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Revision of the wavy ornated cystiscids (Volutoidea Cystiscidae) from the Dhofar (southern Oman) and description of new taxa

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ABSTRACT

The cystiscids species (Volutoidea Cystiscidae) from the Dhofar (southern Oman) with wavy ornated shells are revised on the ground of semi-intensive samplings, mainly operated off Mirbat (Central Dhofar) and more incidentally in other places off Central and Western Dhofar. This species complex, alternatively placed by authors in the genus *Persicula* Schumacher, 1817 or in the genus *Gibberula* Swainson, 1840, is considered to belong to a well-distinctive disbranching among the Cystiscidae, and its placement in a new genus *Sagittalia* n. gen. is proposed, with *Marginella sagittata* Hinds, 1844 as type species. Seven cystiscid species from the Dhofar are proposed in this new genus, two of them previously described as *Persicula masirana* Roth et Petit, 1972, and *Gibberula peterbonuttii* Cossignani et Lorenz, 2018, four of them being described as new: *Sagittalia anapaulae* n. sp. from Mirbat and the Saadah (Central Dhofar), *S. willeminae* n. sp. from Salalah (Western Dhofar), *S. eloiseae* n. sp. from Western and Central Dhofar, *S. vickydobsonae* Boyer et Childs n. sp. from Mirbat and the Saadah (Central Dhofar), and an undescribed species of *Sagittalia* sp. A only known by one specimen collected at 24–28 m depth off Mirbat are discussed. Two main phenetic clusters are recognized in this fauna: the cluster *S. anapaulae*/*S. willeminae* and the cluster *S. eloiseae*/*S. vickydobsonae*/*S. peterbonuttii*, whereas the relationship of *S. masirana* and of *Sagittalia* sp. remains unstated, despite their closely matching animal chromatism. Comparison is proposed with other wavy ornated species from the Arabian Region and from other regions of the Indo-Pacific and Atlantic Provinces, with the analogous fossil fauna documented from the French mid-Eocene and with Recent brother-groups of zig zag ornated cystiscids with reduced number of waves.

KEY WORDS Cystiscidae, Persiculinae, *Persicula*, *Gibberula*, Arabian Region, sibling species, Tethyan relation.

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INTRODUCTION

In his study about the cystiscids from upper reef levels of New Caledonia, Boyer (2003) revised one species and described two new species as belonging to a vast complex of "zig zag ornated *Gibberula* species", and suggested a close relationship with the Australian *G. pulchella* (Kiener, 1834) for at least one of the new species. Boyer (2004) initiated a more methodical study of the *Gibberula*-looking species with oval shell outline and undulated shell decoration or derived decoration patterns, hypothesizing the occurrence of three "major phenetic groups" in this worldwide ranging species complex, corresponding to the three most anciently described species: *Voluta catenata* Montagu, 1803, erroneously described from Cornwall (Great Britain) but commonly found in most of the northern and eastern Caribbean Sea (Figs. 49, 50: holotype NHMUK); *Marginella frumentum* Sowerby, 1832 controver-

sially described from Ecuador but documented from southeastern Caribbean Sea [lectotype pictured in Boyer (2004: Figs. 4, 5)]; and *M. pulchella* Kiener, 1834 [two syntypes pictured in Boyer (2003: Figs. 1–4)], described from Sydney (NSW, Australia) but never recognized since then, among a great number of similar Australian forms. The species belonging to this complex were alternatively placed in the genus *Persicula* Schumacher 1817 or in the genus *Gibberula* Swainson, 1840 by subsequent authors. Boyer (2003 & 2004) did choose to place them in *Gibberula*, without providing any explanation about this point.

While waiting for further observations about the *G. catenata* phenetic group characterized by dominant spiral decoration and considered as "specially complicated", Boyer did focus his 2004 study on the strictly "zig zag ornated" cystiscid from Western Atlantic, proposed to belong either to the phenetic group of *G. frumentum* or to that of *G. pulchella*. In this frame, Boyer recognized three species in the *G. frumentum* species group, revising the nominal *G. frumentum* (Sowerby, 1832) with documented representants in the southeastern Caribbean Sea but plausible type locality in Ecuador (Boyer, 2004), revising also *G. sagittata* (Hinds, 1844), described from Brazil and commonly collected off the central coats of this country, and describing a new species from Central Brazil proposed in the same species group as *G. moscatellii* Boyer, 2004, sibling species of *G. sagittata*. Boyer did recognize only one Western Atlantic species in the group *G. pulchella* Kiener, as *G. fluctuata* (C.B. Adams, 1850), described from Jamaica and documented from most of the Caribbean Sea (live animal in Fig. 45).

In his Discussion section, Boyer noted the occurrence of other "phenetic groups" beside the complex of "undulated *Gibberula*", reporting especially the case of *G. lucia* Jousseaume, 1877 and of *G. almadiensis* Pin et Boyer, 1995, both described from Northwestern Africa, characterized by "very different decoration patterns" and said to be closer to the subpyriform banded species *G. oryza* Lamarck, 1822 ranging in the same region, as far as shell features are concerned. Two undescribed species from Brazil were said to belong also to a "different phenetic group", and the affinities of *G. thomensis* (Tomlin, 1919), described from São Tomé, Central West Africa, were considered as uncertain. From these considerations, Boyer did infer that the complex of cystiscid species with undulated decoration was possibly not monophyletic, noting that similar type of wavy shell decoration is found in other groups such as the Olividae and that the undulated shell decoration might have appeared (or have been retained) several times and may characterize several independent evolutionary twigs.

In the last twenty years, no further study was conducted on this phenetic complex of wavy ornated cystiscids and on its taxonomy. Furthermore, despite the high number of morphospecies occurring in this complex in the Western Atlantic field and over all in the Indo-West Pacific waters, and despite the increasing number of works dedicated to the marine micro-gastropods, a very restricted number of wavy ornated species were described until now. Only five new wavy ornated cystiscids or derived forms were described during the two last decades, as *Gibberula agricola* Faber, 2005 from Margarita Island, Venezuela (with tiny punctuate squared shell matching better the morphology found in the *G. philippii* species group), *G. bagne* (Faber, 2006) from French Guiana (with swollen shell, rostrate top and sharply angled zig zag decoration), *G. peterbonuttii* Cossignani & Lorenz, 2018 from the Dhofar Province, Southern Oman (with slender oval shell, rostrate top and conspicuous spiral lines over blurred and disorganized axial flames), *G. moretzsohni* (Coltro, 2020) from Central Brazil (with oval shell, bulged top and scale-shaped undulate decoration) and *G. domenechi* (Ortea, 2020) from Caribbean Costa Rica, the last one being possibly conspecific with *G. fluctuata* (C.B. Adams, 1850) described from Jamaica (personal data).

Obviously, to understand the content and the taxonomic place of this cystiscid complex characterized by wavy ornated shells, a more in-depth study of the phenetic disparity at work, of the prevailing diversity range, and of possible affinities with other *Gibberula*-looking groups, is required.

The present article is dedicated to a phenetic and taxonomic investigation about the wavy ornated cystiscids and derived forms, through the case study of the assemblage of seven species documented from the upper reef levels (0–35 m) of the Dhofar Province (Southern Oman) during the recent years, which looks to be the most diversified assemblage ever observed until now for this group.

MATERIAL AND METHODS

Material

The material under study is mostly composed of live specimens and empty shells obtained from dive samplings (rocks brushing) at 12–35 m depth off Mirbat (Central Dhofar) by Sandro Gori (Livorno, Italy) during the years 2014–2016, in association with Jose Rosado (Maputo, Mozambique) in 2015–2016. Additional samplings were made from beached shells by the present author in November 2019, and again in November 2023 in association with Jose and Ana Paula Rosado for snorkeling groups at 2–6 m off Mirbat and the Saadah coves (Central Dhofar) and off the Fazayah beaches (Western Dhofar). No dredging operations were tempted on soft bottoms. Complementary beached material from Salalah (Western Dhofar) was loaned for study by Leo and Wil van Gemert (Zeist, the Netherlands), and beached material from Mirbat and the Saadah coves (Central Dhofar) was loaned by Andrew Childs and Vicky Dobson (Paphos, Cyprus). Most of the live collected material was washed and dried immediately after the sampling parties, except for some specimens sketched by the author or photographed in-vitro by Jose Rosado, before individual conservation in ethanol.

Regional marine biogeography

The distribution observed in some groups of marine gastropods (principally the marginelliforms, the columbellids and the genus *Ancilla*) allows to propose three roughly defined biogeographical subdivisions for the coasts of the Administrative Province of Dhofar:

- The Western coast, from the Yemen border to Salalah, characterized by steep rocky shores and great depths, strong upwelling currents and heavy seasonal monsoon influence. Due to the west-east orientation of this coastal Section, the fauna from Western Dhofar is probably extending for the most to the coasts of the Mahrah Province in Eastern Yemen.

- The Central coast, from Mirbat to Hasik, presenting about the same climatic and oceanographic conditions as the Western coast, but separated from it by a low sandy coast running from Raysut to Mirbat, along about 80 km. This low coast seems to constitute a barrier for the distribution of some species, even if similar environments seem to occur west of Raysut and east of Mirbat. For instance, one of our wavy ornated *Gibberula* species was collected as empty shells on the Salalah beach but it was not found off Mirbat, despite semi-intensive samplings. Same for the cysticid species *Extra extra* Jousseaume, 1894, described from Perim (Strait of Bab El Mandeb, Western Yemen) and found in shell grit of the Salalah beach (personal data based on L. & W. van Gemert's sampling), but not found in the semi-intensive brushed samplings worked from 2 m to 35 m off Mirbat.

- The Eastern coast, from Hasik to Sharbithat, constitutes in fact a transitional zone, where the Dhofar coastal mountains are joining the Eastern continental Plateau of Oman (running from Hasik up to the surrounds of Ras Al-Hadd at the northeast tip of Oman, with Masirah Island located at its northern third part). The Archipelago Jazirat Al Hallaniyat (former Khuriya Muriya Islands), located on the southern border of the Plateau, belongs to this Eastern Section. Despite the great latitudinal expanse of the Eastern continental Plateau of Oman, it seems that its marine gastropods fauna is quite homogeneous, and mostly differing from the fauna of the Central Dhofar. Naturally, some species are overlapping these two coastal Sections, at least partially. For instance, *Volvarina arabica* Boyer, 2015, described from Masirah Island and distributed from southern Persian Gulf to the Eastern continental Plateau of Oman, is reaching the Saadah coves, midway between Mirbat and Hasik, but it does not reach Mirbat and its surrounds (personal data).

Consulted documentation

In the frame of this review, extensive research of references about the wavy ornated cystiscids was paid in the scientific literature and in the grey literature. Out of his personal archives, the author consulted the abundant documentation entrusted by Tony McCleery (Guernsey, United Kingdom) about his samplings and observations of live cystiscids in the Caribbean Sea. Some additional documentation about the Caribbean fauna was communicated by Andrew Wakefield (Buckhurst Hill, Sussex, Great Britain). The collection of beached marginelliform gastropods sampled around the Arabian Region by the Dekker-Winkel team (ZMA, the Netherlands)

was also consulted. Important cystiscid material from Sri Lanka and from the Maldives was communicated by Sandro Gori, and important photographic documentation (shells and live animals) about the cystiscid fauna from Sri Lanka and from Mozambique was communicated by Jose Rosado. Documentation and material about the cystiscid populations of the Pacific Archipelagos was obtained from Scott and Jeanette Johnson (Goleta, California) and from Bret Raines (Wichita Falls, Texas).

As far as the general supra-specific classification of the cystiscid fauna is concerned, our hypothesis about the monophyletic status of the wavy ornated cystiscids was tested with reference to previous works of Coovert & Coovert (1995), of Boyer (2019: September 18th, ZooBank datum) and of Fedosov et al. (2019: September 20th, ZooBank datum). The revision proposed by Coovert & Coovert (1995) as well as that proposed by Boyer (2019) are based on integrative analysis of morphologic and anatomic data, whereas the revision proposed by Fedosov et ali is based on analysis of molecular data.

Using the **Persicula** *and* **Gibberula** *concepts*

The respective identities of the genera *Persicula* Schumacher, 1817 and *Gibberula* Swainson, 1840 were never strictly defined and remain unclear, despite the unconvincing binary discrimination tempted by Coovert & Coovert (1995) and based on supposed differences in spire shape (immersed versus non-immersed), external varix (distinct or negligible), shell decoration (complex "patterned" decoration versus monochromatic shaded or simple spiral bands) and siphon length (long or short). In fact, all kinds of intergrades are observed at the specific level (personal data) and such variations, combined or not, look to characterize a series of species groups better than two evident genera. The unity of the *Persicula-Gibberula* series is basically found in suboval, rounded or subpyriform smooth shells with long aperture, very short, obsolete or immersed spire, type 4 animal sensu Coovert (1987) with slit head, long frontal lobes, short to long tentacles, short to long siphon, stretched foot deprived of mentum pleat, Type 3 radula sensu Coovert (1989) with modified rachiglossan radula deprived of lateral teeth and having strongly arched central plate with 6–11 subequal cusps, and paired odontophoral cartilage plates (Coovert & Coovert, 1995). These shared features, exclusive from other cystiscid groups, are characterizing in fact the subfamily Persiculinae Coovert et Coovert, 1995 sensu Boyer (2019).

Coovert & Coovert (1995) accepted three good genera in their subfamily Persiculinae, as *Persicula* Schumacher, 1817, *Gibberula* Swainson, 1840 and *Canalispira* Jousseaume, 1875, but in his revision, Boyer (2019) did replace *Canalispira* in a new cystiscid Subfamily Canalispirinae Coovert & Coovert, 1995 [the same proposition was made by Fedosov et al. (2019)], on the ground of special features of the animal slit head deprived of tentacles and of the absence of shell siphonal notch (Wakefield & McCleery, 2007). The present work will contribute to show that beside *Persicula* and *Gibberula* sensu stricto (respectively, the species matching closely *Persicula persicula* and *Gibberula oryza*), the cystiscid Subfamily Persiculinae is composed of several other groups with strong identity deserving potentially to be recognized at the genus level.

Investigating the generic composition of the Subfamily Persiculinae

We propose to place provisionally in *Persicula* sensu stricto the species with large and thick shells, obsolete spire, stepped outer labrum and deeply notched siphonal canal, represented by the type species *Voluta persicula* Linnaeus, 1758 and its sibling species *V. cingulata* Dillwyn, 1817, both ranging off northwest Africa and characterized by thick rounded shell with richly patterned decoration (regularly distributed brown rounded spots in *Persicula persicula*, regularly spaced diagonal spiral lines in *P. cingulata*). We propose to associate provisionally in *Persicula* the species group of *Marginella cornea* Lamarck, 1822 distributed off northwest Africa and in northwest Indian Ocean. We note that all these species have a short siphon.

We propose to place provisionally in *Gibberula* sensu stricto the species with small shells, short spire, non-stepped outer labrum and moderately notched siphonal canal, represented by the type species *Volvaria oryza* Lamarck, 1822, distributed off northwest Africa and characterized by a subpyriform shell with spiral colour bands. Beside the

species matching *G. oryza* for their similar shell morphology, undecorated or banded shell decoration and short siphon, we propose to accept also in *Gibberula* the species with tiny white shells matching the *G. philippii* species group (Gofas, 1990; Boyer & Renda, 2022), while waiting for a deeper investigation of this group. At least, we provisionally place also in *Gibberula*, but with more reserve, two species being compatible with the *Gibberula oryza* species group for its shell morphology, but wearing a shell decoration derived from a "reduced zig zag pattern" (only 3 to 4 main unequal arrow-heads pointing to the left side, instead of 8 to 12 main arrow heads in the "*G. frumentum* group"): namely *G.* cf. *lucia* and *G. almadiensis* documented from Senegal (personal data). These two allied species present the same shell shape matching the *G. oryza* species group, the same type of shell decoration, and the same kind of animal chromatism found in most of the *Gibberula* species from the Lusitania Province, with bigger white patches grouped along the sides of the foot. Depending on the specimens, *G.* cf. *lucia* from Senegal has a short or a medium sized siphon, whereas *G. almadiensis* has always a short siphon (personal data). This small group deserves also deeper investigation, and it might prove to have a distinct phyletic status beside *Gibberula* sensu stricto, and beside the main complex of wavy ornated cystiscids characterized by a shell decoration based on 8–12 arrow heads pointing to the left, regularly dispersed white patches or spots on the foot associated to brown stains or venules, and long siphon. A pair of sibling species ranging at bathyal levels off New Caledonia (*Persicula quemeneri* Cossignani, 2001 from northern NC and *Gibberula nebulosa* Boyer, 2002 from southern NC), characterized by slender-cylindrical shells decorated by zig zag axial lines forming 4 unequal arrow heads pointing to the left, could constitute a brother-group of the *G. lucia*/*G. almadiensis* cluster.

According to us, at least four other main cystiscid groups deserve to be recognized as pertinent genera in the Subfamily Persiculinae, beside the genera *Persicula* and *Gibberula* sensu stricto:

- The genus *Pachybathron* Gaskoin, 1853, known from the southern Caribbean Sea and recently discovered off eastern Oman (unpublished datum), with short to obsolete spire, narrow aperture and short siphon (Wakefield et al., 2002). *Pachybathron* was placed in synonymy with *Persicula* by Coovert & Coovert (1995) but the subsequent work of Wakefield et ali did demonstrate the deep originally of this group and the pertinence of *Pachybathron* as genus concept.

- The species complex of *Voluta interruptolineata* Megerle von Mühlfeld, 1816, distributed in southern Caribbean Sea and central Panamic Province, with obsolete spire, strong outer labial varix, deep siphonal notch, spiral pattern of shell decoration with continuous or discontinuous lines or with rows of spots, and long siphon (Coovert & Coovert, 1995). The species group of *Marginella tessellata* Lamarck, 1822 presents the same distribution and it is supposed to belong to the same complex, but this still remains unverified.

- The species complex of *Marginella maculosa* Kiener, 1834, with obsolete spire, non-stepped outer margin, deep siphonal notch, ocellate shell decoration and long siphon. This complex is mostly distributed in the southern Caribbean Sea, with few representants in the central Panamic Province and in the Arabian Region (personal data). Live specimens of the species *M. maculosa*, *M. phrygia* Sowerby, 1846, *M. calculus* Redfield, 1870, *Persicula cordorae* De Jong et Coomans, 1988 and *P. vanpeli* Moolenbeek et van der Bijl, 2008 were examined in live condition (personal data).

- The species complex of wavy ornated cystiscids and derived shell decorations based on 8–12 arrow heads pointing to the left, very short or obsolete spire, non-stepped outer margin, poorly notched siphonal canal, long siphon, and regularly dispersed white patches or spots on the foot associated to reddish-brown stains or venules, these animal features being controlled positively on five Caribbean species and on ten Indo-Pacific species. *Marginella thomensis* Tomlin, 1919 from São Tomé is provisionally placed in this complex, due to its shell morphology matching that of *M. frumentum*, and to its shell decoration with crescentic marks derived from a zig zag pattern of 6 main arrow heads pointing to the left. These similitudes were underlined by Gofas & Fernandes (1988). The status of *M. thomensis* remains however quite uncertain for three reasons: its foot chromatism made of fragmented and regularly dispersed yellowish spots on a translucent-whitish ground but associated with dispersed small orange and green spots, this tricolour pattern being usual in various *Gibberula* groups but unrecorded in the zig zag patterned species with 8–12 main arrow heads

and in the derived forms, where the usual pattern is made of regularly dispersed white patches associated to reddish-brown stains or venules; the occurrence of a short siphon observed through many specimens by Gofas & Fernandes, versus a long siphon documented in the *Marginella frumentum* group and in derived forms; the shell decoration of *M. thomensis* derived from a "reduced pattern" based on 6 arrow main heads, looking by the fact as intergrading between the pattern observed in *M. frumentum* and allied species (8–12 main arrow heads and derived forms) and the pattern observed in *Gibberula lucia* and *G. almadiensis* (derived from 3 main arrow heads). Deeper investigations about *Marginella thomensis* are required, in view to verify if its placement in the same twig as *M. frumentum* and allied species is really pertinent, or if *M. thomensis* is constituting a distinct twig by its own, like it might occur for *Gibberula lucia* and *G. almadiensis* as well.

The present work about the seven wavy ornated cystiscid species documented from the Dhofar is conceived as a test for the resolution of the taxonomic status of this species complex, and as a contribution to the organisation of the Subfamily Persiculinae. Otherwise, the species complexes of *Voluta interruptolineata* and of *Marginella maculosa* are under study by the author.

ACRONYMS AND ABBREVIATIONS. DMNH: Delaware Museum of Natural History, Wilmington (DE), United States; MHNG: Muséum d'Histoire Naturelle de Genève, Switzerland; MMM: Malacologia Mostra Mondiale, Cupra Marittima, Italy; MNHN: Muséum national d'Histoire naturelle, Paris, France; NHMUK: Natural History Museum United Kingdom, London, Great Britain; NMW: National Museum of Wales, Cardiff, Great Britain; ZMA: Zoölogisch Museum Amsterdam, the Netherlands; CAW: collection Andrew Wakefield, Great Britain; CCD: collection Andrew Childs & Vicky Dobson, Cyprus; CDW: collection Dekker-Winkel, the Netherlands; CFB: collection Franck Boyer, France; CJR: collection Jose Rosado, Mozambique; CSG: collection Sandro Gori, Italy; CTMC: collection Tony McCleery, Great Britain; CVG: collection Leo and Wil van Gemert, the Netherlands; spm: live collected specimen; sh: empty shell; ad: adult; subad: subadult; juv: juvenile; L: length size; idem: same as the previous citation.

RESULTS

Systematics

Superfamilia VOLUTOIDEA Rafisnesque, 1815
Familia CYSTISCIDAE W. Stimpson, 1865
Subfamilia CYSTISCINAE W. Stimpson, 1865

Genus ***Sagittalia*** n. gen.
https://www.zoobank.org/A472DF90-B2BC-49DB-B606-1CAF18ECE4C8

TYPE SPECIES. *Marginella sagittata* Hinds, 1844. The lectotype of *M. sagittata* Hinds (NHMUK) is pictured in Boyer (2004: Figs. 4, 5).

DESCRIPTION. Shell morphology. Oval shell sizing 4–12 mm, with narrow aperture and obsolete spire, weakly thickened outer these pleats decreasing in size from the base to the top, moderately to faintly notched siphonal canal. Shell decoration: basic pattern of axial zig zag or wavy lines, making 8 to 12 spiral series of more or less thickened arrow heads pointing to left-hand, sometimes with dark spots or small vertical dashes nested in the concave side of the right-hand curves; derived forms showing dominant spiral series of dark spots; derived forms showing dominant spiral lines or spiral series of dashes.

Animal morphology. Slit head with faintly arched lateral lobes and short pointing frontal tips, long thin tentacles, black eyes behind the base of the tentacles, prominent siphon, widely stretched foot deprived of anterior mentum. Animal chromatism. Beige to greenish ground, foot with medium to large dispersed white spots, small red-brown stains or venules often connecting and forming honeycomb networks, especially at the distal end of the metapodium, on the head and on the siphon.

Radula. Only documented for three species (Coovert, 1989), all having tiny arched plates wearing 7 to 11 subequal cusps: *Voluta catenata* Montagu, 1803 with 7 cusps, *Marginella pulcherrima* Gaskoin, 1849 with 9 cusps, and *Marginella thomensis* Tomlin, 1919 with 10–11 cusps. The morphology of these plates looks as very similar to that represented in *Gibberula* sensu stricto (cf. above), as well as in *Voluta persicula*, whose plate is however more deeply notched on its concave side and wears 11 cusps on the convex side (Coovert, 1989).

Odontophore. Paired odontophoral cartilage plates, with narrow, slender and bended outline in

"*Persicula masirana* Roth & Petit, 1972" (our new genus), versus slender club-shaped outline in "*Persicula interruptolineata* (Megerle von Mühlfeld, 1816)" (Coovert & Coovert, 1995).

Biochemistry. The results displayed by Fedosov et al. (2019), through their molecular-based cladistic tree, report the wavy ornated cystiscids as constituting a homogeneous clade noticeably distant from the other Persiculinae groups and looking to be closer to the *Cystiscus*-*Crithe* complex, itself implicitly interpreted as sharing an exclusive common ancestor with the wavy ornated cystiscids. The two wavy ornated species tested by Fedosov et al. (2019) in this frame are "*Gibberula*" aff. *moscatellii* Boyer, 2004 from French Guiana and "*Persicula*" *pulcherrima* Gaskoin (1849) from Martinique. "*Gibberula*" aff. *moscatellii* is in fact *Persicula bagne* Faber, 2006 described from Iles du Salut, French Guiana, and "*Gibberula*" *pulcherrima*, described originally in the genus *Marginella*, is correctly identified by the authors (personal data). *Persicula bagne* has a squat rounded shell with sharp axial zig zag decoration, a long siphon and the usual animal chromatism found in this species complex, with yellow spots and a reddish venules network especially concentrated on the distal part of the metapodium (live specimen pictured by Fedosov et al. in their Fig. 1E). *Marginella pulcherrima*, well-known from Martinique where it is quite common in weeds on rocks at shallow levels of protected places (pers. obs.), has a more pyriform shell, a derived shell decoration with dominant spiral pattern (Figs. 53, 54), a long siphon, the animal being decorated with greenish shaded spots and with two long whitish club-shaped patches, made of concentric layers and distributed on both sides of the metapodium (Fig. 55).

Remarks. The choice of *M. sagittata* Hinds, 1844 as type species of our new genus is due to the fact that the other species formerly described and belonging to our new genus still retain an uncertain identity to different degrees. The validity of the type material of *Voluta catenata* Montagu, 1803 remains to be verified, as the NMW "possible syntypes" (Lyons collection) proposed by Oliver, Talbot, Fredriksson, Tomlinson, Lewis & Fraser (2020) is contradicted by the occurrence of an holotype registered in NHMUK (Figs. 49, 50); the identity, the type material and the type locality of *Marginella frumentum* Sowerby, 1832 remain unclear (Boyer, 2004); the identity of *Marginella pulchella* Kiener, 1834 remains to be stabilized through a formal revision and the recognition of a live population (Boyer, 2003). Among the oldest described species belonging to our new genus, *Marginella sagittata* Hinds, 1844 looks to have the most evidenced identity, with revised type and recognized live populations (Boyer, 2004).

The placement of our new genus in the subfamily Persiculinae Coovert et Coovert, 1995 is proposed despite the abandon of this Subfamily by Fedosov et al. (2019). These authors gave up apparently the use of this subfamily due to the fact that their cladistic tree presented a lateral branch diverging from the rest of the Cystiscidae and bearing two neighbouring twigs: the complex *Cystiscus*-*Crithe* on one hand, and on the other hand two "*Gibberula*-looking species" belonging to our new genus (as "*Gibberula"* aff. *moscatellii* Boyer, 2004 and "*Persicula" pulcherrima* Gaskoin, 1849). Despite the important differences occurring otherwise between the complex *Cystiscus*-*Crithe* and these two "*Gibberula*-looking species" (shell morphology, animal type and radula type), Fedosov et al. (2019) interpreted implicitly the coexistence of the complex *Cystiscus*-*Crithe* and of two *Gibberula*-looking species on the same branch as the proof that the taxonomic distinction between the two Subfamilies Cystiscinae W. Stimpson, 1865 and Persiculinae Coovert & Coovert, 1995 was not appropriate.

Our interpretation is different: the cladistic tree proposed by Fedosov et al. (2009), based on simple molecular tests of 5 genetic markers of few individuals in each morphospecies, allows only to infer that for these biochemical clues, the couple *G.* aff. *moscatelli*/*P. pulcherrima* (our new genus) seems to be genetically closer to *Cystiscus*-*Crithe* than to the other *Persicula*-*Gibberula* looking groups. However, an integrative analysis incorporating the rest of the documentation at disposal (shell morphology, animal morphology, radula morphology and shape of the odontophore plates) leads to consider that the couple *G.* aff. *moscatellii*/*P. pulcherrima* (our new genus) has a closer global relationship with the other *Persicula*-*Gibberula* looking groups than with the complex *Cystiscus*-*Crithe*, and for this reason the couple *G. moscatellii*/*G. pulcherrima* (our new genus) deserves to be conserved in the Subfamily Persiculinae, even if showing some alleles variations comparable to that observed in in the complex *Cystiscus*-*Crithe*. Such an occurrence might possibly come for instance

from simple plesiomorphic remains, and in any case, it does not allow to infer the evidence of an exclusive common ancestor uniting our new genus to the complex *Cystiscus-Crithe*, out of the Persiculinae branch. In other words, our new genus seems to have some genetic distance with the rest of the Persiculinae, but Subfamilies are composed of various non-synchronic disbranchings, and in the present state integrative taxonomy is better defending the distinction of the Subfamilies Cystiscinae and Persiculinae, and the placement of our new genus in the last one.

Sagittalia anapaulae n. sp.
https://www.zoobank.org/D5E2A1E6-C514-4C20-8FBB-097D9C876508

TYPE MATERIAL. Holotype. Oman • sh; Dhofar, east Mirbat; L = 3.8 mm, beached, ex-CFB, Figs. 1, 2; MHNG-MOLL-159456. Paratypes. Oman • 12 sh; Dhofar, east Mirbat; L = 3.6–4.6 mm; CFB.

OTHER MATERIAL EXAMINED. Oman • 5 sh; Dhofar, east Mirbat; beached; CFB • 1 sh ad; Dhofar, east Mirbat; 2–4 m depth; CFB • 1 spm ad; Saadah coves; 2–4 m depth; CFB • many ad & juv spm; Dhofar, Mirbat; 20–35 m depth; CJR • 1 ad spm; Dhofar, east Mirbat; 3–6 m depth; Fig. 3; CJR • many ad & juv spm; Dhofar, Mirbat; 12–35 m depth; CSG.

DESCRIPTION. Shell (from the holotype: Figs. 1, 2): oval subcylindrical outline, flat top with produced teat-like protoconch; very high aperture, narrow in its posterior part, slightly widened in its anterior part, moderately dilated anal canal; shouldered labrum, thin lip with numerous tiny obsolete denticles, not visible at the middle part of the inner labrum where the lip is slightly wrapping; no outer margin, a very thin varix running all along the ventral edge of the lip; four distinct columellar plaits and two very tiny ones in form of lirations, the two lower plaits long and strong, the first one slightly sinuous and subvertical in its central part, and making a moderate angle near to the base; moderately notched siphonal canal, surrounded by a stepped basal callus running from the third plait on the ventral side to the base of the labial lip, narrowing progressively around the dorsal side of the siphonal notch and transforming into the sharp labial varix in a solution of continuity.

The top of the shell is dark brown, the round colour mark being conspicuously delimited by the lower suture and surrounded by a spiral ring of few spaced brown squared spots, protoconch dark brown; body whorl decorated of yellow mustard sinuous axial lines, making eight spiral series of large arrow heads pointing to the left backed by white oval patches, whereas the arrow heads pointing to the right are smaller, thinner and often disrupted; brownish thickening nested in the intervals of the bigger left-pointing arrow heads, between the 2nd and the 3rd spiral series, the 4th and the 5th spiral series, and the 7th and 8th spiral series, central series being the most conspicuous; a small brown mark at the upper third part of the ventral edge of the lip, a bigger one at the middle part.

Animal (Fig. 3). Slit head with weakly rounded lateral sides bearing black eyes, moderately long tentacles, short pointing frontal lobes, quite long and strong siphon; large stretched foot deprived of propodium mentum. Ground colour greenish, with a network of reddish-brown venules making a mosaic figure, quite disorganised and making small patches on the head, the siphon and the propodium, more organised on the posterior part of the metapodium, with more conspicuous and larger patches; few tiny white spots on the head and on the tentacles, medium-sized white spots on the sides of the foot, and two large club-shaped white patches distributed on both sides of the posterior part of the metapodium.

DISTRIBUTION. *Sagittalia anapaulae* n. sp. is only known from Central Dhofar, where it seems to be quite common from 2–4 m to 35 m.

ETYMOLOGY. From Ana Paula Rosado, who contributed with her husband Jose to help the author in the 2023 expedition to the Dhofar.

REMARKS. The variability of the species is characterized by two principal shell variants: the smaller squat form (3.8–4.6 mm) found in shallow water (2–6 m) and less commonly deeper (12–35 m), with 7 main spiral row of big arrow heads pointing to the left side (Figs. 1–3), and the bigger slender form (5.9–6.2 mm) found exclusively at mid-reef levels (12–35 m), with 8 main spiral rows of big arrow heads pointing to the left side, and frequently additional interstitial rows of smaller arrow heads (Figs. 8–11). But intergrades are occurring at mid-reef levels, with medium sized shells (5.5–5.8 mm) showing 8th main row of arrow heads progressively formed

on the last half of the body whorl (Figs. 4–7). In other words, the typical populations found in shallow water off Mirbat and off Saadah looks to be very homogeneous with small squat shells with 7 rows, whereas the comparable populations found at mid-reef levels off Mirbat look to be more variable, from small squat shape with 7 main rows of arrow heads to larger slender shells with 8 rows of arrow heads, including syntopical intergrading forms.

From our observations on a great number of specimens from various stations, it seems that the growth genetic program of this species is coordinating the number of rows of arrow heads with the adult size of the individual, illustrating a case of ontogenetic allometry. From this observation, we infer that no evident gap is occurring within the variation range of the morphospecies, and we propose to consider that all the observed forms are conspecific.

Sagittalia anapaulae n. sp. can be easily distinguished from other wavy ornated species from the Western Indian Ocean by its subcylindrical outline and by its dark flat top and teat-like protoconch. Comparable flat top (without teat-like protoconch) are found in some Caribbean species characterized by dominant spiral decoration derived from a wavy ornated pattern), such as *Voluta catenata* Montagu, 1803 (Figs. 49, 50) and *Marginella pulcherrima* Gaskoin, 1849 (Figs. 53–55), as well as in *Persicula masirana* Roth & Petit, 1972 (Figs. 46, 47) described from Masirah Island (another species with a dominant spiral decoration) or in *Marginella deburghi*, A. Adams, 1864 (Figs. 33, 34), described from Western Australia and showing a punctuated shell decoration, also derived from a wavy pattern (see below). On the contrary, *Sagittalia anapaulae* n. sp. is less easily separable from a sibling species discovered in the vicinity (Salalah, Western Dhofar) and described below.

We note that double club-shaped white marks observed in *Sagittalia anapaulae* (Fig. 3) are occurring also in *Marginella pulcherrima* (Fig. 55) and in *Persicula masirana* (Fig. 48): this uncommon feature might be considered as the clue of a special relationship between these spiral-decorated species sharing the same type of flat spire. This point will be tackled in the Discussion.

Sagittalia willeminae n. sp.
https://www.zoobank.org/2878D9A6-69B3-45B1-A64F-22EFEB03C765

Type material. Holotype. Oman • sh; Salalah; L = 5.5 mm, beached, (Figs. 12, 13); MHNG-MOLL-159461. Paratypes. Oman • 1 sh; Salalah; L = 6.2 MM, Figs. 14, 15; paratype 1 CFB ex-CVG • 1 sh; Salalah; paratype 2 CVG.

Description. Shell (from the holotype: Figs. 12, 13): squat oval outline, flat top with poorly produced bumped protoconch; very high aperture, narrow in its posterior part, slightly widened in its anterior part, moderately dilated anal canal; shouldered labrum, moderately thickened lip with numerous tiny obsolete denticles, not visible at the middle part of the inner labrum where the lip is slightly wrapping; no outer margin, a very thin varix running all along the ventral edge of the lip; four distinct columellar plaits and two very tiny ones in form of lirations, the two lower plaits long and strong, the first one slightly concave and subvertical; moderately notched siphonal canal, surrounded by a stepped basal callus running from the third plait on the ventral side to the base of the labial lip, narrowing progressively around the dorsal side of the siphonal notch and transforming into the sharp labial varix in a solution of continuity.

The top of the shell covered by a rounded dark brown mark, surrounded by a spiral ring of few spaced brown squared spots below the suture, protoconch dark brown; body whorl decorated of yellow mustard sinuous axial lines, making eight spiral series of large arrow heads pointing to the left backed by white oval patches, whereas the arrow heads pointing to the right are smaller, thinner and often disrupted; brownish thickening nested in the intervals of the bigger left-pointing arrow heads, between the 2nd and the 3rd spiral series, the 4th and the 5th spiral series, and the 7th and 8th spiral series, central series being the most conspicuous; a small brown mark at the upper third part of the ventral edge of the lip, a bigger one at the middle part.

Animal: unknown.

Distribution. The species is only known from three beached shells collected on the beach of Salalah, Western Dhofar, and it is clearly absent from all the Mirbat area (Central Dhofar).

Etymology. From Willemina (Wil) Adriana van Gemert, who collected with her husband Leo many micro-shells on the beach of Salalah, and loaned kindly their marginelliforms collection for study.

REMARKS. *Sagittalia willeminae* n. sp. can be considered as a twin species of *S. anapaulae* n. sp. Both species are very similar both for shell morphology and for shell decoration, the only noticeable difference being in the shell outline and proportions, *S. willeminae* n. sp. having a swollen and slightly subpyriform shell, versus subcylindrical in all the variants of *S. anapaulae* n. sp.

The attribution of a specific status to this morph is founded on the fact that the three shells collected on the beach of Salalah look to be very homogeneous and that this form is not found in Central Dhofar, off Mirbat as well as off Saadah, and does not belong to the variability documented in *S. anapaulae* n. sp. On the other hand, no shell matching neither the "squat shallow form" of *S. anapaulae* n. sp. nor the slender form of this species was found on the Salalah Beach, despite extensive sampling of the beach sediments in the place and the distance of 60 km occurring between the Salalah Beach and Mirbat. So, it is inferred that the morph *S. willeminae* n. sp. is replacing the form *S. anapaulae* n. sp. off Salalah, and probably off the rest of Western Dhofar.

In the reported conditions, the occurrence of this "swollen form" as a simple geographic population of *S. anapaulae* is naturally not impossible, but statistically less likely than an autonomous species status, due to the limited coastal gap between the two populations, which would facilitate reproductive mixing and phenetic intergrades if both populations were not reproductively separated. This proposition of *S. willeminae* n. sp. as autonomous species is naturally hypothetical, and it deserves to be confirmed by future observation of live populations from this morph, including about the chromatism of the live animal.

Sagittalia eloiseae n. sp.
https://www.zoobank.org/1415654F-06C6-4C73-BC25-87B154F30C92

TYPE MATERIAL. Holotype. Oman • sh; Dhofar, east Mirbat; beached, Figs. 20, 21, L = 8.7 mm; MHNG-MOLL-159457. Paratype. Oman • 13 sh; Dhofar, east Mirbat; L = 8.0 mm–9.0 mm, Figs. 23, 24, 26–27; CFB.

OTHER MATERIALE EXAMINED. Oman • many sh+ many spm; Dhofar, east Mirbat; 2–4 m depth; CFB • 1 sh ad; Dhofar, Old Mirbat; 1 m depth; CFB • 1 sh ad; Dhofar, Fazayah beaches; 1 m depth; CFB • 1 spm subad; Dhofar, Saadah coves; 3 m depth; CFB • many spm; Dhofar, Mirbat; 20–35 m depth; CJR • many spm; Dhofar, Mirbat; 12–35 m depth; CSG • many sh; Central Dhofar; beached; CCD. Yemen • 1 sh ad; Mahrah Province, Saqr; beached; CDW.

DESCRIPTION. Shell (from the holotype: Figs. 20, 21): Oval outline, slightly rostrated top with immersed protoconch; very high aperture, narrow in its posterior part, slightly widened in its anterior part, moderately dilated anal canal; shouldered labrum, thin lip with numerous tiny packed denticles on the posterior part, bigger and spaced on the anterior part, not visible at the middle part of the inner labrum where the lip is slightly wrapping; labrum outer profile slightly angled at its mid-part, slightly concave below, no outer margin, sharp ventral edge of the lip; six distinct columellar plaits, poorly produced, and six tiny lirations, the first plait short, oblique and slightly concave, the second plait stronger and straighter, the other ones decreasing progressively in size; faintly notched siphonal canal, surrounded by a low-stepped basal callus running from the third plait on the ventral side to the base of the labial lip, narrowing progressively around the dorsal side of the siphonal notch.

The top of the shell is dark brown, making a star-shape; body whorl decorated of yellow mustard sinuous axial lines, making eight spiral series of large and sharp arrow heads pointing to the left backed by white oval patches, whereas the arrow heads pointing to the right are smaller, thinner and often disrupted; brownish thickening nested in the intervals of the bigger left-pointing arrow heads, between the 2nd and the 3rd spiral series, the 4th and the 5th spiral series, and the 7th and 8th spiral series, central series being the most conspicuous, many short vertical threads between the left-pointed arrow heads, giving a dominant weave-look to the decoration pattern; eight small to moderate brown marks distributed on the ventral edge of the lip.

Animal (Figs. 22, 25, 28): Slit head with weakly rounded lateral sides bearing black eyes, moderately long tentacles, short pointing frontal lobes, quite long and strong siphon; large stretched foot deprived of propodium mentum.

Ground colour whitish cream, with a network of pale reddish-brown venules making a quite disorganised mosaic figure on the posterior part of the metapodium, more fragmented and elusive on the propodium, the head and the siphon.

Distribution. The species is documented from Western and Central Dhofar, and also from the Mahrah Province, in Eastern Yemen. It was collected in live condition from 2–4 m to 35 m depth and it seems to be quite common.

Etymology. From Eloise Bosch, who was a pioneer in the discovery of the marine molluscan fauna of Oman, with her husband Donald.

Remarks. *Sagittalia eloiseae* n. sp. is generally identified in private collections as "*Persicula brinkae* Bozzetti, 1993", a large species with wavy ornated shell described from Cape Ras Hafun, Somalia and only known from its holotype (L = 13.4 mm) said to be dredged at 150–200 m (Figs. 16, 17). *Sagittalia eloiseae* n. sp. differs in fact from *Persicula brinkae* by a smaller and quite squatter shell, less numerous, less packed and less conspicuous labial denticles, 8 rows of sharper main spiral arrow heads pointing to the left (instead of 7 rows of blunt arrow heads), and a well-defined star-shaped dark mark on the top of the shell (instead of a smaller comblike fringed mark). A species somewhat resembling to *P. brinkae* is occurring in Sri Lanka (pers. doc.).

The animal chromatism of *Sagittalia eloiseae* n. sp. is very original among the species documented from Indo-Pacific, as limited to fragmented remains of the basic red-brown network of venules generally found in the genus. The most resembling animal chromatism is that reported for *Persicula domenichi* Ortea, 2020, described from Caribbean Costa Rica and only differing from the typical form of *Marginella fluctuata* C.B. Adams, 1850 by a continuous network of venules apparently not associated with any other colour spots (Ortea, 2020: plate 3).

Another *Sagittalia* species collected in the same locality and depth as *S. brinkae*, described as *Gibberula gabryae* Bozzetti, 1993 (Figs. 18–19) with small oval shells (L = 6.0–6.6 mm) and very narrow aperture, looks to belong to another species group, together with *Persicula maldiviana* Cossignani, 2001 described from the Maldives, and with some undescribed species from South Africa and from Australia (pers. doc.).

Sagittalia vickydobsonae Boyer et Childs n. sp. https://www.zoobank.org/3B53E5CD-ABE6-4B5E-B333-01F1954D92B3

Type material. Holotype. Oman • sh; Dhofar, east Mirbat; beached, L = 8.2 mm, Figs, 29, 30; MHNG-MOLL-159460 ex CFB. Paratype. Oman • 11 sh; Dhofar, east Mirbat; L = 7–8.2 mm; CFB.

Other materiale examined. Oman • many sh; Dhofar, east Mirbat; beached; CFB • 2 spm ad; Dhofar, east Mirbat; 2–4 m depth; CFB • 1 spm ad; Dhofar, Saadah coves; 3 m depth; CFB • many sh; Dhofar, Mirbat; beached; CCD.

Description. Shell (from the holotype: Figs. 29, 30): oval outline, slightly rostrated top with immersed protoconch; very high aperture, narrow in its posterior part, slightly widened in its anterior part, moderately dilated anal canal; shouldered labrum, thin lip with numerous tiny packed denticles on the posterior part, bigger and spaced on the anterior part, not visible at the middle part of the inner labrum where the lip is slightly wrapping; labrum outer profile slightly angled at its mid-part, slightly concave below, no outer margin, sharp ventral edge of the lip; six distinct columellar plaits, poorly produced, and six tiny lirations, the first plait short, oblique and slightly concave, the second plait stronger and straighter, the other ones decreasing progressively in size; faintly notched siphonal canal, surrounded by a low-stepped basal callus running from the third plait on the ventral side to the base of the labial lip, narrowing progressively around the dorsal side of the siphonal notch.

The top of the shell is dark brown, making a star-shape; body whorl decorated of yellow mustard sinuous axial lines, making eight spiral series of large and sharp arrow heads pointing to the left backed by white oval patches, whereas the arrow heads pointing to the right are smaller, thinner and often disrupted, some of these axial sinuous lines are more or less obsolete; dark brown rounded spots nested in the intervals of the left-pointing arrow heads, giving a punctuated-look to the decoration pattern, no vertical threads; three faintly suggested brown marks distributed on the outer border of the ventral edge of the lip.

Animal: not fully observed, only noticed in retracted position. The animal chromatism in the fringes of the foot and in the tentacles looked to match the chromatism observed in *G. eloiseae*.

Distribution. It is only known from Central Oman, where it seems to be uncommon and to live only in shallow water (not collected in 12–35 m).

ETYMOLOGY. From Vicky Dobson, who contributed noticeably to the discovery of the coastal micro-molluscs of Oman, in cooperation with her devoted partner Andrew Childs.

REMARKS. The shell morphology of *Sagittalia vickydobsonae* n. sp. is identical to that of *S. eloiseae* n. sp., except for its slightly smaller average shell length of 7.4–8.2 mm, versus 8–9 mm for *S. eloiseae*. The specific separation is established from the shell decoration, with spiral series of rounded dark spots and blurred axial wavy lines in *S. vickydobsonae* n. sp., versus random moon-crescent shaped spots associated to well-defined axial wavy lines in *S. eloiseae* n. sp. No intergrade was found, despite numerous beached shells and live specimens collected in Central Dhofar. Furthermore, *S. vickydobsonae* n. sp. has a shallower bathymetric distribution than *S. eloiseae* n. sp., being collected only as beached shells and or as live specimens at 2–4 m, and never at 12–35 m.

From these elements, we infer that *S. vickydobsonae* n. sp. must be considered as a quite evident sibling species of *S. eloiseae* n. sp. The punctuated decoration of *S. vickydobsonae* n. sp. looks to be clearly derived from the axial wavy decoration found in *S. eloiseae* n. sp., and their closely matching features lead to suppose that *S. vickydobsonae* n. sp. is directly disbranched from *S. eloiseae* n. sp., occurring like a case of probable local speciation rarely documented in the field.

Other punctuated forms derived from wavy ornated patterns are occurring in the Indo-West Pacific Region, such as *Marginella deburghi* A. Adams, 1864 from Western Australia (Figs. 33, 34) and *Gibberula cincta* Boyer, 2003 from Noumea, New Caledonia (Figs. 35, 36). For its flat top with conspicuous dark mark, *Marginella deburghi* presents some affinity with *Sagittalia anapaulae, S. willeminae* and *Persicula masirana*. Several sibling forms from Western Australia closely matching *Marginella deburghi* are wearing axial wavy lines together with spiral rows of rounded spots or dots (pers. doc.), and it is unclear if these variants are belonging to the natural variability of *M. deburghi* or if a series of sibling species is occurring. The same thing occurs about *Gibberula cincta*, with a form from Koumac (north-west New Caledonia) mixing wavy axial lines and spiral rows of dots (pers. comm. of David Massemin, New Caledonia): we do not know if this northern form is just a geographic variant of *G. cincta* or if it is a distinct species. We note also that the shell morphology of *G. cincta* is differing a lot from the shell morphology observed in the wavy ornated cystiscids from the Indian Ocean, and it presents more affinity with the shell morphology represented in the genus *Gibberula* sensu stricto (*G. oryza* species group). The same situation occurs with a tiny species from the Caribbean, described as *Gibberula agricola* Faber, 2005 from Margarita Island, Venezuela, showing a dotted decoration on a shell morphology matching better the genus *Gibberula* sensu stricto (*G. oryza* or *G. philippii* species groups). These different situations are suggesting that the spiral decoration and the punctuated forms in cystiscids species are possibly not of monophyletic order. This point will be tackled in the Discussion.

Sagittalia peterbonuttii (Cossignani et Lorenz, 2018)
Gibberula peterbonuttii Cossignani et Lorenz, 2018: 33.

TYPE MATERIAL. Holotype. Oman • sh; Mirbat; L = 8.5 mm; MMM. Paratypes. Oman • 11 sh; Mirbat; L = 7–9.4 mm; in various collections.

OTHER MATERIALE EXAMINED. Oman • many sh; Dhofar, east Mirbat; beached, Figs. 37–42; CFB • 1 spm ad; Dhofar, east Mirbat; 2–4 m depth; CFB • 2 spm ad + 3 sh ad; Dhofar, Mirbat; 20–35 m depth; CJR • 1 spm ad; Dhofar, east Mirbat; 3–6 m depth; Fig. 43; CJR • 3 spm ad + 2 sh ad; Dhofar, Mirbat; 12–35 m depth; CSG • many sh; Dhofar, Mirbat; beached; CCD.

DESCRIPTION. Shell (original description): see in Cossignani & Lorenz (2018). Animal (Fig. 43). Slit head with weakly rounded lateral sides bearing black eyes, moderately long tentacles, short pointing frontal lobes, quite long and strong siphon; large stretched foot deprived of propodium mentum. Ground colour light greenish, with a mosaic network of reddish-brown venules circling polygonal white spots, with few bigger white spots on the sides of the foot, and tiny whitish spots on posterior axis of the metapodium.

DISTRIBUTION. *Sagittalia peterbonuttii* is only known from Mirbat, Central Oman, where is seems to be uncommon and mostly distributed in shallow water.

REMARKS. Due to its similarities with *S. brinkae* n. sp., *S. eloiseae* n. sp. and *S. vickydobsonae* n. sp. for its shell morphology, *S. peterbonuttii* seems to belong to the same species group and to be derived from a punctuated form of the kind of *S. vickydonsonae*. The high disparity of the dominant spiral decorations observed in *Sagittalia* species (*S. catenata* and *S. pulcherrima* in the Caribbean, *S. peterbonuttii* and *S. masirana* in the Indian Ocean) suggests that this feature is possibly of polyphyletic order, or more precisely that it occurred on several times in the diversification of different wavy ornated lineages.

Sagittalia sp. A

This species (Fig. 44) is known from only one live specimen (CJR), collected at 24–28 m depth off east Mirbat, Central Dhofar. The shell morphology seems to be very similar to that observed in the *Sagittalia eloiseae* species group, but the shell decoration and the animal chromatism are deeply differing from the other species studied from the Dhofar Province. The shell decoration is characterized by alternate series of light-mustard and white axial zig zag narrow bands, and spiral series of small vertical brown dashes alternated with beige dots. The animal chromatism is made of subequal medium sized white spots and red-brown dots regularly distributed on a greenish ground, the tentacles are mostly reddish, the head wears reddish stains mostly concentrated around the eyes and medium sized white spots mostly packed on the front-head, on both size of the head slit, the siphon is whitish mottled with reddish-pink shades in its medium part. Its drafted spiral shell decoration and axial bands, as well as its animal chromatism, remember somewhat the ubiquist *Sagittalia masirana* (Roth & Petit, 1972) revised below.

Sagittalia masirana (Roth et Petit, 1972)
Persicula masirana Roth et Petit, 1972: 80, Figs. 1, 2

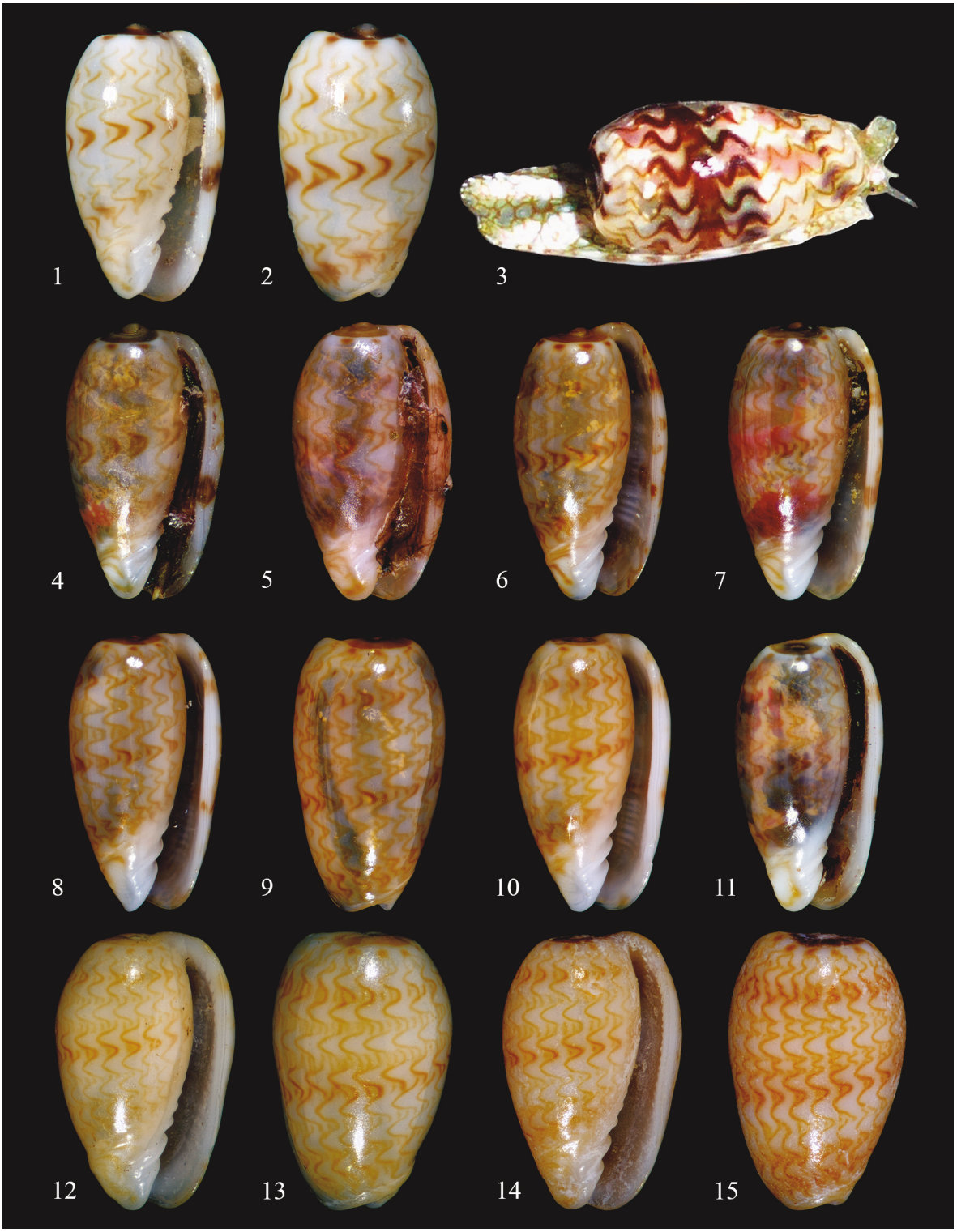
TYPE MATERIAL. Holotype. Oman • sh; NE Masirah Island, Ras Jidufah; L = 10 mm; DMNH 51327.

OTHER MATERIALE EXAMINED. Oman • 2 spm; Muskat; CFB • many spm; Masirah Island (Sur Bay and South Cape); CFB • 10 spm; N of Masirah Island; 10–20 m depth; dredged; CFB • many sh; Dhofar, east Mirbat; beached; CFB • 2 spm; Dhofar, east Mirbat; 12–35 m depth; CSG • 2 spm; Dhofar, east Mirbat; 20–35 m depth (Figs. 46, 47); CJR • many sh; Dhofar, Mirbat; beached; CCD.

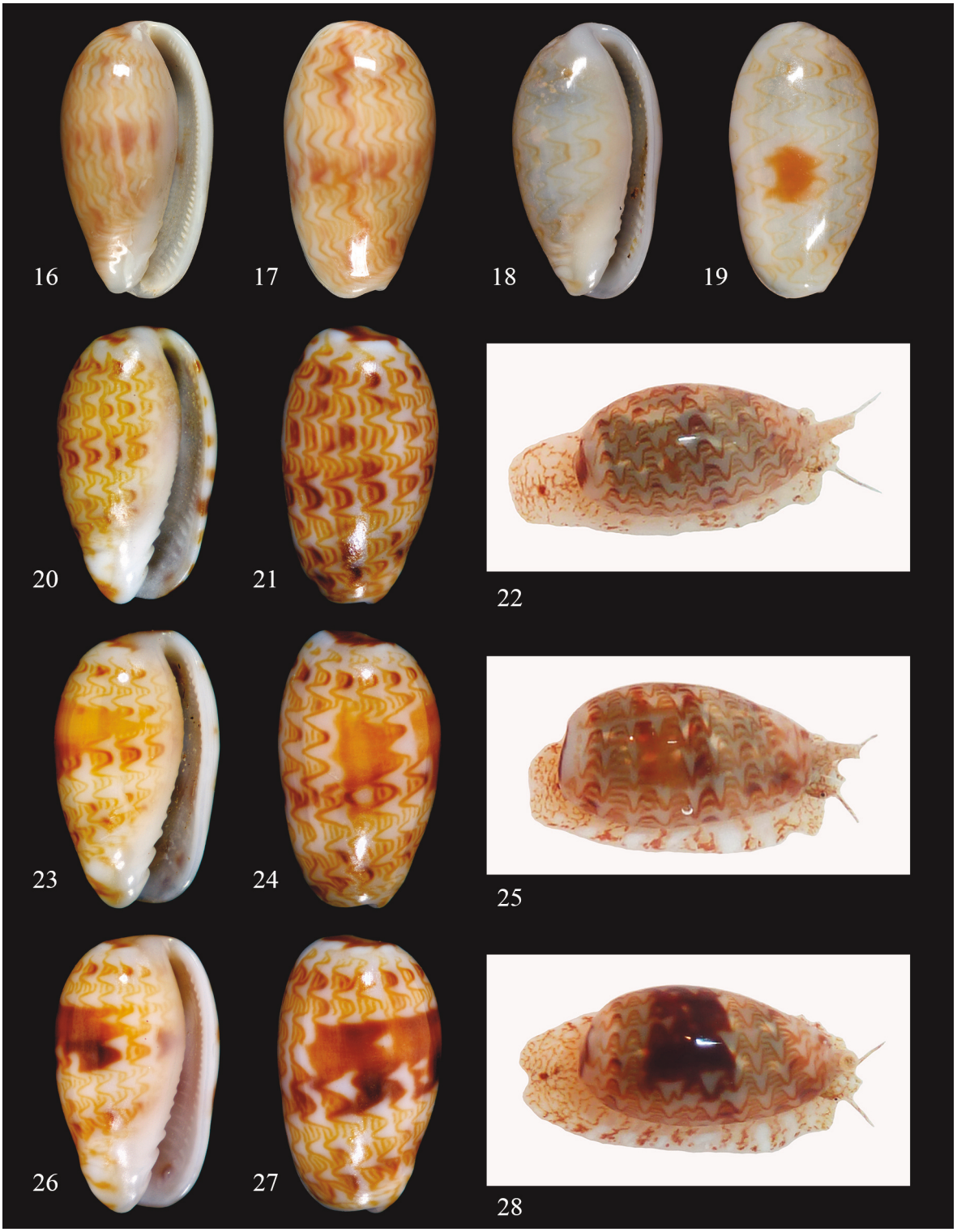
DESCRIPTION. Shell (original description): see in Roth & Petit (1972). Animal (Fig. 48): Slit head with weakly rounded lateral sides bearing black eyes, moderately long tentacles, short pointing frontal lobes, quite long and strong siphon; large stretched foot deprived of propodium mentum. Light greenish ground, regularly distributed subequal medium sized white spots and red-brown dots on the foot, smaller white spots on the head, the tentacles have two long dark green stains, medium green marks around the eyes, darker behind them, siphon light greenish mottled with small whitish spots in its lower part.

DISTRIBUTION. Distributed from the Gulf of Oman to the Dhofar Province, *Sagittalia masirana* (Roth & Petit, 1972) presents the most important distribution among the documented *Sagittalia* species from the Western Arabian Sea.

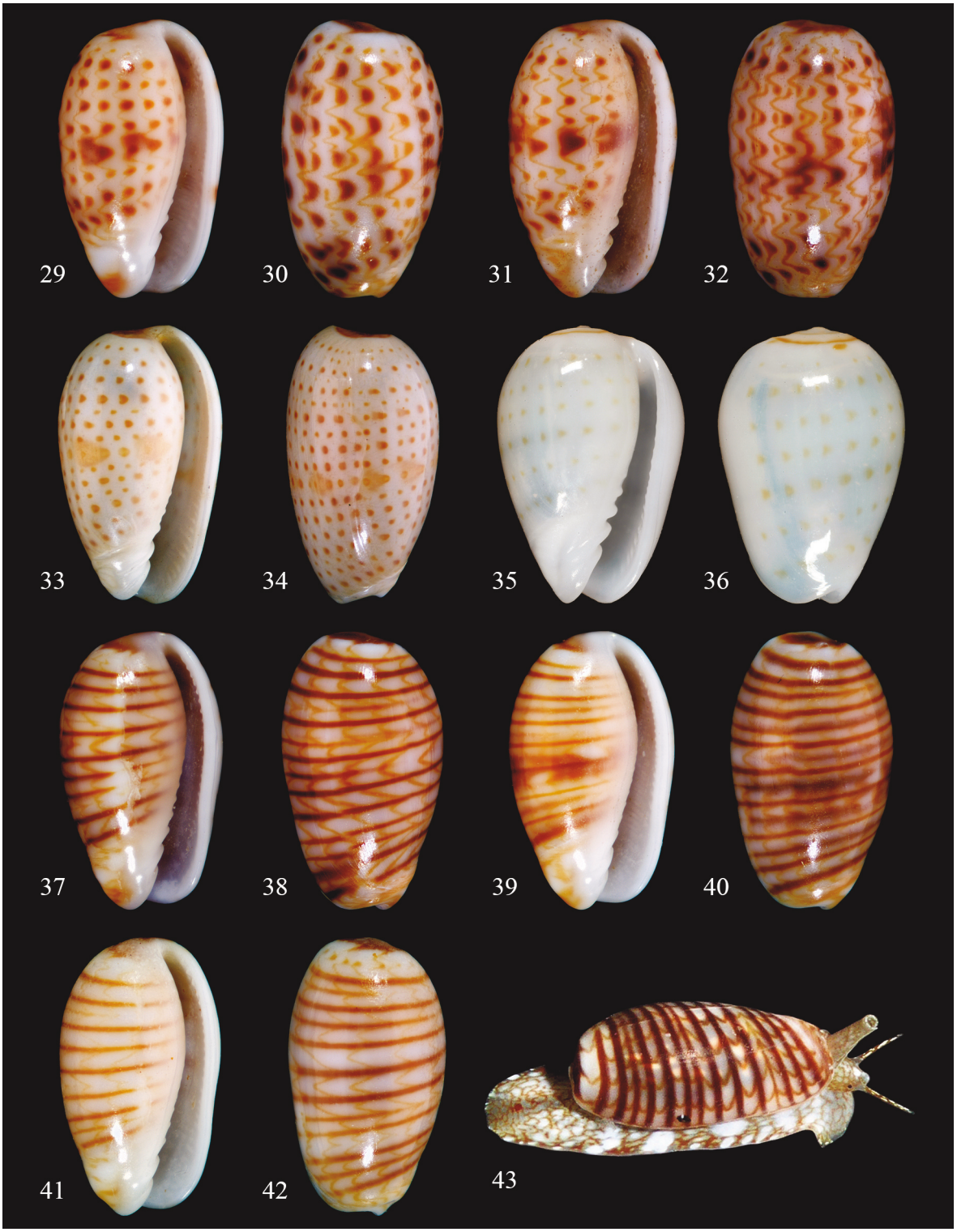
REMARKS. Due to its flat top with conspicuous round dark mark, *Sagittalia masirana* (Roth et Petit, 1972) seems to belong to the same species group as *S. anapaulae* and *S. willeminae*. It differs however noticeably from them by its bulged subpyriform outline and by its dominant spiral shell decoration made of alternate long white dashes and shorter brown dots, what patterns look to be quite similar to that found in the Caribbean species *S. catenata* (typical form, Figs. 49, 50) and *S. pulcherrima* (Figs. 53–55). *Sagittalia masirana* shows also noticeable resemblance with *Sagittalia* sp. A for its drafted spiral shell decoration on a yellow-beige ground with diluted axial brownish flames, and for its animal chromatism, with a foot showing subequal medium sized white spots and red-brown dots regularly distributed on a greenish ground. On the other hand, the shell morphology of *S. masirana* is differing significantly from that of *Sagittalia* sp. A, especially for its bulged subpyriform outline (versus slender oval outline in *Sagittalia* sp. A) and overal for its flat top with conspicuous dark mark (versus rostrate top and weak off-center dark spot in *Sagittalia* sp. A). From these elements, the phyletic proximity between these two species is reserved.



Figures 1–11: *Sagittalia anapaulae* n. sp. Figs. 1, 2: holotype MHNG-MOLL-159456, east Mirbat, Dhofar, beached sh, L = 3.8 mm, ex-CFB. Fig. 3: live spm, east Mirbat, 3–6 m, CJR. Figs. 4–7: Mirbat, 20-35 m, rocks brushing, L = 4.1 mm, 4.6 mm, 5.8 mm, 5.5 mm, CSG. Figs. 8–11: Mirbat, 26-28 m, rocks brushing, L = 6.1 mm, 5.9 mm, CJR. Figures 12–15: *S. willeminae* n. sp. Fig. 12, 13: holotype MHNG-MOLL-159461, Salalah, Dhofar, beached sh, L = 5.5 mm, ex-CVG. Figs. 14, 15: paratype CFB, Salalah, Dhofar, beached sh, L = 6.2 mm, ex-CVG.



Figures 16, 17: *Sagittalia brinkae*, holotype MNHN, Ras Hafun, Somalia, 150-200 m, L = 13.4 mm. Figures 18, 19: *S. gabryae*, holotype MNHN, Ras Hafun, Somalia, 150–200 m, L = 6.6 mm. Figures 20–27. *S. eloiseae* n. sp. Fig. 20, 21: holotype MHNG-MOLL-159457, east Mirbat, Dhofar, beached sh, L = 8.7 mm, ex-CFB. Fig. 22: live spm, Mirbat, 20-35 m, CJR. Figs. 23, 24: paratype 1 CFB, east Mirbat, beached sh, L = 8.2 mm. Fig. 25: live spm, Mirbat, 20–35 m, CJR. Figs. 26, 27: paratype 2 CFB, east Mirbat, beached sh, L = 8.0 mm. Fig. 28: live spm, Mirbat, 20–35 m, CJR.



Figures 29, 30: *Sagittalia vickydobsonae* n. sp., holotype MHNG-MOLL-159460, east Mirbat, beached sh, L = 8.2 mm, ex-CFB. Figures 31, 32: *S. vickydobsonae* n. sp., paratype 1 CFB, east Mirbat, beached sh, L = 7.4 mm. Figures 33, 34. *S. deburghi*, Western Australia, L = 14.6 mm, CFB. Figures 35, 36. *S. cincta*, holotype MNHN, Noumea, New Caledonia, 10 m, L = 4.2 mm. Figures 37–43. *S. peterbonuttii*. Figs. 37–42: east Mirbat, beached sh, L = 8.6 mm, 8.7 mm, 8.8 mm, CFB. Fig. 43: live spm, east Mirbat, 3–6 m, CJR.

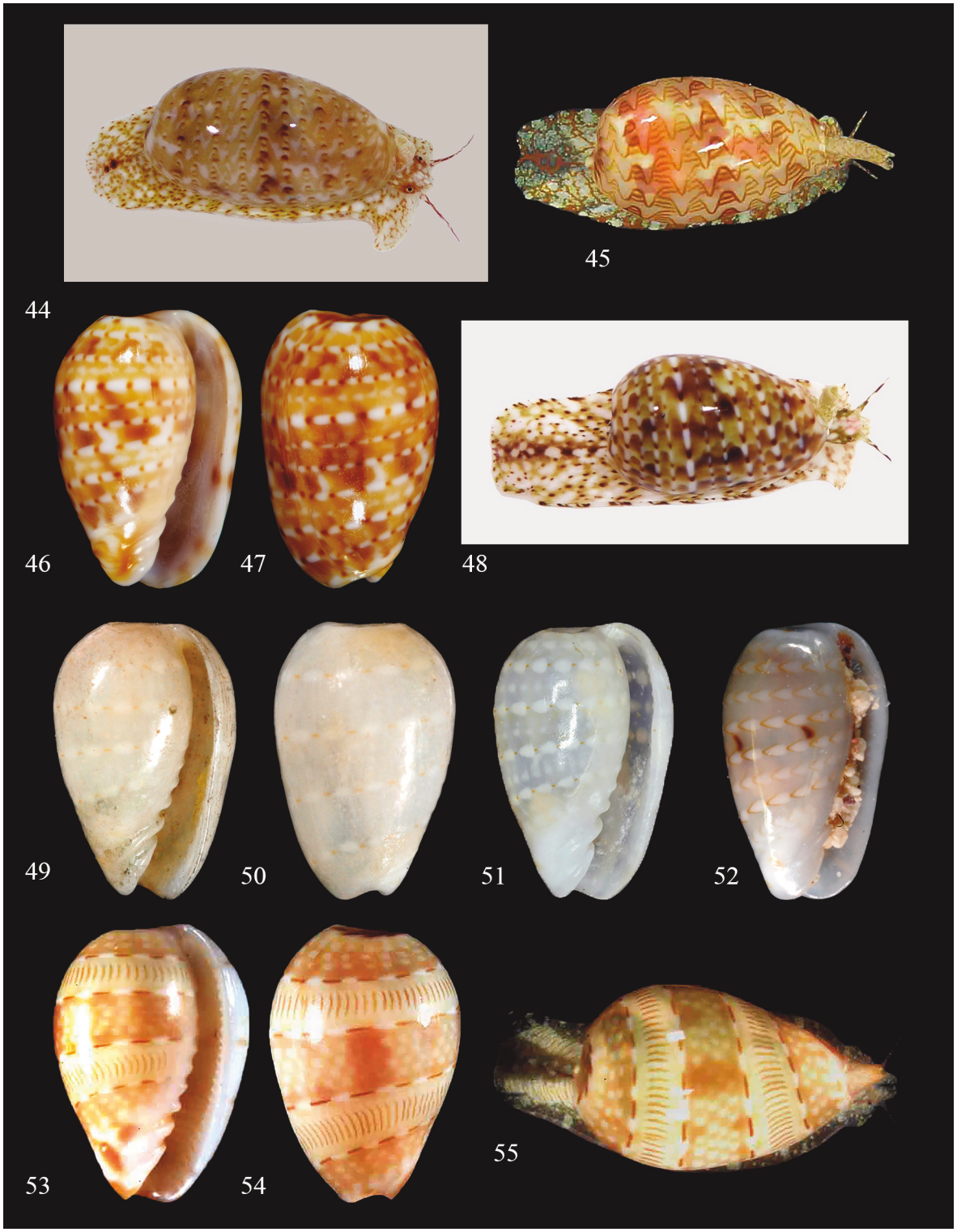


Figure 44. *Sagittalia* sp. A, live spm, Mirbat, 20–35 m, CJR. Figure 45. *S.* cf. *fluctuata* (C.B. Adams, 1850), live spm, San Blas Islands, Caribbean Panama, CTMC. Figures 46–48: *S. masirana*. Figs. 46, 47: Mirbat, 20-35 m, L = 9.3 mm, CJR. Fig. 48: live spm, Mirbat, 20–35 m, CJR. Figures 49–52. *S. catenata.* Figs. 49, 50: holotype NHMUK 1998075, "Mus. Montagu, British", L = 4.8 mm. Fig. 51: alleged syntype, Museum Lyons, NMW, "Cornwall", L = 4.34 mm. Fig. 52: La Blanquilla, Islas Sotavento, Venezuela, L = 4 mm, CAW. Figs. 53–54: *S. pulcherrima*, Aruba, 70 m, L = 7 mm, CTMC. Fig. 55: *S. pulcherrima*, live spm.

DISCUSSION

Species diversity and patterns disparity of Sagittalia *in the Dhofar*

The seven cystiscid species from the Dhofar revised above are sharing several features allowing to accept them without reserve in our new genus *Sagittalia*: principally the medium sized to long siphon, the animal chromatism with small red-brown stains or venules associated to more or less large and dispersed white spots or patches, the shell decoration made of axial wavy lines or of derived spiral patterns with rows of dark dots or of alternate dark and white dashes, or with dark spiral bands. In fact, the local assemblage of *Sagittalia* species from the Dhofar is giving a pretty good representation of the phenetic disparity prevailing more generally in this genus, even if it does not resolve the genus limits by itself.

To recognize species groups of closely related species in this local assemblage is less evident. For instance, *Sagittalia anapaulae* n. sp. and *S. willeminae* n. sp. resemble each other closely for their shell features, principally their quite produced protoconch, flat top with conspicuous dark spot delimited by lower suture, spiral row of dark spots on the shoulder, and similar wavy axial decoration on the rest of the last whorl. They can be considered as twin species. On the other hand, *Sagittalia masirana* presents shell features similar to that of *S. anapaulae* n. sp. and *S. willeminae* n. sp. for the flat top of its shell with conspicuous round dark spot delimited by lower suture, and spiral row of dark spots on the shoulder, but the rest of its shell decoration is deeply differing from that of the couple *S. anapaulae* n. sp./*S. willeminae* n. sp., with a pattern of spiral rows composed of alternated white and dark dashes, on a yellow-beige ground with diluted axial brownish flames. Moreover, the foot chromatism of *S. masirana* is noticeably differing from that of *S. anapaulae*, showing dispersed white spots and small brown stains on a greenish ground, instead of a honeycomb pattern in *S. anapaulae* n. sp., with brown venules circling polygonal light green patches, and two large club-shaped marks on each side of the posterior part of the metapodium. The animal chromatism of *S. masirana* proves to be very similar with that of *Sagittalia* sp. A, above all due to the same original foot chromatism, and homologous chromatism pattern for the head, tentacles and siphon, the greenish parts of *S. masirana* being replaced by reddish parts in *Sagittalia* sp. A. This animal chromatism pattern proves to be uncommon in the genus *Sagittalia* but it presents also the basic ingredients developed in all the animal chromatism forms observed in the genus. This animal chromatism pattern could be considered either like a derived feature shared by a limited number of species from the Arabian Sea, or like an ancestral feature conserved in a panchronic lineage. This cannot be resolved in the frame of this study due to insufficient data and tools at disposal.

On the other hand, *S. masirana* and *Sagittalia* sp. A are deeply differing for their shell morphology (swollen oval-square outline with flat top in *S. masirana*, slender oval outline with rostrate top in *Sagittalia* sp. A) and for their shell decoration, despite sharing spiral rows of alternate white and dark marks on a flamed ground (diffuse brown patches in *S. masirana*, alternate series of light-mustard and white axial zig zag narrow bands in *Sagittalia* sp. A). The different shell top patterns found in these two species do not give an evident indication about their degree of relationship, in the same way as the fact of sharing the same structure of spiral decoration, because these derived features probably appeared on several times in various lineages from ancestral patterns of bulged/flat shell top and of axial zig zag decoration (see below about the fossil *Sagittalia* fauna). However, the most likely hypothesis from our point of view is that *S. masirana* and *Sagittalia* sp. A have a common ancestor with the same animal chromatism of dispersed small white and brown spots on the foot, a wavy axial shell decoration, and most probably a bulged or a flat top, as the morphological evolution from a bulged/flat top to a rostrate top looks to be a more practicable architectural change than the opposite process (about this, see Thomson, 1917).

The three other *Sagittalia* species from the Dhofar with rostrate shell top seems to be closely related, even if not in direct line, and they present a demonstrative series of the successive stages driving from a zig zag shell decoration pattern to a spiral banded decoration, from basic zig zag axial pattern for *S. anapaulae*, to punctuate pattern (both axially and spirally oriented) in *S. vickydobsonae* n. sp., and to spiral banded pattern (over dilute and disorganized axial zig zag lines) in *S. peterbonuttii*.

The occurrence of such a coherent evolutionary series in the Dhofar is reinforcing the hypothesis of a transformation process of the shell decoration appearing in various lineages across time.

Diversification process and "characters hierarchy" in Sagittalia

The variable combination of three main categories of discriminatory features (flat or rostrate shell top, axial zig zag decoration or derived patterns, striped or punctuate animal chromatism) in the assemblage of *Sagittalia* species observed in the Dhofar is posing puzzling problems of interpretation, but all these concurrent features have probably not the same signification and weight from an evolutionary and phyletic point of view. So, a better understanding of the phyletic aspects and of the evolutionary processes at work in this fauna is probably requiring an overview on its documented history and on the general pattern of phenetic disparity prevailing in the Recent.

The wavy ornated cystiscids documented from the mid-Eocene of France (Lutetian) is characterized by Le Renard & van Nieulande (1985), through few contrasted species: *Gibberula vittata* (Edwards, 1854) (idem, fig. 18) with a quite high triangular spire, a produced bulged protoconch, and an axial scale-shaped shell decoration 10 rows of left-oriented scales); another individual (idem: fig. 19) is also named as "*G. vittata*", but it clearly belongs to a different species, characterized by a low triangular spire, a wide and low lenticular protoconch, and a zig zag ornated shell decoration with very angled arrow heads arranged as an irregular combination of lightning bolts sketches (5 to 7 unequal left-oriented arrow heads in each axial figure, not organized in spiral rows); *G. constantinensis* Le Renard & van Nieulande, 1985 (idem: fig. 20) also with a low triangular protoconch but with a small narrow protoconch, and a punctuated shell decoration of 10 spiral rows of dots); *G. prunicallosa* Le Renard et van Nieulande, 1985 (idem: fig. 22) with a domed spire and quite wide teat-like protoconch, and a shell decoration of 10 narrow spiral bands.

In a nut, these four mid-Eocene species present two types of spire morphology: three of them have quite high to low triangular spire, and another species has a domed spire with teat-like protoconch. Naturally, this documentation is not exhaustive and many other *Gibberula*-looking species with zig zag decoration or derived pattern did surely occur, in the mid-Eocene of France and moreover in the adjacent Tethys Sea and other oceanic fields. So, we cannot be sure at all that this limited mid-Eocene fauna from northwestern France is really representative of the shell disparity prevailing at that time among the zig zag ornated *Gibberula*-looking species and their derived forms. However, we observe that any triangular spire is not represented in the analogous Recent fauna, whereas domed spire are quite common, besides flat tops and rostrate tops, both looking as derived from a bulged/domed top. We note that rostrate tops were common in the rest of the *Gibberula*-looking fauna from the French mid-Eocene, but apparently only in species deprived of shell decoration, and their shell morphology series are suggesting that these rostrate forms were derived from domed tops better than from triangular tops (Le Renard & van Nieulande, 1985: Figs. 1–6). We observe on the contrary that the main shell decoration patterns observed in the Recent fauna of zig zag ornated cystiscids (wavy pattern, punctuate pattern and banded pattern) were already all represented with evidence since the mid-Eocene. We note however that *Gibberula*-looking species deprived of any kind of colour decoration and that prove to be closely allied phyletically with the zig zag decorated species might occur as well in the mid-Eocene, as a result from a process of decoration loss (either directly from a zig zag decoration stage or from a banded stage), but this would not be detectable in the fossil material. In the same way, such undecorated forms of *Sagittalia* might occur in the Recent, but they would remain undetected without paying a careful attention to live populations, especially concerning the length of the siphon and the animal chromatism.

Despite the limited documentation at hand, two evolutionary data can be stated about the zig zag ornated cystiscid fauna: the disappearing of the triangular-shaped spire in the Recent and the early diversification of the zig zag pattern and derived forms as far as the Eocene. From this situation, the Recent fauna looks to be very conservative. Along an evolutionary trip of 45 mya, the modern genus *Sagittalia* gave up the triangular spire shape and it established frequent evolution towards the rostrate spire shape, beside the old domed spire shape,

often associated to a more or less produced teat-like protoconch. And after all this time, the shell decoration patterns in *Sagittalia* remain basically the same. Otherwise, the phyletic relationships prevailing among the Recent *Sagittalia* species remain unclear. The most evident thing is the evolution from zig zag decoration patterns to punctuate patterns, and in spiral patterns; this is confirmed by the ontological development of juvenile shells of punctuated or banded forms, which show always a zig zag draft on their very early shell whorls (personal data). The evolution from domed spire to flat top or to rostrate spire seems to be also the usual trend in the Recent, but probably all the present *Sagittalia* rostrate species are not recently derived from ancestry with domed or flat top, as rostrate lineages could as well be established since long. Methodical study of the fossil occurrences from the Eocene of other regions, but also from Miocene and Pliocene beds, will help to a better understanding of this question, as well as a deeper biochemical documentation about the Recent *Sagittalia* fauna could be.

The phyletic unity prevailing in the Recent *Sagittalia* fauna seems to be evidenced mostly by our present study, however with three important reserves dealing with the "limits of the genus":

1° - cryptic *Sagittalia* species might occur as "undecorated shell pattern" (see above) and they remain to be detected,

2° - several zig zag decorated *Gibberula*-like radiations might have deeply diverged in time, saving similar phenetic features but resulting in deep phylogenetic gaps, what would make our new genus a bit artificial for the Recent,

3° - several species or species groups with "reduced wavy shell decoration" or punctuate shell decoration placed with reserve in *Sagittalia* (such as *S. thomensis* from São Tomé) or provisionally not proposed in this genus (such as *Gibberula agricola* from Margarita Island, Venezuela, the couple *G. lucia*/*G. almadiensis* from Senegal, or the couple *G. quemeneri*/*G. nebulosa* from New Caledonia) deserve special studies in view to evidence possible brother-genera of *Sagittalia*. We note that the unequal arrow heads decoration found in the couple *G. lucia*/*G. almadiensis* and over all in the couple *G. quemeneri*/*G. nebulosa* show some resemblance with the pattern found in *G*. non-*vittata* from the French Lutetian.

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