below to represent also another species, with Cythara garretti Pease, 1860 as possible synonym name and Columbella sublachryma Hervier, 1900 as more dubious synonym; the Family status of Columbella (Anachis) pusiola Dunker, 1971 as well as that C. (Anachis) nana Dunker, 1871 remain uncertain, the first name being not recorded in WORMS and the second name being synonymized with the columbellid species Columbella (Seminella) peasi Martens & Langkavel, 1871; Mitrolumna iki Kay, 1979 is verified to be non-conspecific with the sympatric A. metula in the waters of the Hawaiian Islands on the ground of its his distinctive color pattern (Dan Polhemus, pers. comm.); Anarithma maesi Drivas & Jay, 1986 is also verified to be nonconspecific with the sympatric A. metula in the wa-

ters of La Réunion on the ground of its distinctive color pattern and of its larger and smoother slender shell (MNHN, pers. obs.).

From the Central Philippines, two morphs commonly confused with *A. metula* are recognized herein as sibling forms and they are described as new species, each of them presenting constant differences with the pattern of *A. metula* in sympatric situation, without evident intergrades despite the high number of checked specimens. Other sibling species of *A. metula* are certainly occurring in other places of the Indo-Pacific Province and they will deserve special inquiries in the frame of region-based studies, such as the distinctive morph pictured from Moorea by Gustav Paulay (https://calphotos.berkeley.edu) or as the distinctive morph pictured from Zululand by Kilburn (1986: figs. 158–160).

**Anarithma bulbosa** n. sp. (Figs. 27–34) https://zoobank.org:act:D3313D0B-E261-45A8-A3BB-93AB701897C1

TYPE MATERIAL. Holotype MNHN–IM–2000–36524 (Figs 27–30), L = 3.9 mm; 7 paratypes FBC (Figs. 31–34), all from the type locality.

OTHER MATERIAL EXAMINED. Not found in lumun-lumun samples from Mactan and from Aliguay.

DESCRIPTION OF THE HOLOTYPE (Figs. 27–30). Stout biconical outline with strong sculpture, protoconch of 4.2 whorls with large bulbous nucleus; protruding spiral cords, thick axial ribs bearing strong nodules at the level of the two upper cords, the nodules of the upper series being less elevated and more stretched along the spiral axis; on the ventral side, the axial ribs present alternatively either a white mark or a brown mark under the strong white nodules, golden yellow lines in the intercostal groove, and thinner golden yellow spiral lines are running on one cord out of two; on the dorsal side, a wide brown patch is spreading on the center of the dorsal side, showing a crenulated pattern on its upper side, the golden lines on the cords and under the ribs being thicker and forming a checkboard pattern, more distinctive on the outer side of the labrum; the two columellar plaits are faintly produced in mature shells and absent in young adults.

Type locality. Balicasag Island, 50–150 m.

DISTRIBUTION. Anarithma bulbosa n. sp. is only known for now from Balicasag Island; it was not found in other places from Central Philippines, and not recorded from the documented areas located in the vicinity at similar latitudes, such as the Marshall Islands (Scott Johnson collection) and Papua New Guinea (MNHN collection). On this ground, the species must be considered as a narrow endemic, despite the presence of a multispiral protoconch.

ETYMOLOGY. From the bulbous aspect of the nucleus.

REMARKS. Anarithma bulbosa n. sp. is differing from the sympatric A. metula by several evident and constant features, such as the slightly shorter protoconch with much bulbous nucleus, squatter angular outline, stronger sculpture with 7 axial ribs visible from the ventral side of the last whorl (instead of 8 ribs in A. metula), deeper anal sinus and more arched labial border, and faint columellar plaits versus strong plaits on a more convex border in A. metula, more numerous and thicker golden spiral lines on the body whorls, presence of intercostal golden lines making a conspicuous checkboard pattern on the left side of the dorsum, dark marks on the upper tip of the ribs and the dorsum are tobacco brown shaded, instead of orange-brown in A. metula. Any kind of intergrade was not observed. The morphology, the decoration and the size range of A. bulbosa look as remarkably constant (L = 3.5 mm to 3.9 mm).

*Anarithma fuscafenestrata* (Chino et Stahlschmidt, 2014) (Figs. 35–38).

Mitromorpha fuscafenestrata Chino & Stahlschmidt, 2014: 23–24, 1 fig. in-text p. 23 and plate 1, figs. 2a–c; Aoré Isl., Santo, Vanuatu, 45–50 m.

Type MATERIAL. Holotype MNHN–IM–2000–23338 (Figs. 35, 36), L = 5.1 mm, paratype MNHN IM–2000–23339, L = 4.9 mm, and 10 further paratypes in various collections (NMSN, collection Poppe and collections of the authors).

Other material examined. FBC: 2 spm from Balicasag, 50-150 m.

DESCRIPTION. Chino & Stahlschmidt, 2014, p.

24: "Shell broad biconic, small to medium sized for the genus, attending 6.1 mm; whorls very weakly convex; teleoconch whorls about 4; base of the body whorl strongly tapering. Aperture somewhat linear; labrum with ridge-like denticles and a tubercle at the level of columella/parietal junction. Columella white, swollen with a small V-shaped notch. Anal sinus fairly deep. Axial sculpture is absent. Spiral sculpture of 3 rather weak threads on first whorl, base of body whorl with about 18 spirals; spirals slightly narrower than intervals, interspeces with microscopic axial sculpture. Ground color white, with two rows of small, brown colored, more or less rectangular shaped, widely spaced spots, the anterior row only visible on body whorl. Protoconch conical, whithish, about 3.5 smooth whorls. Animal unknown".

TYPE LOCALITY. Aoré Island, Espiritu Santo, Vanuatu, 45–50 m.

DISTRIBUTION. Due to dubious data and comparisons attached to the original description of the species (see in Remarks), *Anarithma fuscafenestrata* can be confirmed only from Espirito Santo (Central Vanuatu: Figs. 35, 36), Balicasag (Central Philippines), Papua New Guinea (MNHN Collection: Fig. 37) and Moorea, Society Islands (Fig. 38).

REMARKS. Chino & Stahlschmidt (2014: 24) are comparing A. fuscafenestrata with a morph designed by them under the name of "Mitromorpha stepheni Melvill & Standen, 1897" and said to be "very similar in regards of the color pattern", but differing from A. fuscafenestrata "in the cylindrical and less biconic shell, the well developed axial sculpture, and the weaker spiral sculpture". As demonstrated previously, the name "A. stepheni" is a junior synonym of A. metula, and the morph compared to A. fuscafenestrata by Chino & Stahlschmidt (2014) belongs in fact to an undescribed sibling species quite common in the Central Philippines and described below.

The authors concept of "Mitromorpha fuscafenestrata" looks to be quite unprecise, as the type material contains eclectic morphs: for instance, the paratypes 7 and 8 belonging to the G. Poppe Collection and apparently coming from the Philippines are ribbed shells belonging to the new species described below.

For the stabilization of the species concept of

A. fuscafenestrata, we propose to refer to the holotype from Espirito Santo, Central Vanuatu (Figs. 35, 36), to the juvenile specimen from Papua New Guinea (MNHN) pictured in Fig. 37, to the live specimen from Moorea pictured in Fig. 38 (UCB), and to the two specimens from Balicasag (FBC). These five specimens are sharing the same morphological and chromatic characters and they are coherent with the original description. We note that in this series, the four adult specimens present a quite inflated shape, which is compatible with the description term of "broad biconical". We note also that the total absence of axial sculpture is well-evidenced, as well as the occurrence of a rather matte milky white color ground and of rounded to squarred dark brown marks. Any kind of intergrade was not observed between A. fuscafenestrata and the sibling ribbed form from the Central Philippines, despite the important material checked here. The documented length size of the shell of A. fuscafenetrata ranges from 5.1 mm (holotype MNHN of A. fuscafenestrata from Espirito Santo) up to 7.0 mm (larger specimen from Balicasag, FBC). The pyramidal protoconch of A. fuscafenestrata has 3.4 to 3.6 whorls (average shell length: 3.5 mm).

Anarithma melvilli n. sp. (Figs. 39–50) https://zoobank.org:act:6013D2A4-DE06-4091-BA23-C24668CB83CB

TYPE MATERIAL. Holotype MNHN–IM–2000–36525 (Figs. 39–42), L = 5.0 mm, and 62 paratypes FBC (Figs. 43–48), all from the type locality.

OTHER MATERIAL EXAMINED. MNHN: Collection Maurice Jay, La Réunion, 0–40 m, numerous spm. FBC: Central Philippines (Mactan Island, Balicasag Island and Aliguay Island), 50–150 m, numerous spm.

DESCRIPTION. On the basis of the holotype (Figs. 39–42): Slender oval outline with moderate sculpture, subhyalinous grey-white ground; white protoconch of 3.5 whorls with moderately bulbous nucleus; thin and packed spiral cords, axial ribs weakly nodulose at the level of the two upper cords; on the ventral side, the axial ribs present alternatively either a white mark or a deep brown rectangular mark axially oriented under the two upper cords; a ring of deep brown chevron-shaped marks

at the mid-part of body whorl, partially merging together; a ring of tiny honey dots is running on the upper cord; aperture rather narrow and sinuous, the columellar border is moderately convex and present a faint notch at its middle part, forming two weak columellar plaits.

Type locality. Balicasag Island, 50–150 m.

DISTRIBUTION. In the present state, the typical form of *Anarithma melvilli* n. sp. is only verified with certainty from the Central Philippines (pers. obs.), but closely matching populations designed here as *A*. cf. *melvilli* n. sp. are documented from Mozambique (J. Horro, pers. comm.), La Réunion (MNHN, pers. obs.) and Espirito Santo, Vanuatu (MNHN, 1 spm from southeast Santo, shallow water).

ETYMOLOGY. From James Cosmo Melvill, author of the name "Columbella stepheni", junior synonym of A. metula Hinds but often used in the literature and in the collections for the designation of our new species.

REMARKS. In Central Philippines, *A. melvilli* n. sp. shows as quite variable for its outline, most time slender but sometimes squatter and more biconical, for its more or less protruding ribs, and for its color pattern, with the two rows of dark brown marks sometimes sometimes merging on the dorsum in a big dark patch, and the row of tiny honey dots on the upper cord sometimes absent. The length size is ranging from 4.0 to 5.2 mm.

Anarithma melvilli n. sp. is differing from A. metula principally by much darker color marks (deep brown instead of light honey brown), the presence of a row of brown marks at the mid part of the body whorl, and slightly less protruding sculptures. The size range of A. melvilli is slightly larger than that of A. metula, but their respective size range are however overlapping (L = 3.0 mm to 4.5 mm for A. metula; 4.0 mm to 5.2 mm for A. melvilli).

Anarithma melvilli n. sp. is differing from A. fuscafenestrata principally by the presence of more or less pronounced axial ribs, but also by its subhyalinous (or vitreous) grey-white ground color, instead of opaque milky white in A. fuscafenestrata, more oblique cords on the anterior part of the body whorl, with narrower interspaces between the cords and less developed thin axial inter-cords striae, more elongated brown marks instead of rounded or squarred marks in A. fuscafenestrata. The average

length size of *A. melvilli* in Central Philippines looks as smaller than the certified sizes in *A. fus-cafenestrata* (its holotype and the 2 specimens FBC), but the respective size ranges are however slighly overlapping: 4.0 mm to 5.2 mm for *A. melvilli* versus 5.1 mm to 7.0 mm for *A. fuscafenestrata*.

In the "peripheral" populations referable to A. melvilli n. sp. and studied from Mozambique and La Réunion, the pattern of variability looks as a bit different from the pattern observed in Central Philippines, as their shell outline is more diversified from narrow and slender shells to squat biconical inflated shells, the axial sculptures are ranging from strong to very weak, and depending on the specimens the dark brown marks are ranging from axially stretched to rounded or squarred. A specimen documented from Espirito Santo, Vanuatu (MNHN) presenting a squat inflated biconical shape, weak axial ribs and small dark brown rounded marks shows the same pattern of diversification towards features typically found in A. fuscafenestrata. We consider however that these different "diverging" morphs belong to the geographical variability of A. melvilli n. sp. and that they can be accepted as A. cf. melvilli n. sp. in the present state, considering the fact that they just present a wider phenetic variability than the typical population from Central Philippines and that they do not share some of the most distinctive features of A. fuscafenestrata sensu stricto, such as the total absence of axial sculpture, the less oblique and more spaced cords, and the opaque milky white ground color.

Anarithma lachryma (Reeve, 1845) (Figs. 51–66)

*Mitra lacryma* Reeve, 1845 : pl. 32, fig. 258 (dorsal view only), no locality.

TYPE MATERIAL. Lectotype NHM Reg. Nb. 1980107-1 (Figs. 51, 52), L=7.3 mm, and 2 paralectotypes NHM Reg. Nb. 1980107-2 and 3 (Figs. 53–56), L=7.3 mm & 6.9 mm, no locality. The lectotype was designated by Cernohorsky (1988: 68, figs. 6, 7) with a wrong size in the text (6.8 mm instead of 7.3 mm here controlled from the scale bar) and both wrong Register Number and wrong size (7.8 mm) in the captions.

OTHER MATERIAL EXAMINED. FBC: Central

Philippines (Mactan Island, Balicasag Island and Aliguay Island), 50–150 m, numerous spm.

DESCRIPTION. Reeve, 1845, sp. 258 (English text): "Shell ovate, attenuated at both ends, rather thin, spire short, somewhat obtuse; whorls longitudinally very finely ribbed at the upper part, transversely marked with obsolete raised stria; white, peculiarly painted at the back with a large orangebrown blotch; columella two- or three- plaited, plaits nearly obsolete; lip effused. Hab. -?".

Type locality. Here designated as Balicasag Island, 50–150 m, Central Philippines.

DISTRIBUTION. Anarithma lachryma is common in the Central Philippines, but it seems to be unusual in Papua New Guinea (MNHN, pers. obs.) like in Mozambique (Juan Horro, comm. pers.). In La Réunion (MNHN, pers. obs.) this species is represented by a rather variable population looking as intergrading between A. lachryma and the twin species discussed in the follow. A specimen from Safaga, Egypt (FBC) looks as intergrading both forms as well. In Mozambique, the population attributable to A. lachryma is more distinctive, but its protoconch seems to have slightly more inflated whorls than the population of A. lachryma from the Philippines.

REMARKS. In most cases (Figs. 57–66), Anarithma lachryma is differing from A. metula (Figs. 19–26) by a larger length size (4.3 to 7.0 mm instead of 3.0 to 4.5 mm), less whorls in the protoconch (about 3.2 to 3.5 whorls instead of 4.00 to 4.75 whorls), less nodulose two upper cords, more protruding upper labrum, more angular upper labial tooth, more swollen central columellar border with more incised notch, flatter and less spaced ribs (generally 10 axial ribs are visible from the ventral side, instead of 8 in A. metula), wider and flatter anterior cords on the body whorl, less conspicuous honey marks on one rib out of two under the two upper cords (instead of more conspicuous brown-orange marks in A. metula), no color marks on the upper cord or very rare thin light honey short axial dashes (instead of a ring of golden honey dots in most of A. metula), 2 to 5 short honey digitations overlapping the outer tip of the second cord (instead of no digitation in A. metula), less conspicuous brownish dorsal patch with posterior dark brown marks making like crenulations alternating with white areas at the level of the shoulder (instead of well-defined

horizontal border of the dark brown-orange patch underlining the second upper cord in *A. metula*), thick axial and spiral light-honey lines crossing on the anterior part of the body whorls (instead of less numerous thin mustard spiral lines and no axial lines in *A. metula*).

In its extreme variations, A. lachryma can reach 7.0 mm in length size, its outline can range from squat biconic to slender suboval, some specimens can show more or less nodulose two upper cords (like in the lectotype for instance), axial ribs are generally lacking on the dorsum of the body whorl and when suggested they are partially crossed by spiral cords, the axial and spiral light-honey lines running on the anterior part of the body can be partially lacking or totally absent. Few sympatric specimens with narrow slender shells and numerous packed axial ribs are provisionally attributed with reserve to the species as A. cf. lachryma. In Central Philippines, A. lachryma is also collected in sympatry with a twin morph tentatively characterized hereunder and attributed to a taxon fallen into disuse since its description.

Anarithma pamila (Duclos, 1848) (Figs. 67–98)

Columbella pamila Duclos, 1848: pl. 22, figs. 11, 12, no locality.

?Cythara garretti Pease, 1860: p. 147, sp. 89, no figure, Sandwich Islands.

?Columbella sublachryma Hervier, 1900: p. 382, pl. 14, fig. 1, Lifou.

?Mitromorpha flammulata Chino & Stahlschmidt, 2009: p. 67, 68, 1 fig. in-text, pl. 3, figs. 1, 2, Kagoshima, Japan.

Type MATERIAL. Six syntypes MNHN–IM–2000–6410 (Figs. 67–70), attached label giving "Mazatlan" as locality. A lectotype is here designated as MNHN–IM–2000–6410–1 (Figs. 67, 68), L=6.7 mm. The five other specimens of the lot are considered as paralectotypes.

OTHER MATERIAL EXAMINED. NHM: *Cythara* garretti Pease, 1860: lectotype NHMUK 19627801(Figs. 71, 72) and 3 paralectotypes NMHUK 1962781, Sandwich Islands, selected by Cernohorsky (1988: 68). MNHN: *Columbella sublachryma* Hervier, 1900: syntype MNHN–IM–2000–6380 (Figs. 79, 80), Lifou. FBC: Central Philippines (Balicasag Island and Aliguay Island),

50–150 m, numerous spm (typical and intergrading form).

DESCRIPTION. No original description. Description from the lectotype here designated (Figs. 67, 68): Biconical suboval shell, rather nodulose spire, wide ribs with narrow interspace on the ventral side of the body whorl, about absent on the dorsal side; two upper spiral cords of the body whorls moderately nodulose on the ventral side and about smooth on the dorsal side, produced strong and spaced spiral cords on the anterior half-part of the body whorls, but flat, smooth and packed on the posterior part of the body whorl. Aperture narrow, moderate notch a bit lower than the mid-part of the columellar border, strong upper labial tooth. Light orange-tan spiral zone under the second cord of the last whorl, presenting a crenulated pattern, spreading downside on the dorsal side of the body whorl; light orangetan digitations running on the two upper cords between the ribs, making a series of alternating short and long subrectangular patches at the top of the last whorl.

Type Locality. The attached reference of "Mazatlan" looks to be wrong, as any similar mitromorphid species was never reported from the Panamic Province since now. So we are designating here Balicasag Island, 50–150 m, Central Philippines, as type locality of the species.

DISTRIBUTION. Out of Central Philippines, *Anarithma pamila* (Duclos, 1848) is documented from Papua New Guinea (MNHN), Marshall Islands (Scott Johnson, pers. comm.), Moorea in the Society Islands (Gustav Paulay, UCB picture) and Mozambique (Juan Horro, pers. comm.).

REMARKS. Anarithma pamila is differing from A. lachryma by several discreet differences, not always evident by their extent but better by their correlation. In most cases, A. pamila shows a more slender outline than A. lachryma, more oval and less strictly biconical, the proportional length of the aperture is longer and the spire is proportionally shorter, the shoulder of the labrum is less thickened and produced, the average length size is slightly larger despite overlapping in most case (5.2–7.1 mm for A. pamila versus 4.3–6.4 mm for A. lachryma), wider and less numerous packed axial ribs on the ventral side (7 to 9 ribs in A. pamila versus 9 to 10 less packed ribs in A. lachryma); the average length of the protoconch of A. pamila (3.70 whorls) is slightly longer than in A. lachryma (3.35 whorls), and its length variability is wider (3.25

to 4.00 whorls in A. pamila, versus 3.20 to 3.50 whorls in A. lachryma); the upper dorsal part of the last whorl is very smooth, the interspace between the cords being about or absolutely not visible, whereas they are more conspicuous in A. lachryma; axial orange-tan or light-tan digitations are running on the two upper cords of the last whorl, both on ventral and dorsal sides, whereas only very few digitations are running on outer tip of the second cord on the dorsal side of A. lachryma; in most cases, A. pamila is decorated of uniform tan-coloured patches and lines, like occurring in most A. lachryma, however A. pamila show light orange-tan to khaki green shades, whereas A. lachryma presents more browny shades and most often dark brown marks under the second cords of the body whorl. Both species show to have a similar protoconch shape.

Depending on the places in the Central Philippines, the degree of occurrence of both species seem unequal and the phenetic discrimation between them is more or less easy. In our lumunlumun samplings from Balicasag, more than 300 specimens of A. lachryma were identified, for about 60 specimens attributed to A. pamila: among these 60 specimens, the half part was initially considered as more or less intergrading with A. lachryma for one or several features, but the identification as A. pamila was finally made with certainty on the ground of unique correlations, such as the occurrence of regular colour digitations running on the two upper cords of the dorsal part of the body whorl, together with the occurrence of uniform khaki-tan colour shades and of smooth upper part of the dorsum of the body whorl. From the lumunlumun sampling made off Mactan Island (80 m), we did identify only 10 specimens of A. lachryma and one ambiguous specimen more or less intergrading between both species. On the contrary, in the dredged sampling from Aliguay Island we found only two specimens of A. lachryma and two specimens of A. pamila, each species looking as pheneticaly very homogeneous, and both looking as deeply contrasting from each other.

Anarithma lachryma and A. pamila look as twin species separable in rather easy conditions in the Central Philippines, and apparently also in Papua New Guinea (MNHN photos collection) and in Mozambique (photos communicated by Juan Horro). In other places, such as La Réunion, populations presenting more or less intergrading fea-

tures are occurring and might prove to belong to an ancestor lineage of the twins, but this point will be studied deeper in a next work. Several described taxa closely matching A. pamila and presented here with contrasted reserve as possible synonym names may prove to represent in fact sibling species belonging to the same radiation A. lachryma/A. pamila. For instance the lectotype of A. garretti (Pease, 1860) from Hawaii (Figs. 71, 72) is matching A. pamila for the smooth upper part of the dorsum of the body whorl and for the few digitations crossing the two upper cords of the body whorl, whereas this lectotype is more closely matching A. lachryma for the other features and its paralectotypes (Figs. 73–78) are fully matching A. lachryma as well. Due to its relatively isolated distribution, this population from Hawaii might however have a distinct endemic status and its morphologic variability deserves deeper investigations. In these conditions, we place provisionally A. garretti in the synonymy of A. pamila with significant reserves. A. sublachryma (Hervier, 1900), described from Lifu (Figs. 77, 78) looks as closely matching the most heavily sculptured of the A. pamila specimens from Balicasag (Figs. 89, 90) and despite serious reserves we place provisionnally A. sublachryma in the synonymy of A. pamila.

On the contrary A. pinguis (Hervier, 1900), also described from Lifu (Figs. 79, 80), presents a very smooth shell in its whole and a very short spire with concave sides, both features never observed in various populations belonging to the A. lachryma/A. pamila species complex (Philippines, La Réunion, Mozambique), and very contrasting with the sympatric form A. sublachryma: so A. pinguis is considered as a probable autonomous species within the A. lachryma/A. pamila complex.

Anarithma flammulata Chino et Stahlschmidt, 2009, more recently described from Kagoshima, Japan (Figs. 81, 82), presents also a rather distinctive appearance with its rather smooth shell surface and its colour pattern of big axial flames flanking big white patches on the upper part of the body whorl. However axial ribs are suggested on the spire of A. flammulata, and both these morphological and chromatic features look as very close to the smooth and most "flamed-shaped" specimens of A. pamila from the Philippines (Figs. 93, 94), so A. flammulata may prove to be an extreme variant of A. pamila or possibly a geographic form of the

species. A cline of intergrades for the smooth surfaces and for the flamed decoration pattern seems to occur in the geographic interval between Central Philippines and Southern Japan, for instance in the Carolines and the Marshall Archipelagos (Scott Johnson, pers. comm.). The robust determination of the taxonomic status of the population from Japan deserves further inquiries, especially about the phenetic variability occurring in the place. Despite these reserves, we place provisionally *A. flammulata* in the synonymy of *A. pamila*.

Anarithma nigricingulata (Chino et Stahlschmidt, 2009) (Figs. 99–102)

Mitromorpha nigricingulata Chino & Stahlschmidt, 2009: p. 66, 67, 1 fig. in-text & pl. 2, figs. 3, 4; Mactan, Philippines, 60 m.

Type MATERIAL. Holotype NSMT–76866 (L = 4.9 mm), paratype MNHN–21855 (L = 4.8 mm) and four other paratypes in various collections, all from Mactan Island except the third paratype which comes from Aliguay Island.

OTHER MATERIAL EXAMINED. FBC: Balicasag, 50–100 m, 6 spm (Figs. 100–102); Punta Engano, Mactan, 80 m, 1 spm.

DESCRIPTION. Chino & Stahlschmidt, 2014, p. 66–67: "Shell small sized for genus, up to 4.9 mm, shell thick, solid, slender fusiform and with semioval outline. Body whorl large (52–53% of the shell length) and slightly swollen. Outer lip solid and thickened on upper side, with a small and shallow sinus situated on the shoulder slope. Protoconch of about 3 whitish transparent whorls. Columella slightly swollen, with two folds. Early whorls with 3 strong spirals, increasing to 15–16 spirals on the body whorl. No axial ribs occurring but spiral becoming granulate on the 3rd to 4th teleoconch whorls. Ground color whitish with around 4-6 dark brown colored spirals forming a band on the middle of the whorl, 6–9 white spots on upper and lowest spiral of the band. Remnants of the color band forming a small dark band near the suture of the penultimate whorl. Early teleoconch remaining whitish colored. Aperture whitish inside. Animal and radula unknown".

Type locality. Mactan Island, Cebu, 60 m.

DISTRIBUTION. Known initially from Mactan and Aliguay, now recognized also from Balicasag and inferred to range in the whole Central Philippines.

REMARKS. Anarithma nigricingulata seems to be endemic from the Central Philippines and it looks to be uncommon in the field. Most of the observed specimens are deprived totally or partially of their protoconch, which proves to be easily lost; this is an original occurrence among the mitromorphid species. This pyramidal protoconch has 3.0 to 3.5 whorls. A. nigricingulata is provisionally accepted in the A. metula species multispiral group, on the ground of its similar multispiral protoconch (Fig. 99) and of its shell decoration pattern which presents some similarity with the chromatic phase of wide central brown spiral band occasionally observed in A. melvilli (see infra). On the other hand, A. nigricingulata is diverging noticeably from the other species here accepted in the A. metula species group, due to its coarse spiral sculpture of spiraloriented packed beads. In the considered case, we propose to give a higher discriminatory value to the chromatic pattern than to the characters of the sculpture, the observation of the A. metula complex leading to consider that the sculpture seems to have a higher plasticity than the colour pattern in this group. In the present case, the coarse beaded axial sculpture is not interpreted as necessarily representative of a major evolutionary distance. Naturally, this point of view is overall intuitive and it may well be contested by new evidences in the next.

# B series: the A. lachryma lecithotrophic species group

In the present state of the documentation, three species are proposed in this series: *Anarithma dorcas* Kuroda & Oyama, 1971 (Figs. 103, 104, 111), *A. rubrimaculata* (Chino et Stahlschmidt, 2009) (Figs. 105, 106, 112), and *A. granulata* (Chino et Stahlschmidt, 2009) (Figs. 107, 108, 113). Despite the noticeable disparity of the protoconchs shape in these three species (Figs. 111–113), they all have exactly 2.25 whorls and they look as being better lecithotrophic, if not strictly paucispiral in the usual meaning. We note that despite its non-planktotrophic protoconch, the first of these three species was correctly described in the genus *Anarithma*, whereas the two latter species the first species were described in the genus *Mitromorpha*.

For its checkerboard decoration, its color shades and its smooth shell surface, A. dorcas looks to be close to A. pamila and to the sibling form A. flammulata. Anarithma rubrimaculata looks to be close to A. lachryma for its finely interlaced sculpture, for its color shades and for its crenulated colour pattern. Despite a simplified decoration, the absence of spiral brown lines and coarser beads, A. granulata looks to be close to A. metula and to the sibling A. bulbosa for other morphologic and decoration features. These close similarities tend to prove that the changes in the protoconch shape and in the larval development do not seem to imply an important evolutionary distance, and that a close relationship seems to occur between the species of the A series and of the B series.

Despite the fact that only immature specimens were studied (original description, MNHN paratype and grey literature), the lecithotrophic species *A. tenuicolor* (Chino et Stahlschmidt, 2009) is associated to this series, as presenting also features closely matching *A. lachryma* for the shell sculpture and for the decoration pattern.

#### C series: the lecithotrophic diverging series

This series of species looks to be more eclectic for the shape and for the number of whorls of the lecithotrophic protoconchs, for the types of shell sculpures, for the decoration pattern and for the colour shades. All these rare to uncommon species were described recently from the Central Philippines by Chino & Stahlschmidt (2009; 2014), and further species belonging to this group remain clearly to describe (documentation by E. Guillot de Suduiraut and G. Poppe: pers. comm.). These species were all described in the genus Mitromorpha, probably due to their non-planktotrophic protoconch, but we propose to replace all of them in the genus Anarithma, on the ground of their variable proximity with the core-group A. lachryma and of the intergrading link made by the species classified in our B series.

We are just illustrating here the species *A. punctata* (Chino & Stahlschmidt, 2009) (Figs. 109, 110, 114), which is mostly diverging from the B series by the presence of a decoration of spiral series of honey dashes not found in the *A. metula* species group (A and B series), its shorter protoconch of 2 whorls and its inflated nucleus do not look as discriminating feature at this stage. *A. poppei* (Chino

et Stahlschmidt, 2009), *A. ambigua* (Chino et Stahlschmidt, 2009) and *A. pylei* (Chino et Stahlschmidt, 2014) have stout biconical angular shells with rather simplified colour decoration, but they are very disparate for their protoconch shape and for their sculpture. *A. candeopontis* (Chino et Stahlschmidt, 2009) with deep white upper whorls and spiral rows of well-defined white patches on uniform honey ground is suggesting rather distant kinship with *A. lachryma*.

Even if its placement in Anarithma seems to be the most appropriated solution, A. fusiformis (Chino et Stahlschmidt, 2009) looks as differing noticeably from the other Anarithma species studied from the Philippines by its slender oval outline, its finely crisscross shell sculpture and its creamy, light brown or mauve uniform color ground with a ring of blurred dark tobacco peripheral patches, and it mostly resembles some Mitromorpha species described from north-eastern Atlantic. The most resembling species are M. gofasi Mifsud, 2001 described from the Canary Islands, and to a lesser degree M. denizi Mifsud, 2001 described from Western Sahara. More detailed comparisons are however required, and such superficial resemblances may result from simple convergence.

By the dominant sculpture of strong spiral cords, the quite smooth peripheral zone and the simple whitish/yellowish band on a light brown ground running at the base of the spire whorls and on the shoulder of the last whorl, Mitromorpha tagaroae Chino et Stahlschmidt, 2009 is presenting some representative features of strictly Mitromorphalooking species ranging in the Philippines, such as M. philippinensis Mifsud, 2001, M. oliva Chino et Stahlschmidt, 2009 and M. unilineata Chino et Stahlschmidt, 2009 (close resemblance with the type species Mitromorpha carpenteri Glibert, 1954 from northeastern Pacific). But by its quite nodulose spire and by the axial ribs suggested on the upper part of its last whorl, M. tagaroae matches also most of the Anarithma species from the Philippines. In the present state of the documentation, M. tagaroae is kept in its original genus Mitromorpha, but like for A. fusiformis we do consider it as a phenetic intergrade between the genera Anarithma and Mitromorpha, possibly without phyletic signifi-

The high specific diversity and the noticeable disparity at work in this lecithotrophic series ac-

count for the important speciation ability allowed by the shortening of the embryonic/larval stage, together with the important rate of lineages survival within the "A. lachryma radiation".

## D series: the planktotrophic polychromatic group

Beyond important specific differences in shell outline, macrosculpture and decoration pattern, this series is constituting a quite homogeneous group of planktotrophic species sharing the same kind of tricolour chromatism, made of white, honey brown and pink or purple shades.

Anarithma purpurata (Chino et Stahlschmidt, 2009) (Figs. 115, 116) is characterized by a pyramidal protoconch of 2.6 to 3.0 whorls, a very oval outline, a very regular sculpture of packed subequal beads, and a mostly purple-pink colour ground with white zones for the upper teleoconch and for the periphery of the last whorl, with few, small and scattered honey-brown stains. A. purpurata was described from Mactan (60 m) and looks to be uncommon at upper and mid-recifal levels, and it is found as much far as Kwajalein in the Marshall Islands (picture in www.underwaterkwaj).

Anarithma alphonsiana (Hervier, 1900) (Figs. 117, 118), described from Lifou, is characterized by a slender pointing protoconch of 3.0 whorls, a narrow and slender biconical outline, a very narrow and straight aperture, strong axial ribs, fat spaced beads on the base of the spire and the upper part of the last whorls, and a decoration of alternated white and purple spiral bands, with spaced spiral series of brown spots alternating with white spots on the axial ribs. The species looks to be very rare in the Philippines, as our specimen from Balicacag 5 Figs. 117, 118) seems to be the single one ever reported from this region. We underline the fact that our specimen from the Philippines looks as very similar with the MNHN syntype (unfigured) from Lifou, except for the protoconch which is removed in the latter and thereby has not been compared.

Anarithma cf. salisburyi (Cernohorsky, 1978) (Figs. 121, 122) looks to be also very rare in the Philippines, as our specimen is also the single one ever reported from the region. It differs principally from the nominal species A. salisburyi described

from Hawaii (unfigured) by a slightly more inflated protoconch of 2.7 whorls, whereas A. salisburyi presents a narrower protoconch of about the same number of whorls. For the other features both forms are very similar, but due to the high distance occurring between Hawaii and the Philippines and to the slight difference in the shape of the protoconch, the conspecific status is reserved. Even if evident similitudes are occurring between A. cf. salisburyi and A. iozona (Hervier, 1900) described from Lifou (Figs. 119-120), especially about the tricolour chromatic pattern, A. iozona presents a more biconical outline, coarser and less numerous axial ribs, and much different columellar plications: in A. iozona occurs a simple notch in the convex columellar border, versus two well-defined columellar plaits in upper position on the oblique columellar border in A. cf. salisburyi. Due to the protoconch being removed in the MNHN syntype of A. iozona (ibid.), the comparison with the protoconch of A. cf. salisburyi was not made.

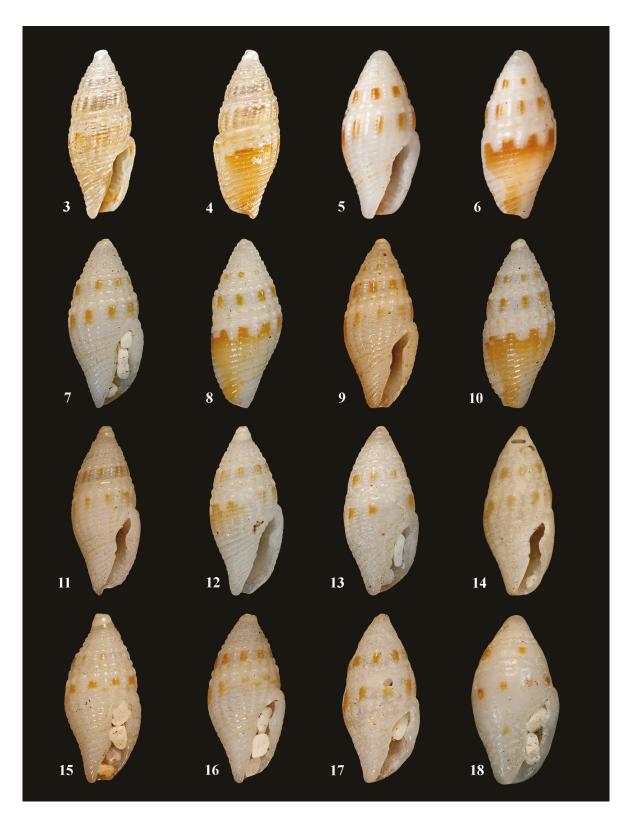
## E series: Anarithma thalaoides (Chino et Stahlschmidt, 2014)

Anarithma thalaoides (here unfigured), described from Lifou, is reported also from the Vanuatu and from the Philippines (Mactan, 60 m) by the authors. It presents very original features in the Anarithma series, with a narrow and slender subcylindrical shell outline, a strong pointing protoconch of about 2.50 whorls, a widely opened anal canal, thick goffered general sculpture and light honey flames on a creamy-white ground, the upper half part of the spire been vitreous and undecorated. Its subpyramidal protoconch with tapered tip is suggesting to be better planktotrophic. Anarithma thalaoides is very close to A. kilburni (Drivas et Jay, 1986), a species described from La Réunion and known also from the Mozambique (J. Horro, pers. comm.). Anarithma kilburni is mainly differing by a squat, bulbous and twisted protoconch of 2.25 whorls looking better as lecithotrophic, and by a full-white color instead of the honey flames on a creamy ground found in A. thalaoides. Both species were described in Mitromorpha but we consider that they clearly belong to the Anarithma field, even if representing a welldistinctive lineage. A similar species is known from Eastern Micronesia (Scott Johnson, pers. comm.).

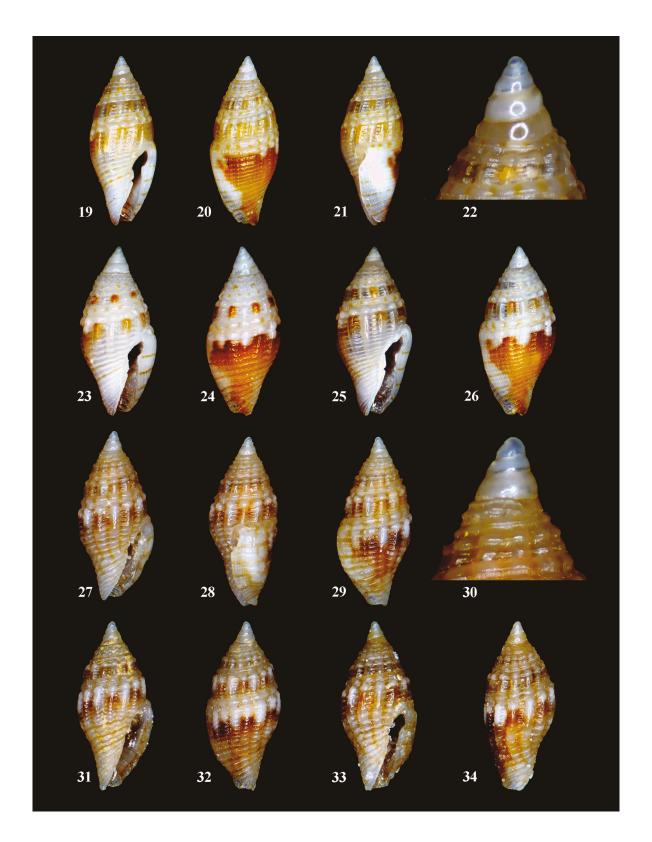
**F series:** Anarithma fischeri (Hervier, 1900) (Figs. 123–126)

Anarithma fischeri described from Lifou looks to be widespread in Western Pacific and it is quite common in the Philippines. Its pyramidal planktotrophic protoconch of 3.5 to 4.0 whorls is similar to the protoconch occurring in the "A. metula planktotrophic group" (A series) and its shell sculpture of rather flat and packed spiral cords deprived of axial ribs is matching the morphology found in the species A. fuscafenestrata revised above. As far as shell features are concerned, the only evident difference between A. fischeri and A. fuscafenestrata lies in the uniform black decoration with white tips occurring in A. fischeri. This black colour shade is very original in the Anarithma field, and it is strongly reminiscent of the dominant colour pattern generally found in the genus Lovellona Iredale 1917. Moreover, the peripheral white blotches as well as the crenulated figure running at the base of the shell are similar in A. fischeri and in some Lovellona species, such as the type species of the genus L. atramentosa (Reeve, 1849) (Figs. 127–130). We note also that A. fischeri is sharing two other shell features with the Lovellona species: rather flat and packed spiral cords and absence of axial ribs.

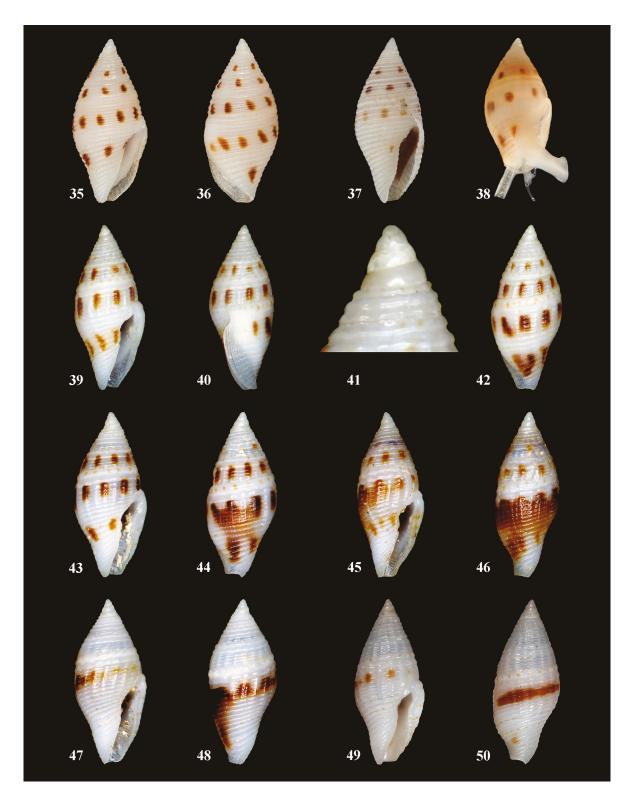
Anarithma and Lovellona are recognized as belonging to the same phyletic clade Mitromorphidae, such similarities cannot be considered as incidental and they cannot be addressed as simple case of convergence. We propose on the contrary to consider this situation as representative of a case of homology, whether it will prove to be plesiomorphic or apomorphic. Lovellona atramentrosa has a very short and small protoconch of 2.0 whorls with tiny nucleus, and lecithotrophic lineages derivate basically from planktotrophic species, the most likely hypothesis here is that the Lovellona group could descend from an ancestor not much different from A. fischeri. The other hypothesis, however less simple, would be the occasional resurgence of a common ancestral chromatic character within the Anarithma radiation. Further inquiries will allow to check what kind of disbranching occurred in the present case, the evolutionary distance between Lovellona and Anarithma being possibly not much different than the distance between Mitromorpha and Anarithma.



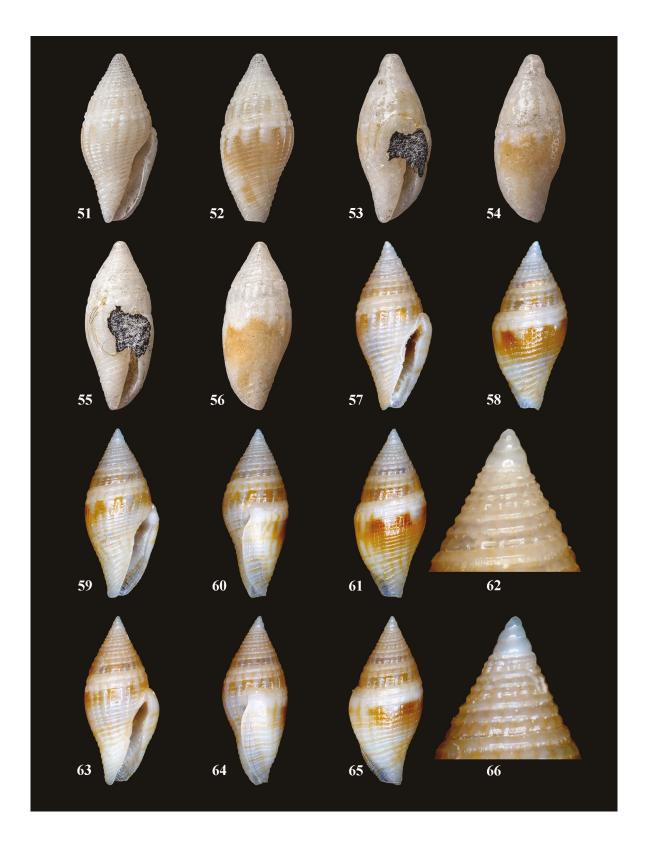
Figures 3–4. *Clavatula metula*, holotype NHM, no locality, L=4.4 mm. Figures 5, 6. *Columbella (Seminella) stepheni*, syntype MM, Lifu, L=4.1 mm. Figures 7–18. *Columbella (Seminella) stepheni*, syntypes A-J NMW, Lifu, L=4.2 mm, 4.4 mm, 4.6 mm, 4.4 mm, 4.3 mm, 4.3 mm, 4.4 mm, 4.2 mm and 3.8 mm.



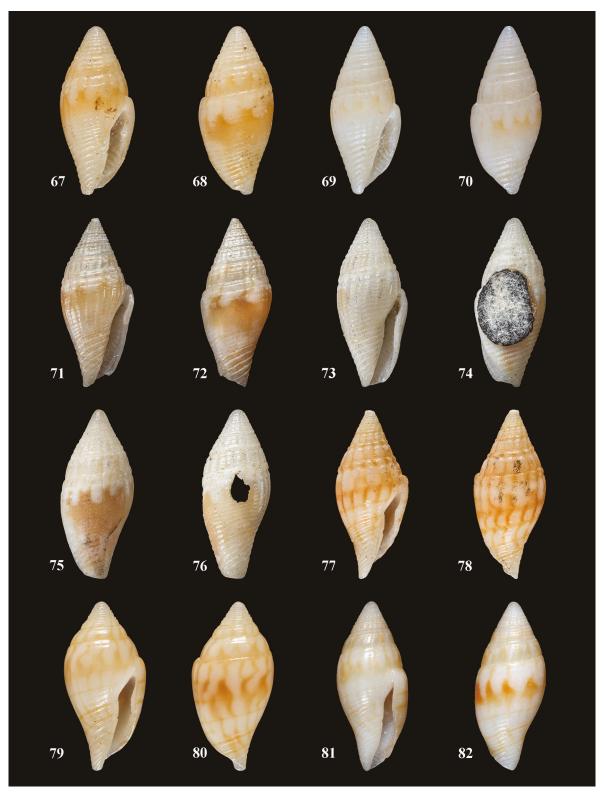
Figures 19–26. *Anarithma metula*, Balicasag, 50-150 m, L=3.8 mm, 3.3 mm & 3.8 mm, CFB. Figures 27-30. *A. bulbosa* n. sp., holotype MNHN, Balicasag, 50-150 m, L=3.9 mm. Figures 31-34. id., paratypes CFB 1 and 3, L=3.9 mm and 3.5 mm.



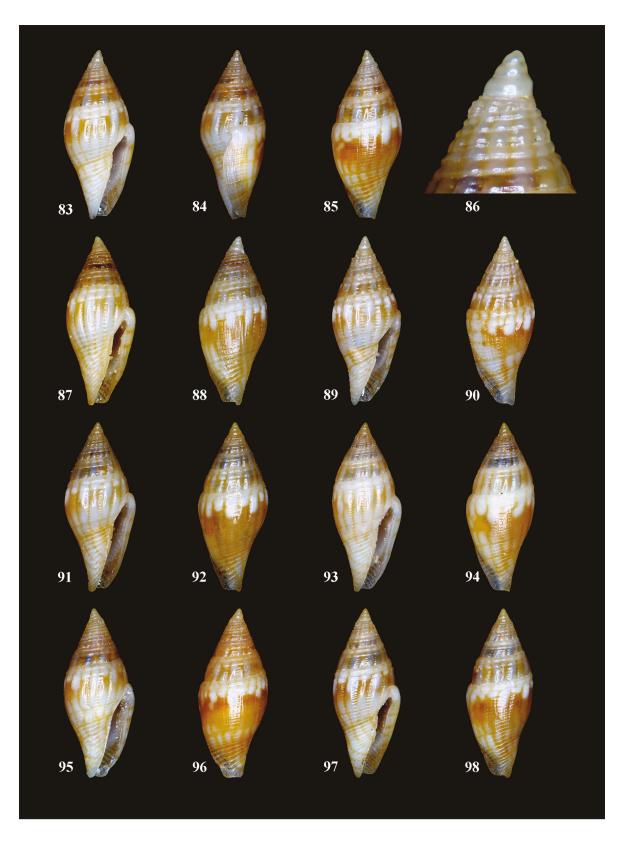
Figures 35–36. *Mitromorpha fuscafenestrata*, holotype MNHN, Espiritu Santo, Vanuatu, 45–50 m, 5.1 mm. Figure 37. *A. fuscafenestrata*, MNHN Collection Papua New Guinea, Tab Is., 31 m, no length size. Figure 38. *A. fuscafenestrata* as « M. cf. *metula* Hinds », live animal, northeast Moorea, French Polynesia, no length size, UCB. Figures 39–42. *Anarithma melvilli* n. sp., holotype MNHN, Balicasag, 50–150 m, L = 5.0 mm. Figures 43–48. id., paratypes 3, 4 & 2 CFB, L = 4.5 mm, 4.9 mm & 4.9 mm. Figures 49–50. *Mitromorpha nigricingulata* Chino & Stahlschmidt, paratype 1 MNHN, Cebu, Mactan, 60 m, L = 4.8 mm.



Figures 51–52. *Mitra lachryma*, lectotype NHM, no locality, L = 7.3 mm. Figures 53–56. idem, paralectotypes 2 and 3 NHM, L = 7.3 mm & 6.9 mm. Figures 57–66. *Anarithma lachryma*, Balicasag, 50–150 m, L = 4.6 mm, 5.1 mm and 5.0 mm, CFB.



Figures 67–70. *Colombella pamila*, syntypes 1 and 2, MNHN, "Mazatlan", L = 6.7 mm & 6.7 mm. Figures 71–72. *Cythara garretti*, lectotype NHM, Sandwich Is., L = 6.8 mm. Figures 73–76. *Cythrara garretti*, paralectotypes A–C, NHM, L = 5.6 mm, 6.0 mm & 5.3 mm. Figures 77–78. *Columbella sublachryma* Hervier, syntype 1, MNHN, Lifou, L = 7.0 mm. Figures 79, 80. *Columbella pinguis* Hervier, syntype, MNHN, Lifou. Figures 81, 82. *Mitromorpha flammulata*, paratype 1 MNHN, Kagoshima, Japan, L = 7.8 mm.



Figures 83–98. *Anarithma pamila*, Balicasag, 50-150 m, L=6.0 mm, 4.9 mm, 5.2 mm, 5.7 mm, 5.9 mm, 6.6 mm and 5.9 mm, CFB.

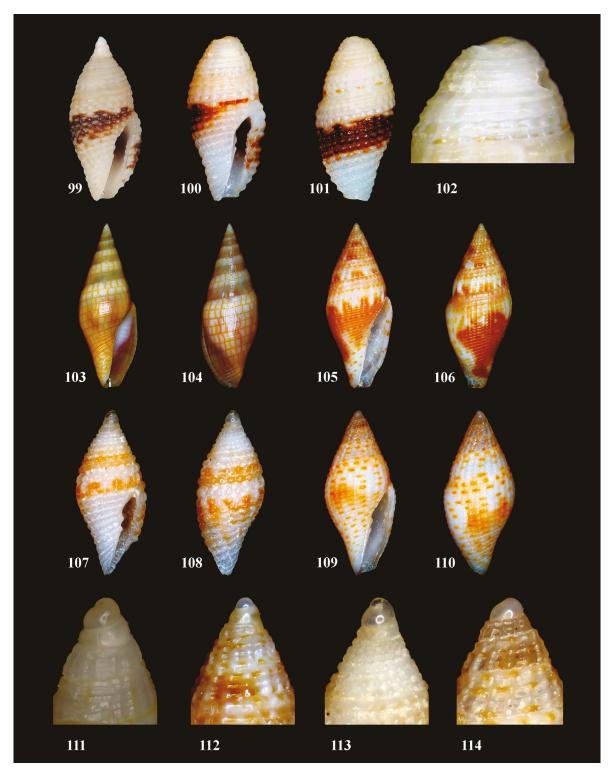
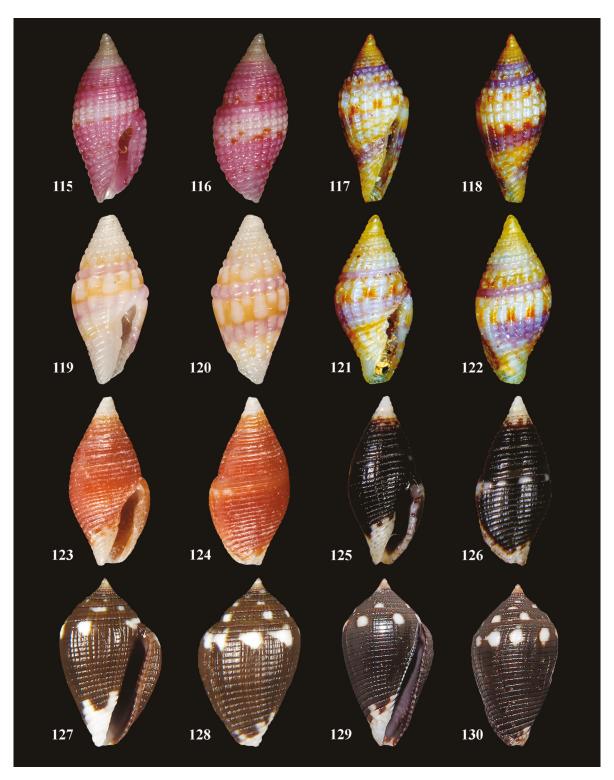


Figure 99. Anarithma nigricingulata, Philippines, L = 4.7 mm, GPC, from www.conchology.be. Figures 100-102. A. nigricingulata, Balicasag, 50-150 m, L = 4.0 mm, CFB. Figures 103-104. A. dorcas, Balicasag, 50-150 m, L = 23.5 mm, CFB. Figures 105-106. A. rubrimaculata, Balicasag, 50-150 m, L = 9.2 mm. Figures 107-108. A. granulata, Balicasag, 50-150 m, L = 3.7 mm, CFB. Figures 109-110. A. punctata, Balicasag, 50-150 m, L = 7.4 mm, CFB. Figure 111. Protoconch of A. dorcas, spm from Figs 103-104. Figure 112. Protoconch of A. rubrimaculata, spm from Figs. 105-106. Figure 113. Protoconch of A. granulata, spm from Figs. 109-110.



Figures 115–116. *Mitromorpha purpurata*, paratype MNHN, Mactan, Cebu, 60 m, L = 4.1 mm. Figures 117–118. *Anarithma alphonsiana*, Balicasag, 50–150 m, L = 5.5 mm, CFB. Figures 119–120. *Columbella iozona*, syntype MNHN, Lifou, L = 5.0 mm. Figures 121–122. *Anarithma* cf. *salisburyi* (Cernohorsky), Balicasag, 50–150 m, L = 3.5 mm, CFB. Figures 123–124. *Columbella fischeri*, syntype MNHN, Lifou, L = 5.0 mm. Figures 125–126. *Anarithma fischeri*, Philippines, no length size, GPC, from www.conchology.be. Figures 127–128. *Lovellona atramentosa*, Philippines, no length size, GPC, from www.conchology.be. Figures 129–130. *L. atramentosa*, Kwajalein, Marshall Is., no length size, from www.underwaterkwaj.

#### **DISCUSSION**

At the geographic scale of the Central Philippines, the phenetic distribution examined above leads to propose the A. lachryma species group as being composed of the A series and of the B series, that means a set of both planktotrophic and lecithotrophic species. On the simple ground of closer phenetic proximity with A. lachryma for the general shell morphology and the decoration pattern of the teleoconch, we accept in this group the planktotrophic A. lachryma, A. metula, A. bulbosa n. sp., A. fuscafenestrata, A. melvilli n. sp., A. pamila and A. nigricingulata, as well as the lecithotrophic A. dorcas, A. rubrimaculata, A. granulata and A. tenuicolor. These different species seem to be closer each together than to the other Anarithma species documented from the Philippines. Due to important morphological or chromatic similarities, some paired species placed in this A. lachryma species group seem to be more closely derived from each other, such as A. lachryma and A. pamila, A. lachryma and A. rubrimaculata, A. pamila and A. dorcas, A. metula and A. bulbosa, or A. melvilli and A. fuscafenestrata. However, nothing allows neither to speculate about any disbranching order in this supposed species group nor to estimate relative evolutionary distances between them. In particular, nothing allows to consider that all the multispiral species are closer together than to such or such lecithotrophic species proposed in this group.

The proposed "lecithotrophic diverging series" (or C series) is apparently composed of a more eclectic assemblage, as lecithotrophic species presenting some affinities with species placed in the *A. lacryma* group, but with some of their features suggesting a higher phenetic drift, which may reflect greater evolutionary distances than what is suggested within the *A. lachryma* group sensu stricto.

Due to the apparent high heritability of the chromatic characters in the *Anarithma* species, and to the originality of their tricolour chromatism with pink/purple shades, the proposed "planktotrophic polychromatic group" (or D series) seems to be quite distant from the *A. lachryma* species group, even if the shell morphologies (and the multispiral protoconchs) look as pretty similar to the most common features occurring in the *A. lachryma* species group. We observe also that this polychromatic species group presents internally quite homoge-

neous morphologic features, which suggests the status of a monophyletic brother group disbranched from the *A. lachryma* species group.

From its side, *Anarithma thalaoides* clearly belongs to a well-autonomous species group known from southwestern Indian Ocean (Mozambique and Mascarene Islands) to Western Pacific (from Eastern Micronesia to Lifou), and it looks also like a monophyletic lineage, quite distant of the *A. lachryma* species group.

Anarithma fischeri presents a special status in the Anarithma complex, looking simultaneously as very close to A. fuscafenestrata and to the A. lachryma species group for morphological features, and as very close to the Lovellona genus for its decoration pattern (mostly black with white tips and crenulated fringe). As such, A. fischeri suggests to be an "intergrading form" between the genera Anarithma and Lovellona, which would deserve to be deeply documented through appropriated investigations, specially comparing the radular features, the internal anatomy and the biochemistry of A. fischeri and of L. atramentosa for instance.

Naturally, further documentation about radular pattern, animal chromatism, internal anatomy or even biochemistry of the Anarithma species might lead to state on quite different ranks of proximity between the considered species, and to change more or less the scope or even the pertinence of the A. lachryma species group within the genus Anarithma. In the same order, further investigation might lead to modify what are the respective boundaries of the mitromorphid genera Anarithma, Mitromorpha and even Lovellona, as suggested by some proxies reported above. However in the present state, it seems that the "hierarchy characters" commonly used for the phenetic study of the mitromorphids is somewhat controversial, in the sense that the larval development and the protoconch shape seem to be very "plastic" in this group, as such not attesting evident phyletic distances, whereas the decoration pattern of the teleoconch seems to be more "heritable" and to attest with more evidence of relative phyletic distances.

From the documentation at hand, we infer that in the *Anarithma* group sensu lato, the change from planktotrophic development to lecithotrophic development is quite easy and frequent, and poorly evidencing evolutionary or phyletic distances. As far as turrid groups are concerned, two recent works

did state similar situations in raphitomid groups through sibling pairs of species mostly differing by their type of protoconch: Fedosov & Puillandre (2012 for the *Kermia-Pseudodaphnella* complex, and Giannuzzi-Savelli et al. (2018) for the Mediterranean *Raphitoma*.

Our own observations about the Mitromorphidae of the Philippines are also suggesting that the distinction between "lecithotrophic species" characterized by protoconch of less than 2 or 2.5 whorls and "planktotrophic species" characterized by protoconch of more than 2 or 2.5 whorls looks to be illusory. Not only all the intergrades in terms of protoconch whorls proved to occur, but other major factors must be taken in account, such as the relative size of the nucleus, as a bulbous nucleus (for instance in the case of A. bulbosa, A. dorcas, A. granulata or A. cf. salisbury) is suggesting important reserves of nutriment for the embryo and implies feeding autonomy for benthic as well as for pelagic early wandering. These occurrences are seriously corroborating the McEdward's prediction (1997) about "a continuum of larval strategies".

#### **CONCLUSIONS**

- 1°) *Mitra lachryma* Reeve, 1845 is restored as type species of the genus *Anarithma* Iredale, 1916.
- 2°) Two undescribed *Anarithma* species are discovered in the course of the study, and described respectively as *A. bulbosa* n. sp. and *A. melvilli* n. sp.
- 3°) On the ground of important affinities suggested by the morphology and chromatism of the teleoconch, the protoconch morphologies observed in the *Anarithma* complex look as more plastic from an evolutionary point of view than the colour pattern for instance, which contradicts the "characters hierarchy" usually applied.
- 4°) Both planktotrophic and lecithotrophic species prove to occur in the *A. lachryma* species group, about all the types of intergrades of morphology and of infered larval development being in fact represented, which supports the McEdward's hypothesis (1997) about "a continuum of larval strategies", here verified at the scale of the *Anarithma* complex. Our samplings are however submitted to a serious bias in favor of the settlement of freedrifting larvae, and the species with direct develop-

ment are probably under-repesented in our study.

- 5°) Eleven species ranging in the Central Philippines are provisionally recognized in the *A. lachryma* species group, namely: the planktotrophic *A. lachryma*, *A. metula*, *A. bulbosa* n. sp., *A. fuscafenestrata*, *A. melvilli* n. sp., *A. pamila* and *A. nigricingulata*, as well as the lecithotrophic *A. dorcas*, *A. rubrimaculata*, *A. granulata* and *A. tenuicolor*.
- 6°) Besides this A. lachryma species group, four other Anarithma assemblages are provisionally recognized at the scale of Central Philippines: a "polychromatic brother group" of planktotrophic species morphologically very close to the core-species of the A. lachryma species group, but presenting distinctive original tricolour patterns; a rather eclectic group composed of lecithotrophic species looking as more distant from the species accepted in the A. lachryma species group; the species A. thalaoides belonging to the uncommon but widespread species group A. kilburni; and the species A. fischeri looking to be morphologically very close to species belonging to the A. lachryma species group but presenting a shell chromatism strongly reminiscent of that found in the mitromorphid genus Lovellona.
- 7°) In the course of the study, three species are provisionally considered to suggest an "intergrading » or "transitional » status between genera: Mitromorpha fusiformis is replaced in Anarithma but considered to show certain phenetic similarities with a few northeastern Atlantic Mitromorpha species; Mitromorpha tagaroae is provisionally conserved in the genus *Mitromorpha* for its strong similarities with M. philippinensis Mifsud and some other species from the Philippines matching the Mitromorpha core-concept (close similarities with the type species Mitromorpha carpenteri, described from "West Coast of North America"), but some of its morphological features look as better compatible with Anarithma; the placement of A. fischeri Hervier in Anarithma is accepted without reserve, but its very distinctive chromatic pattern pleads in favor of special investigation about its possible evolutionary links with the genus *Lovellona* Iredale, 1917.
- 8°) From these thoughts, a more complete delimitation of the genus *Anarithma* Iredale, 1916 and of its internal organization seems to require a documented revision of the brother genera *Mitromorpha* Carpenter, 1865 (type species: *Mitromorpha carpenteri*, replacement name of *Daphnella filosa*

for homonymy with *Columbella filosa* Dujardin, 1837; northeastern Pacific) and *Lovellona* Iredale, 1917 (type species: *Conus atramentosus* Reeve, 1849; Indo-West Pacific). Despite few unevident intergrading forms, the separation between the genera *Mitromorpha* and *Anarithma* seems to be quite easy at the scale of the Indo-Pacific Province, but it seems to be less evident in the Atlantic waters and in any case the phyletic limits of the *Mitromorpha* radiation deserves further inquiries.

#### ACKNOWLEDGEMENTS

I am indebted to the late Emmanuel Guillot de Suduiraut for giving lumun-lumun material in the early 2000's, which allowed to sort out representative series of mitromorphid species from Balicasag Island. I am also indebted to Sandro Gori (Livorno, Italy) for giving the opportunity to consult further mitromorphids of Balicasag from his lumun-lumun samplings. For the access to the type material and constant help despite the difficult sanitary conditions, I must warmly thank Andreia Salvador (NHMUK) and Harriet Wood (NMW). A great help came as ever from Walter Renda (Amantea, Italy), who skillfully performed macro-photos of the material under study, arranged the pictures and mounted the plates. Thanks also to Juan Horro (Vigo, Spain) and to Dan Polhemus (Hawaii) for useful discussions about the Indo-Pacific mitromorphid radiations. For the access to original pictures, I must acknowledge Guido and Philippe Poppe (Cebu, Philippines), Gustav Paulay (UFL) and Scott Johnson (Santa Barbara, USA). Photographic credits: MNHN material: Maria Hennion and Manuel Caballer (Recolnat ANR-11-INBS-0004); NMW material: Harriet Wood (Collections Curator); NHM material: Kevin Webb (Photographic Unit).

#### REFERENCES

- Bouchet P., Kantor Y., Sysoev A. & Puillandre N., 2011. A new operational classification of the Conoidea (Gastropoda). Journal of Molluscan Studies, 77: 273–308. https://doi.org/10.1093/mollus/eyr017
- Bouchet P. & Warén A., 1979. Planktotrophic larval development in deep-water gastropods. Sarsia, 64: 37–40.

- Cernohorsky W.O., 1978. New species of Mitridae, Costellariidae and Turridae from Hawaiian Islands with notes on *Mitra sphoni* in the Galapagos Islands. The Nautilus, 92: 61–67.
- Cernohorshy W.O., 1988. Taxonomic notes on the Mitromorpha group of the Family Turridae (Mollusca: Gastropoda: Borsoniinae). Records of the Auckland Institute Museum, 25: 63–73.
- Chino M. & Stahlschmidt P., 2009. New Turrid Species of the *Mitromorpha*-complex (Gastropoda: Conidae: Clathurellinae) from the Philippines and Japan. Visaya, 2: 63–82.
- Chino M. & Stahlschmidt P., 2014. Descriptions of four new shallow water *Mitromorpha* species from the Western Pacific (Gastropoda: Mitromorphidae). Visaya, 4: 21–27.
- Duclos P.L., 1848. *Columbella*. In: J.C. Chenu, 1846–50: Illustrations conchyliologiques ou description et figures de toutes les coquilles connues vivantes et fossiles. Classées suivant le système de Lamarck modifié d'après les progrès de la science et comprenant les genres nouveaux et les espèces récemment découvertes. Paris. Pls 19–25.
- Fedosov A.E. & Puillandre N., 2012. Phylogeny and taxonomy of the *Kermia-Pseudodaphnella* (Mollusca: Gastropoda: Raphitomidae) genus complex: a remarkable radiation via diversification of larval development. Systematics and Biodiversity, 10: 447–477. http://dx.doi.org/10.1080/14772000.2012.753137
- Giannuzzi-Savelli R., Pusateri F. & Bartolini S., 2018. A revision of the Mediterranean Raphitomidae (Gastropoda: Conoidea) 5: loss of planktotrophy and pairs of species, with the description of four new species. Suppl. to Bollettino Malacologico, 54 (suppl. 11): 1–77.
- Hervier R.P.J., 1900. Le genre *Columbella* dans l'Archipel de la Nouvelle-Calédonie. *Journal de* Conchyliologie, 47: 305–391.
- Hinds R.B., 1843. On new species of *Pleurotoma*, *Clavatula*, and *Mangelia*. Proceedings of the Zoological Society of London, 11: 36–46.
- Horro J., Gori S., Rosado J. & Rolán E., 2021. Little Conoidean Shells From Dhofar, Oman, With Description of 35 New Species. Visaya (Supplement 16): 5–87, pl. 1–74.
- Iredale T., 1916. On some new and old molluscan generic names. Proceedings of the Malacological Society of London, 12: 27–37.
- Kantor Y., Puillandre N., Olivera B. & Bouchet P., 2008. Morphological proxies for taxonomic decision in turrids (Mollusca, Neogastropoda): a test of the value of shell and radula characters using molecular data. Zoological Science, BioOne (Zoological Society of Japan), 25: 1156–1170.

https://doi.org/10.2108/zsj.25.1156

Kilburn R.N., 1986. Turridae (Mollusca: Gastropoda) of southern Africa and Mozambique. Part 3. Subfamily Borsoniinae. Annals of Natal Museum, 27: 633–720.

- Lieberman B.S. & Vrba E.S., 1995. Hierarchy Theory, Selection and Sorting. A phylogenetic perspective. Bioscience, 45: 394–399.
- McEdward L.R., 1997. Reproductive strategies of marine benthic invertebrates revisited: facultative feeding by planktotrophic larvae. The American Naturalist, 150: 48–72.
- Melvill J.C. & Standen R., 1896. Notes on a collection of shells from Lifu and Uvea, Loyalty Islands, formed by the Rev. James and Mrs Hadfield, with list of species. Part II. Journal of Conchology, 8: 273–315, pl. 9–11.
- Melvill J.C. & Standen R., 1897. Notes on a collection of shells from Lifu and Uvea, Loyalty Islands, formed by the Rev. James and Mrs Hadfield, with list of species. Part III. Journal of Conchology, 8: 396–421.
- Mifsud C., 2001. The genus *Mitromorpha* Carpenter, 1865 (Neogastropoda: Turridae) and its sub-genera

- with notes on the European Species. Pp. 1–32. Privately published, C. Mifsud, Malta.
- Pease W.H., 1860. Descriptions of New Species of Mollusca from the Sandwich Islands. Part II. Proceedings of the Zoological Society of London, 28: 141–148.
- Polhemus D.A., 2020. New Records and Update Distributional Data for Marine Micromollusks (Mollusca: Gastropoda) from the Mesophotic Depth Zone of the Hawaiian Islands. Bishop Museum Occasional Papers, 133: 1–29.
- Reeve L.A., 1845. Monograph of the genus *Mitra*. In: Conchologia Iconica, vol. 2: pl. 1–39. L. Reeve & Co., London.
- Reeve L.A., 1849. Monograph of the genus *Conus*. Supplementary plates 1–9 and unpagined text. In: Conchologia Iconica [supplement to vol. 1]. L. Reeve & Co., London.
- Thorson G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews, 25: 1–27.