ABOUT *VOLVARINA EUMORPHA* (MELVILL, 1906) (MARGINELLIDAE) AND CLOSELY RELATED SPECIES, WITH DESCRIPTION OF A NEW SPECIES FROM THE GULF OF OMAN

FRANCK BOYER¹ & WALTER RENDA²

¹4, impasse Pasquier, 30190 – Garrigues Sainte Eulalie, France ²Via Bologna 18/A, 87032 – Amantea (Cosenza), Italy

Abstract Volvarina eumorpha (Melvill, 1906) is redescribed and its distribution revised to range from the Persian Gulf to Dhofar at upper reef level (6–35m), but not reaching the shallow infralittoral. V. eumorpha is thought to belong to a species group restricted to the far Western Indian Ocean and aggregating two other species: V. dekkeri sp. nov. described from Muscat as sibling species of V. eumorpha and restricted to the upper infralittoral of the southern Gulf of Oman, and V. kilwaensis Boyer, 2015 known from southern Kenya to Kilwa Island in southern Tanzania. Some extant and Late Miocene species from the Atlantic and Mediterranean fields are interpreted as brother-groups separated from the V. eumorpha species group since at least the closure of the Western Tethys Seaway; the final closure being dated from about 14 Ma/13,8 Ma (Langhian, Mid-Miocene).

Key words Volvarina, Marginellidae, Gulf of Oman, Masirah, Dhofar, relict species, Tethyan relationship.

INTRODUCTION

Volvarina species in the Indian Ocean remain poorly studied and the principal published works, produced only in recent years by Boyer (2015a, 2015b, 2017 & 2018), tackle only a limited number of species groups and localities. These works, however, brought to light an unsuspected species diversity, combining species groups apparently restricted to certain geographic areas of the Indian Ocean, together with species groups that suggest affinities with the Atlantic fauna (Boyer, ibid.).

Additional material and data obtained since the previous revision of *V. eumorpha* (Melvill, 1906) (Boyer, 2017), hitherto documented its distribution from the Mekran Coast (southeastern Iran) down to Masirah Island (eastern Oman), lead to this revision, also prompting the assessment of the affinities of this species in the context of the Indian Ocean, as well as the Atlantic.

MATERIAL & METHODS

Apart from the type specimens documented from public institutions (MNHN and NHM) the material examined is mainly based on the personal collection of the first author (Muscat, Masirah, Kenya-Tanzania, northwestern Africa and Brazil), the loan of two lots from the Musandam Peninsula (UAE & Oman) by Henk Dekker, two lots from Dhofar (southern Oman) by Sandro

Corresponding author : franck.boyer7@orange.fr

Gori and Jose Rosado, and three lots from Muscat belonging to the collections de Morgan and Maindron in the Paris Museum. Data about the animal's chromatism were obtained for *V. eumorpha*, for its sibling species from the Gulf of Oman and for the syntopic *V. arabica* Boyer, 2017. Data about the radulae were obtained for the sibling species of *V. eumorpha* and for the syntopic *V. arabica* as well.

Photographic credits are detailed in the Acknowledgements.

Acronyms & Abbreviations

MNHN:	Muséum national d'Histoire naturelle,
	Paris
NHM:	Natural History Museum, London
ZMA:	Zoological Museum Amsterdam
CFB:	collection Franck Boyer
CWR:	collection Walter Renda
CHD:	collection Henk Dekker
spm:	specimen
sĥ:	shell
ad:	adult
juv:	juvenile

Systematics

Superfamily: Muricoidea Rafinesque, 1815 Family: Marginellidae Fleming, 1828 Genus: *Volvarina* Hinds, 1844

Type species: *Marginella nitida* Hinds, 1844=*Voluta mitrella* Risso, 1826. Subsequent designation by Redfield, 1870.

Volvarina eumorpha (Melvill, 1906) (Figs 1–12, 29).

Marginella (Volvaria) eumorpha Melvill, 1906: 76–77, pl. 8, fig. 19.

Type material Lectotype (Figs 2–3), L= 8.85mm, and paralectotype (Fig. 4), L=8.50mm, here designed, NHM Reg. Nb. 1906.6.13.10–11, L=8.85mm, "Persian Gulf, Gulf of Oman, Maskat. 15 fathoms".

Other material examined 1 sh, Charbar, Iran, 20 fms (Figs 5–6); 1 sh, Masirah North, Oman, 10m (Figs 7–8); 3 juv sh +1 ad fragment, Masirah North, 11–17m; 1 ad spm +1 ad sh, Masirah North, 20m (Figs 9–10); 1 ad spm, Mursays, Sur Bay, West Masirah, 6m (Figs 11–12) CFB . 2 spm +2 juv spm, Mirbat, 35m Coll. Sandro Gori. 1 spm, East Mirbat, 26–32m (Fig. 29) Coll. Jose Rosado.

Original description

"M. testa nitidissima, laevigata, polita, oblongocylindrica, albida vel pallide stramineo-brunnea, subpellucida anfractibus 5, quorum apicales conici, apice ipso magno, omnino laevissimis, ultimo spiraliter obscure trizonato, zonis rufulis, apertura oblonga, labro incrassato, nitido, simplice, columella obliqua, 4-plicata. Long. 9, lat. 4mm".

Complementary description

Shell (lectotype, Figs 2–3): slender fusiform outline, high subconical spire, moderately produced lenticular protoconch, rounded base; aperture narrowed in its posterior half-part, widened in its anterior half-part; rather flexuous labrum with a slope discontinuity forming a flat spot in its posterior third part, outer margin moderately wide and thickened; four subvertical columellar plaits, quite distant, decreasing in size from the lower one to the upper one, the first plait strong, long and very sinuous, the three next ones very thin and poorly arched. Ground colour subhyaline whitish, with two diffuse light pinky spiral bands suggested at the lower and upper third steps of the last whorl.

Shell variability (Figs 2–12): the shell outline is poorly variable, the protoconch can be less produced (Figs 9–10), the outline more oval, the spire more massive and the labrum more angular (Figs 9–12). In fresh specimens (Figs 9–12), a pattern of three diffuse pink spiral bands can be more or less marked, on a whitish (Figs 11–12) or flesh coloured background (Figs 9–10, 29), the middle band being the widest and the subsutural band being the most elusive.

Animal (Fig. 29) Type 2 animal sensu Coovert & Coovert (1995); the general background colour is opaque milky white, a cluster of purplish-brown dots is scattered over the anterior part of the propodium and another cluster is scattered over the posterior part of the metapodium, the siphon is more densely dotted, whereas the tentacles are marked by few spaced dots; visible through the light pink shell, the internal mantle shows clusters of darker flecks and few scattered white dots; the subhyaline external mantle shows few scattered purplish-brown dots on its lateral sides and some larger purple-brown flecks along the fringe, interspaced by few white dots.

Radula Unknown.

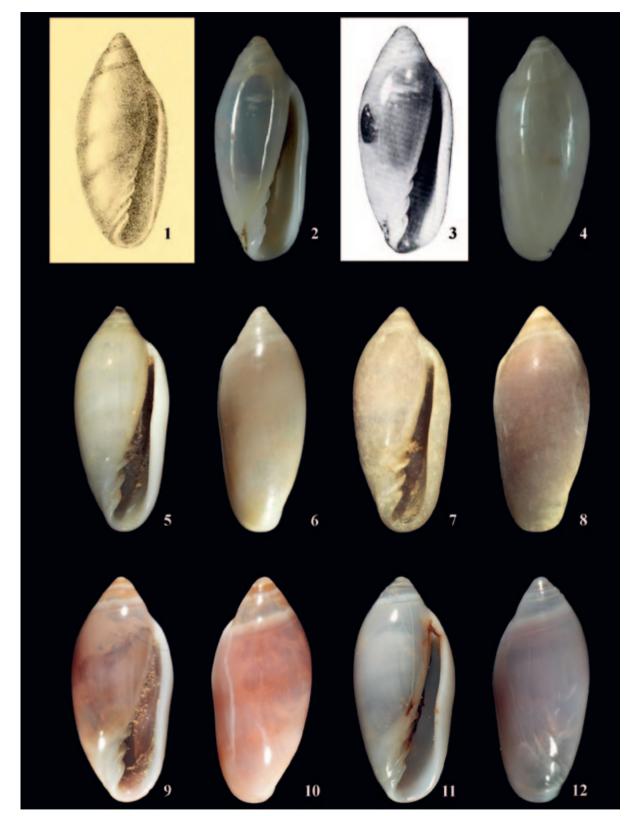
Type locality "Persian Gulf, Gulf of Oman, Maskat. 15 fathoms".

Distribution V. eumorpha is only known by a very limited number of specimens from the Gulf of Oman, from Masirah and from Dhofar and Melvill (1906: 77) reports it in the Persian Gulf. Its documented bathymetric distribution (live specimens) ranges from 6 to 35m, the upper level being reported from a very protected place and looking to constitute an exceptional occurrence. Despite heavy exploration of the littoral environment in northern Oman (R. Moolenbeek, comm. pers.), Masirah Island (obs. pers.) and Dhofar (S. Gori, J. Rosado and obs. pers.), the species has never been collected live in the five first meters or as a beached shell.

Habitat Off Masirah, live specimens were dredged on a silty-detritic bottom in a very protected bay (6m) as well as on a sandy-rubble bottom in open water (20m), whereas in Dhofar (Mirbat) the live specimens were collected by brushing on hard and mixed bottoms (26–35m).

Remarks V. eumorpha seems to be scarce, at least at the upper reef levels. However, these levels might just correspond to the upper limit of the bathymetric distribution of the species, and possibly the principal population of *V. eumorpha* may thrive at lower reef levels.

VOLVARINA EUMORPHA AND CLOSELY RELATED SPECIES 191



Figures 1–16 1 type figure of *Marginella (Volvaria) eumorpha* Melvill, 1906 (plate 8, fig. 19). 2 *Volvarina eumorpha*, lectotype NHM, here designed, Reg. Nb. 1906.6.13.10, L=8.85mm, "Persian Gulf, Gulf of Oman, Maskat. 15 fathoms". 3 *V. eumorpha*, same specimen pictured in Kaicher Card Nb 2636. 4 *V. eumorpha*, paralectotype NHM, here designed, Reg. Nb. 1906.6.13.11, L=8.50mm, same locality. **5–6** *V. eumorpha*, Charbar, Iran, 20 fms, L=10.1mm, CFB. **7–8** *V. eumorpha*, Masirah North, 10m, L=10.2mm, CFB. **9–10** *V. eumorpha*, Masirah NNE, 20m, L=8.3mm, CFB. **11–12** *V. eumorpha*, Mursays, Sur Bay, Masirah, 6m, L=7.5mm, CFB.

192 F BOYER & W RENDA

In the Indian Ocean *V. eumorpha* differs well from the other *Volvarina* groups documented until now (Boyer, 2015a 2015b, 2017 & 2018), only matching a species described recently from southern Tanzania as *V. kilwaensis* Boyer, 2015 and a sibling species restricted to the littoral of northern Oman and described below. Some fossil and Recent species distributed in the Atlantic suggest more distant relationships with *V. eumorpha* and its species group from the Indian Ocean. The point is tackled in the Discussion section.

Volvarina dekkeri sp. nov. (Figs 13–20, 30, 39–43)

Zoobank new taxon number: urn:lsid:zoobank.org:act: 85B5B3EC-317B-442D-A128-A879F60E4611.

Holotype MNHN-IM-2000–36520 (Figs 13–14, 39–42), L=9.7mm.

Paratypes 1 MNHN, L=8.0mm; 1 CFB, L=8.1mm; 1 CWR, L=9.4mm; 1 CHD, L=8.7mm; all from "Mascate" (ex-collection de Morgan).

Other material examined Volvarina dekkeri sp. nov. 13 spm, "Mascate", old collection, L=8.2–9.1mm (Figs 15–16) CFB. 1 spm, Fujeirah, Al Kubus, EAU, Gulf of Oman, L=9.1mm (Figs 17–18); 1 spm, 1 sh, Limah, Musandam, Feb. 2004, L=8.7mm (Figs 19–20) CHD.

V. arabica Boyer, 2015, for comparison as sympatric material. MNHN, holotype, Mursays, Sur Bay, Masirah, low tide, 16.5mm (Figs 31–32). 15 spm, 1 juv spm, L=9.9–12mm, "Mascate" MNHN, coll. de Morgan. 5 spm, L=9.9–12mm, "Mascate" MNHN, coll. Maindron. 35 spm, "Mascate", L=9.5–14mm (Figs 33–38) CFB, old collection. 15 spm as "*M. obscura* Reeve, Muscat, Oman, low tide in sand near rocky reef", L=13.3–17mm. CFB, ex-P. Clover. 8 spm, Muscat, L=11.6–13.2mm CFB, self-sampling 2013.

Description

Shell (Figs 13–14, 39–42): slender-oblong outline, high ogival (gothic arch-shaped) spire, rounded base; low and wide, lenticular protoconch, blunt apex, high ogival spire of three whorls, wide whitish deposit on the suture and visible false suture on orange background; vertical and almost straight outer lip, enveloping internal border in its central part, with a receding shoulder and a slope discontinuity forming a flat spot in its posterior third part; outer margin faintly

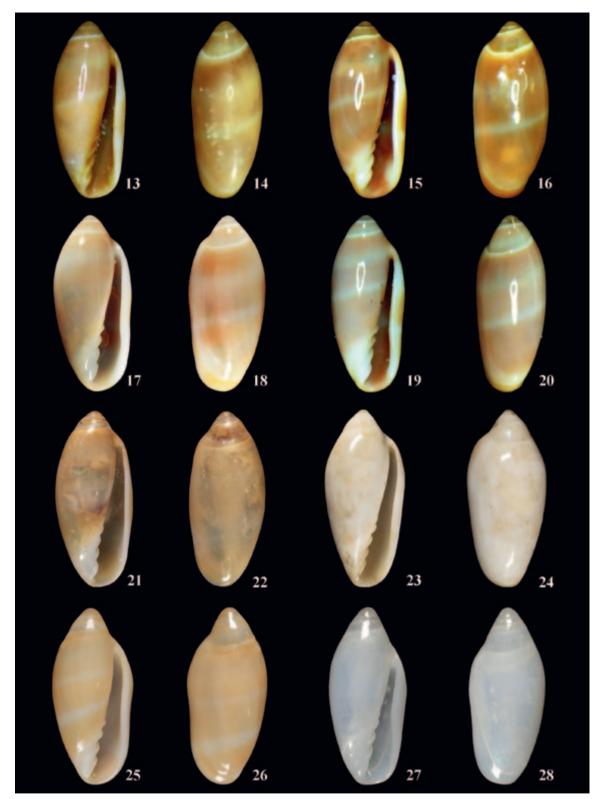
thickened, rather wide in its central and its lowest parts, much narrowing in its upper part; very narrow aperture in its upper half-part, moderately widening towards the base; four columellar plaits, quite short and oblique, the first plait being faintly sinuous and much shorter than the second plait; background colour of the shell lighttan, with three wide, spiral orange-brown bands on the last whorl, spreading respectively on the ventral side just below the suture, just above the medium part of the whorl, and just below the medium part of the whorl down to the level of the upper columellar plait; these spiral bands leave clearer narrow gaps, the most narrow and conspicuous being situated at the medium part of the whorl, the larger one being situated at the base of the shell, and the medium-sized and more diffuse one being situated at the level of the anal canal; the ventral side of the outer lip is whitish, its dorsal side is orange tinted, this shade overflowing towards the ventral side in the central part of the labrum.

Shell variability (Figs 15–20): The background colour is creamy-white to light-tan, the colour bands are pinkish to orange-brown, the height of the spire may be slightly shorter, the labrum may be slightly sinuous, but on the whole the species must be considered as poorly variable.

Animal (Fig. 30, from two field sketches and notes of R. Moolenbeek): Type 2 animal, sensu Coovert & Coovert (1995); background colour light flesh; foot shows very few white cloudshaped marks, some red-purple spots more concentrated on the most anterior and the most posterior parts; few red-purple dashes and small spots on the siphon and on the head; few white cloud-shaped marks on the subtransparent outer mantle; the inner mantle is not visible through the shell.

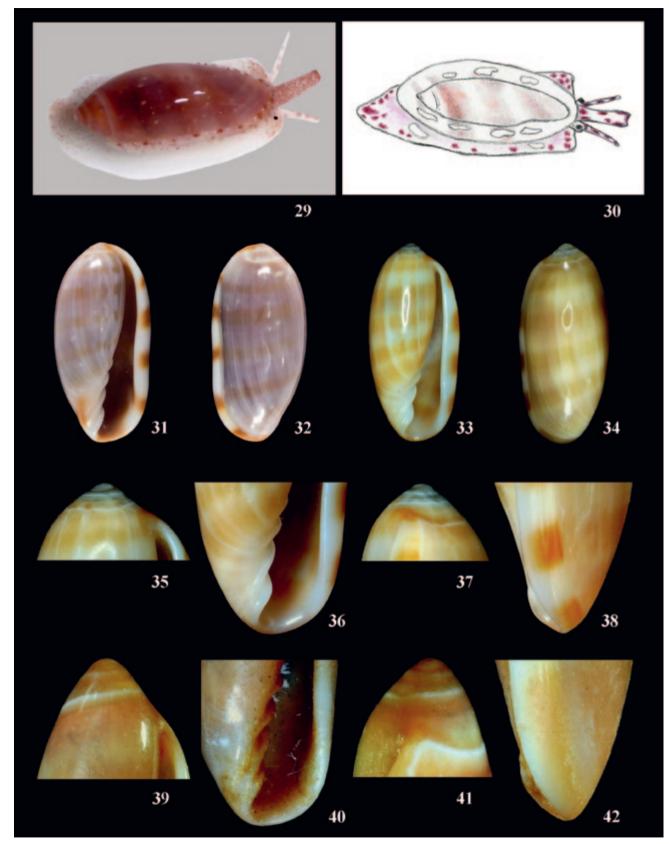
Radula (Fig. 43): From the drawing of a radula studied by Coovert & Coovert (1990: 53–54), extracted from a specimen of the undetermined species sp. O-1 collected at low tide in Muscat and said to be "closely related to *obscura* of authors" (our *V. arabica*) but "differing in smaller shell size and different color as well as other features". In the context of this locality, this sp. O-1 can only be our new species.

Type 6 radula sensu Coovert & Coovert (1990), plate showing a comb-like pattern with relatively few cusps (18–19) with a large central cusp, flanked by some very faint cusps in the central



Figures 13–28 13–14 Volvarina dekkeri sp. nov., holotype MNHN (IM-2000–36520), coll. De Morgan, Mascate, Oman, L=9.7mm. 15–16 : V. dekkeri, Muscat, L=8.6mm, CFB.17–18 V. dekkeri, Fujeirah, Al Kubus, EAU, Gulf of Oman, L=9.1mm, CHD. 19–20 V. dekkeri, Limah, Oman, Gulf of Oman, L=8.7mm, CHD. 21–22 V. kilwaensis Boyer, 2015, holotype MNHN, Kilwa Island, Tanzania, L=8.1mm. 23–24 Marginella parvula var. elongata Locard, 1897, syntype MNHN, "Côtes du Sahara, 175m", L=11mm. 25–26 Volvarina tunicata Boyer, 2000, holotype MNHN, Guarapari, Espirito Santo, 20–25m, L=8.1mm. 27–28 Marginella (Volvaria) serrei Bavay, 1913, syntype MNHN (lot de 14 syntypes), Bahia, Brésil, 5mm.

194 F BOYER & W RENDA



Figures 29–42 29 *Volvarina eumorpha*, East Mirbat, 26–32m, live specimen, rec. and ph. Jose Rosado, Nov. 2016. **30** *Volvarina dekkeri*, Muscat, from field sketches by Robert Moolenbeek. **31–32** *V. arabica* Boyer, 2015, holotype MNHN, Mursays, Sur Bay, Masirah Island, Oman, L=16.5mm. **33–34** *V. arabica*, Muscat, Oman, L=11.7mm, CFB. **35–38** details of the shell morphology **39–42** *V. dekkeri*, holotype.

third part, and medium-sized cusps towards the outer third parts. This peculiar pattern among the "comblike radulae" is designated by Coovert & Coovert (1990) as representative of the Caribbean "*rubella* group", in which the shells are said to have a short spire. In the present case, *V. dekkeri* must be considered as having a rather high spire, so the unity of this "*rubella* group" deserves to be verified and the radula represented by *V. dekkeri* might be as well considered as a convergence case.

Type locality Muscat, Oman.

Distribution Only known from southern part of the Gulf of Oman from Muscat to the Musandam Peninsula. Not recorded from the Persian Gulf, and not collected in Masirah (Boyer, 2017) or in Dhofar waters (pers. obs).

Habitat Under stones and boulders, at low tide and in very shallow waters.

Derivation of name From Henk Dekker (ZMA), who devoted to extensive sampling duties along the coasts of the Arabian Region, and who kindly loaned material for various studies.

Remarks Volvarina dekkeri sp. nov. differs from the allopatric V. eumorpha by several subtle but constant shell characters : the outline is more oval, the spire is more ogival and the apex is more pointed; the first columellar plait is shorter and less sinuous; the pattern is made of three wide orange-tan colour bands separated by two conspicuous narrow intervals, versus three diffuse pinkish bands separated by wider intervals of progressive dilution in V. eumorpha; an orange spot is spreading to the mid-part of the ventral side of the labrum, versus limited to the lateral side of the lip in V. eumorpha. The two species differ in their respective animal chromatism: the foot, the siphon and the head having a subhyalinous fleshy background decorated with scattered purplish dots in V. dekkeri, versus a milkywhite background decorated with concentrations of purplish-brown dots on the front-part of the propodium, the distal part of the metapodium and the entire siphon, and no purplish dots spreading along the lateral sides of the foot in V. eumorpha.

Volvarina dekkeri is collected in syntopy with *V. arabica* Boyer, 2015 in Muscat, in shallow water,

under stones and boulders (R. Moolenbeek, pers. comm.). Despite a superficial resemblance in shell between both species when a population of V. dekkeri (L=8.0-9.7mm) is cohabiting with a small-sized population of light brown-shelled specimens of V. arabica (L=9.5–14mm), evident differences are revealed when comparing the shells feature by feature (Figs 35-42). The difference occurring in the animal chromatism of both species is no less evident, as in its main distribution range (pers. obs: from Muscat down to Masirah Island) the soft parts of V. arabica have a general flesh colour background striped by a network of radiating arachnid white veins (Boyer, 2015a: fig. 5). V. dekkeri differs also noticeably from V. arabica by the shape of its radular plates (Figs 43-44), the latter presenting the most usual "comblike pattern" with a less prominent central cusp and higher number of subequal cusps, whereas the radular plate of V. dekkeri is closely matching the "rubella pattern" which presents generally a fewer number of cusps, with a big central one separated by a gap from the lateral ones. However, due to the diversity of shell patterns and animal chromatisms documented in the species presenting the "rubella radular pattern" (pers. obs.), this feature is not evidenced as an homologous character in each case and it might prove to be occasionally a convergent feature occurring in distant lineages.

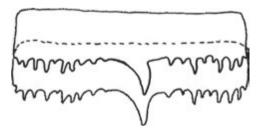


Figure 43 Radula of *Volvarina dekkeri*, as "*Volvarina sp*. O-1" from Muscat, Oman, in Coovert & Coovert, 1990, p. 53–54, fig. 124, radula no. 282, radula width: 0.395mm, shell length: 11.97mm.



Figure 44 Radula of *V. arabica*, as "*Volvarina obscura* of authors" from Muscat, Oman, in Coovert & Coovert, 1990, p. 52–53, fig. 120, radula no. 058, radula width: 0.510mm, shell length: 16.72mm.

V. dekkeri and V. arabica seem to be no more closely related to each other than to other congeners. On the ground of its distinctive animal chromatism, V. arabica does not seem to have close relatives in the Atlantic or the Indian Ocean, except a species designed as Volvarina sp, collected in Indonesia and illustrated live on the website https://www.meerwasser-lexikon.de/ tiere/4896_Volvarina_sp.htm by four photos taken in a seawater tank. This Volvarina sp. shows important similarities with V. arabica, including the same pattern of whitish arachnid veins on the soft parts (even if less densely arranged), with few light-brown patches on the center of the foot, and the oblong shell decorated by six orange spiral bands on a light-tan hyalinous background, the two upper bands more or less merge together. V arabica and this Indonesian Volvarina sp. must be considered as constituting a small isolated "V. arabica group" now ranging in discontinuous conditions at the two tips of Northern Indian Ocean.

DISCUSSION

V. eumorpha and V. dekkeri can be considered as sibling or near-sibling species, and they seem to have diverged towards different bathymetric levels from a close common ancestor. No particularly close relative to them is known from the Recent in the Indo-Pacific waters, except V. kilwaensis Boyer, 2015 (Figs 21-22), described from southern Tanzania (Kilwa Island) and also reported from shallow waters of southern Kenya and of Zanzibar (Boyer, 2015a: 23). V. kilwaensis shows more affinities with V. dekkeri on comparing the strongly oval outline and ogival spire, but it compares closely with V. eumorpha with its rather long and sinuous first columellar plait and the diffuse colour decoration of its shell. In any case, these three species must be considered as forming a "V. eumorpha species group", quite isolated in Far-Western Indian Ocean.

This *V. eumorpha* species group presents close similarities with some living and fossil species of the Atlantic area. Among the Recent species from this area, *V. attenuata* (Reeve, 1865) and some other undescribed species from the circalittoral of northwest Africa (Western Sahara: coll. Franco Gubbioli, coll. Jose Maria Hernandez and CFB: 60–100m; Mauritania and Senegal: CFB: 80–100m) show close affinities with *V. eumorpha* for their slender subconical shell outline. That is especially the case for *V. parvula elongata* (Locard, 1897) (Figs 23–24), collected at 175m off Western Sahara and considered as a variety of *V. attenuata* (Gofas, 1989: 161–166): this phenon differs from *V. eumorpha* mostly by its shorter spire, its more inflated last whorl, its shorter first columellar plait and the occurrence of a tiny fifth plait. Several other species from the Lusitanian Province, such as *V. mitrella* (Risso, 1826) from the infralittoral of Mediterranean or *V. ptychasthena* Gofas, 1989 from the upper bathyal of the Açores, suggest also some affinities with *V. eumorpha*, but with less evidence.

Another case of close shell resemblance occurs between V. dekkeri and the species V. tunicata Boyer, 2000 (Figs 25-26), described from southern Brazil (Guarapari, Espirito Santo, at 20-25m). V. tunicata has a slightly higher spire than V. dekkeri, the outline of the stouter shell is more biconical than subcylindrical, the suture is not underlined by a wide whitish spiral band, the two most conspicuous colour gaps are located in a lower position, and no orange shading overflows on the ventral side of the labrum. However, for all the other features, the shells look identical in both species, especially concerning the shape of the labrum and of the columellar plaits, but also the general outline of the shell and the general pattern of the colour decoration. The species V. serrei (Bavay, 1913) (Figs 27–28), belonging to the same group as V. tunicata and inhabiting the intertropical zone of Brazil (the type locality is Bahia), also shows very similar traits compared to V. dekkeri, but it differs principally by a more pronounced spire, a thinner and shorter first columellar plait, and a fully white or light-tan colour background. Despite the long distance between the respective ranges of these species, a case of morphologic/ chromatic convergence seems to be dubious, and the V. serrei species group must be considered with high probability as closely related to the V. eumorpha species group.

Among the fossil references, the species most resembling *V. eumorpha* seems to be a phenon illustrated as *V. oblongata* (Sacco, 1980) by Sosso *et al.* (2015: fig. 3M) from the Tortonian (Upper Miocene) of northeast Italy. The identity of *V. oblongata* remains not well-characterized and the authors seem generally to refer to a rather eclectic assemblage of species : for instance Sosso *et al.* referred the identity of *V. oblongata* to three different species (ibid: figs 3M; 3-N-O–P; 3Q).

Among these species, *V*. cf. *oblongata* pictured in fig. 3M greatly resembles *V. eumorpha* as well as *V. attenuata* despite its more vertical and thinner columellar plaits. *V.* cf. *oblongata* shares its very slender near-biconical outline with *V. attenuata*, as well as the ogival spire observed in *V. dekkeri* and in *V. kilwaensis*, the only difference is its more vertical columellar plaits, the first one being very straight.

The Recent V. attenuata species group and V. serrei species group as well as the fossil V. oblongata species group from the Upper Miocene are interpreted as brother-groups separated from the V. eumorpha species group since at least the closure of the Western Tethys Seaway, the final closure is dated from about 13.8 Ma/14 Ma, in the Middle Miocene (Hamon et al., 2013; Bialik et al., 2019). In previous works (Boyer, 2000, 2014, 2015a, 2015b and 2017), the first author tackled several cases of close affinities suggested between Marginellidae species from the Oman (or more widely from northern or western Indian Ocean) and species distributed off West Africa or in the Caribbean. The point of such Tethyan relationships remains under study and it is intended that it be addressed in a following work focusing on the biogeographic affinities of the marginelliform gastropods from the waters of Oman.

ACKNOWLEDGEMENTS

We are indebted to Robert Moolenbeek (ZMA) for giving his sketches and field notes about the marginelliform species he collected in Muscat during his two sampling trips in the place during the years 1990. We are also indebted to Henk Dekker (ZMA) for loaning the marginelliform material that he collected throughout the Arabian Region, specially the lots of *Volvarina dekkeri* here reported from the Musandam Peninsula.

Thanks are also due to Gérard Hervillard (Maisons-Alfort), for help in the field during the sampling trip to Muscat made with the first author in December 2013.

Wa are grateful to Alain Robin (Le Mesnil-Saint-Denis) for the photo of the live *V. arabica* taken at Masirah Island, to Jose Rosado (Maputo) for the photo of the live *V. eumorpha* he collected

off East Mirbat, and to Sandro Gori (Livorno) for the loan of material from Dhofar.

Lastly, we are grateful to the anonymous referee and to the Editor, Anna Holmes, for their helpful review and correction of the manuscript.

The photos of the holotype of *V. arabica, V. kil-waensis, V. parvula elongata, V. tunicata* and *V. ser-rei* were performed by Manuel Caballer (MNHN) on 2016, in the frame of the Project RECOLNAT (ARN-11-INBS-0004).

References

- BIALIK M, MARTIN F, BETZLER C, ZAMMIT R & WALFMANN ND 2019 Two-step closure of the Miocene Indian Ocean Gateway to the Mediterranean. *Scientific Reports* 9 / 8842: 1–10.
- BOYER F 2000 The genus *Volvarina* (Volutacea: Marginellidae) in Brazil. Part 1: Revision of the species described by A. Bavay and closely related species. *Novapex* 1 (2) 35–55.
- BOYER F 2014 Etude du complexe Glabella denticulata (Link, 1807). Xenophora Taxonomy 4 12–29.
- BOYER F 2015a Sur quelques *Volvarina* (Marginellidae) de l'Océan Indien occidental. *Xenophora Taxonomy* **6** 19–31.
- BOYER F 2015b Le groupe *Volvarina angustata* (Sowerby, 1846) dans l'Océan Indien septentrional. *Xenophora Taxonomy* **7** 35–47.
- BOYER F 2017 Révision des Marginellidae du récifal supérieur de l'île de Masirah. *Xenophora Taxonomy*, 17 3–31.
- BOYER F 2018 Révision des gastéropodes marginelliformes dans le récifal supérieur des Maldives. *Xenophora Taxonomy* **21** 23–47.
- COOVERT GA & COOVERT HK 1990 A Study of Marginellidae Radulae. Part I: Type 6 Radula, "Prunum/Volvarina" Type. Marginella Marginalia 8 (1–6) & 9 (1–6) 1–68.
- COOVERT GA & COOVERT HK 1995 Revision of the Supraspecific Classification of the Marginelliform Gastropods. *The Nautilus* **109** (2–3) 43–110.
- GOFAS S[°] 1989 Le genre *Volvarina* (Marginellidae) dans la Méditerranée et l'Atlantique du Nord-Est. *Bollettino Malacologico* **25** (5–8) 159–182.
- HAMON N, SEPULCHRE P, LEFEBVRE V & RAMSTEIN G 2013 The role of eastern Tethys seaway closure in the Middle Miocene Climatic Transition (ca. 14 Ma). *Climate of the Past* **9** 2687–2702.
- Sosso M, BRUNETTI M & DELL'ANGELO B 2015 The family Marginellidae Fleming, 1828 in the Miocene (Tortonian) of South Piedmont (Italy), with the description of three new species. *Archiv für Molluskenkunde* 144 (2) 242–258.