

THE MARGINELLIDAE OF ANGOLA: THE GENUS *GIBBERULA*

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Abstract: The Angolan species of the genus *Gibberula* (Gastropoda, Marginellidae) are reviewed, and five new species are described: *G. cristata*, *G. mimetica*, *G. tantula*, *G. mendacis* and *G. confusa*. The colour patterns of soft parts is described for these and for all previously described Angolan species, and is held to be essential for species recognition.

Résumé: Les espèces angolaises du genre *Gibberula* (Gastropoda, Marginellidae) sont revisées, avec cinq espèces nouvelles: *G. cristata*, *G. mimetica*, *G. tantula*, *G. mendacis* and *G. confusa*. Le polychromatisme des animaux vivants est décrit pour toutes les espèces, en soulignant son importance pour la taxonomie au niveau spécifique.

Resumo: As espécies angolanas do género *Gibberula* (Gastropoda, Marginellidae) são revistas, e cinco espécies novas vem descritas: *G. cristata*, *G. mimetica*, *G. tantula*, *G. mendacis* e *G. confusa*. O policromatismo dos animais vivos vem descrito para todas as espécies, frisando-se a sua importância para a taxonomia a nível específico.

Marginellids are remarkably diverse and successful in most West African littoral environments. There is nevertheless little in common between those, best known, found north of the Gulf of Guinea (mostly Senegal and Mauretania) and those recorded to the south, which will be dealt with herein.

Dautzenberg (1913), Odhner (1923) and Knudsen (1956) have referred to marginellids of this area and described some of the species. The author has observed these species alive and encountered several other hitherto undescribed.

MATERIALS AND METHODS

Material for this study was collected along the entire coastline of Angola (Fig. 1) excepting the Cabinda and Soyo areas, in a survey carried out during the years 1981–1987, jointly with Francisco Fernandes, of Luanda. Material collected by the author, including all holotypes of new species, is deposited in Museum National d'Histoire Naturelle of Paris. Paratypes have been distributed to various Institutions as listed. Relevant material is also in F. Fernandes' private collection.

Collecting

- (1) Infralittoral algal mat (low water mark to 2–3 m) on hard bottoms was sampled by brushing and collecting residue in a 0.5 mm nylon mesh net mounted on a frame.
- (2) Infralittoral soft bottoms (low water to 1.5 m) were sampled with a small dredge with a wire-mesh of 5 mm, mounted on a 2 m handle.
- (3) Deeper environments, down to 120 m, were collected by conventional dredging from a small boat.

Residues were immediately sieved in sea water (mesh 5 mm, 1 mm and 0.35 mm); the smaller fractions were placed in a bucket with plenty of sea water and observed for the small molluscs emerging. Living animals were observed, and drawings made of all the species.

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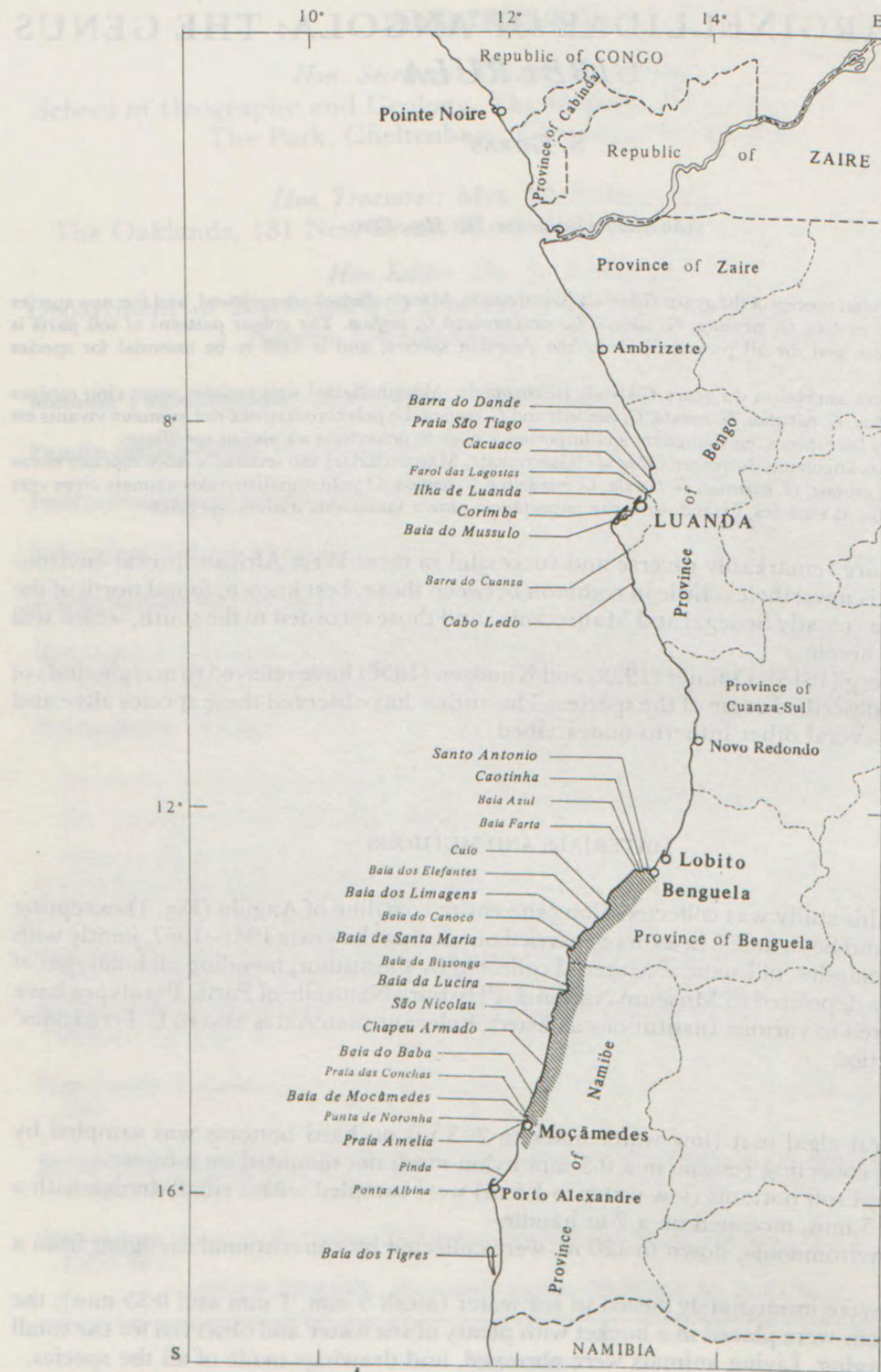


Fig. 1. Map of coastal Angola, to show localities of collecting; hatched area shows predominantly rocky shore. Scale: 1/8 000 000.

SYSTEMATIC PART

Generic features

The type species of *Gibberula* Swainson, 1840 is *G. zonata* Swainson (= *Volvaria oryza* Lamarck, 1822), the animal of which I have described elsewhere (Gofas, in press). The most closely allied representative in Angola is *G. cristata* n. sp.

Other genus-group names are available for small shells resembling *Gibberula*. These include *Granula* Jousseaume, 1875 (type species *Marginella bensoni* Reeve, 1865, subsequent designation by Coan, 1965) and *Kogomea* Habe, 1951 (type species *Erato novempromontialis* Yokoyama, 1928 by original designation). They are distinguished from *Gibberula* only on smaller size and tenuous conchological grounds. The observations of living specimens of all species listed herein does not show any essential difference with the type species of *Gibberula*.

Shell characters

Shell 1.5 to 10 mm in length, ovoid, stout, with a small, low spire. Outer lip thickened but without external varix, usually denticulated inside. Columella with several plaits on a thickened rim, decreasing in size towards posterior end (differing in this respect from *Marginella* and *Hyalina* where the foremost plait is the smallest). Siphonal canal distinctly notched. Shell material colourless or with spiral lines or bands.

The outer lip of immature specimens is thin. In species where the adult has a denticulated aperture, this character may be seen on juvenile specimens, as spiral grooves deep inside the aperture but not reaching its margin.

Head/foot

The head of *Gibberula* is deeply divided in two. There are two short cephalic tentacles and two small anterior lobes. The eyes are a short distance behind the tentacles, somewhat laterally but not protruding as in *Marginella*. The mouth is provided with an extensible proboscis.

The foot is only slightly longer than the shell when extended. In some species, the sole lies flat on the substrate when the animal is crawling. Others have the edge of the propodium raised, developed as parapodia which fit the head/tentacles in the manner of many tectibranchs. This character is stable for a given species, the typical attitude is resumed as soon as the animal is moving. It may be related to ecological preference of the particular species, the latter morphology better fitted to motion on a soft substrate or within a sediment-infilled algal mat.

The colour pattern of the head/foot is a useful taxonomic character in all the species.

Mantle

The mantle of *Gibberula* does not extend over the shell during normal activity. A tongue shaped, translucent lobe may be seen on the left side in some instances.

The internal mantle is usually visible through the shell. It may be brightly coloured in the smaller species with a featureless, translucent shell, and its pattern is then continued into the spire over the visceral mass.

Mantle design is very stable in some species (e.g. *G. aurata*, *G. atlantidea*, *G. mimetica*) where it may be used as a taxonomic character; it is more unpredictable in others (e.g. *G. pallata*, *G. cristata*) where only basic colours are stable but not patterns. Similar colour pattern is found in closely related species, and interpreted as persistence of a common ancestral character in the local radiation.

The siphon is short and un conspicuous, often bordered by a small pad.

Radula

The teeth in the rachiglossate radula of *Gibberula* are strongly arched, and indented with strong cusps of which the most prominent is usually axial. There is much variability of the teeth along the same radula, and the detail in cusp morphology is seldom identical on two successive teeth.

Among the species examined, there is no correlation between shell size and size of radula teeth. The smallest teeth were seen in *G. gruveli*, a relatively large species.

An unusual pattern has been seen on one of the species examined (*Gibberula aurata*), where a regularly alternating morphology is developed between two successive teeth, in order to fit the exceedingly long lateral cusps (see Fig. 22).

Reproduction

All species of marginellids have a direct development without planktonic phase. Egg cases, containing a single developed embryo, have been observed for *G. atlantidea* and *G. gruveli*. The latter were attached to other shells, including shells and opercula of *Turritella praeterrissa* Dautzenberg, 1913, on a muddy bottom in Bay of Mussulo, province of Luanda (Fig. 15).

Dwarf specimens

Smaller individuals, evidently adult judging from completely formed outer lip but about half the size of average individuals and constituting a discrete size class, were found together with populations of *G. pallata* and *G. mimetica*. No definitive character other than size could be reported, and the significance of these dwarf specimens is not known. Size range of other species seems rather stable within one area, whereas series of sibling species differing apparently only in size are documented for *Marginella*.

***Gibberula cristata* n. sp.** (Figs. 2–5, 46–47)

Etymology: from Latin *cristatus*, a, um (adj.), provided with a crest (allusive to the raised suture).

Type locality: Bay of Corimba, Praia Etambar (province of Luanda) on infralittoral rocks lined with muddy algal mat, 0–1 m.

Type material: Holotype (MNHN) and 126 paratypes (86 adults and 40 juveniles) from the type locality (MNHN, BMNH, IIT, UAN, FF). 6 paratypes (MNHN): Dredging (10 m) between Cacucaco and Farol das Lagostas (prov. Luanda).

Other material examined

Northern Angola: Barra do Dande, on rocks 0–1 m: 15 adult specimens and 20 juveniles. Bay of Corimba, dredging 10–20 m on gravel: 4 specimens. Off Ilha de Luanda, dredging 40–50 m: 14 specimens.

Southern Angola: Caotinha, infralittoral rocks 0–1 m: 1 specimen. Bay of Santa Maria, dredging 8–10 m: 2 specimens. Bay of Lucira, infralittoral rocks 0–1 m: 12 specimens, and dredging 10–15 m on calcareous algae: 7 specimens.

Abbreviations used in the text

MNHN: Muséum National d'Histoire Naturelle, Paris – Laboratoire de Malacologie

BMNH: British Museum (Natural History), London

IIT: Instituto de Investigação Científica Tropical (Centro de Zoologia), Lisbon

SAM: South African Museum, Cape Town

UAN: Universidade Agostinho Neto (faculdade de Ciências, dep. Biologia), Luanda

FF: private collection of Francisco Fernandes, Luanda

'Specimens' refers to specimens collected alive, as opposed to 'shells'

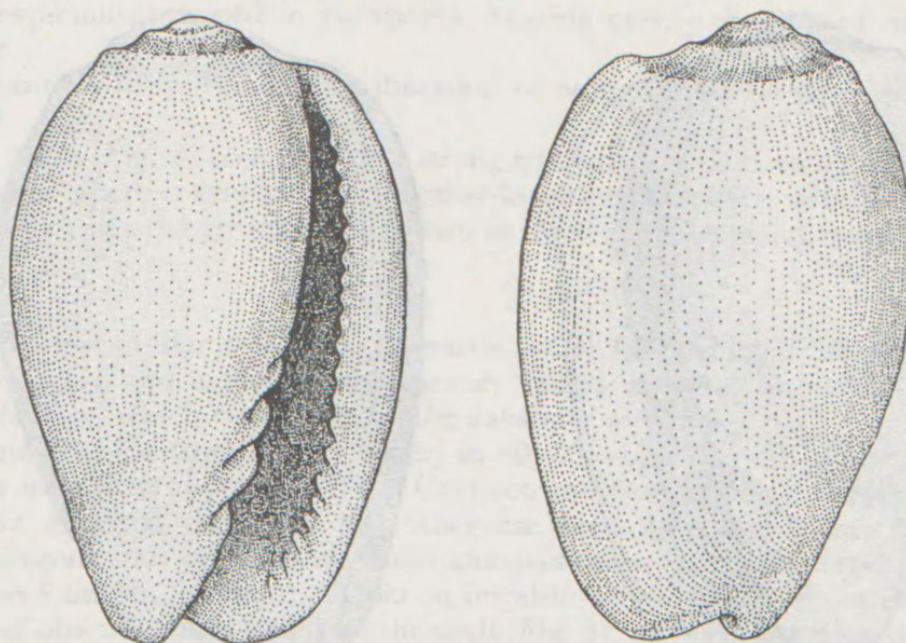


Fig. 2. *Gibberula cristata* n. sp.: holotype, from Praia Etambar. Actual size: 5-7 mm.

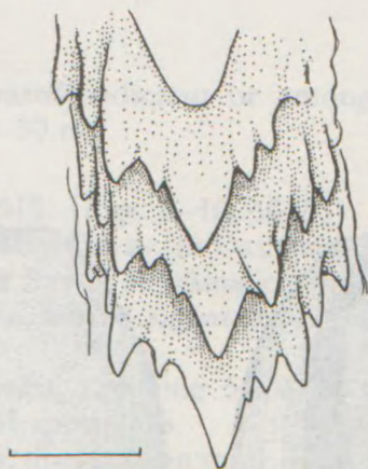


Fig. 3. *Gibberula cristata* n. sp.: same locality, three teeth of the radula; scale bar is 10 μ m.

Description

Shell 5 to 7 mm in length, rather solid. Suture characteristically raised in a low spiral ridge. Outer lip thickened, very slightly protruding posteriorly, with some 20 definite denticles on the inner side. Columella with 5 to 6 plaits, evenly decreasing in size posteriorly. Shell translucent, whitish to orange or tan in colour, with a dark sutural band; the subsutural area and anterior part of body whorl are rather porcellaneous and opaque.

Head bearing two cylindrical tentacles and conspicuous anterior lobes; its profile is slightly swollen next to the eyes. Some orange and yellow spots are irregularly scattered on the head and tentacles; a greyish stain is occasionally present behind the eyes.

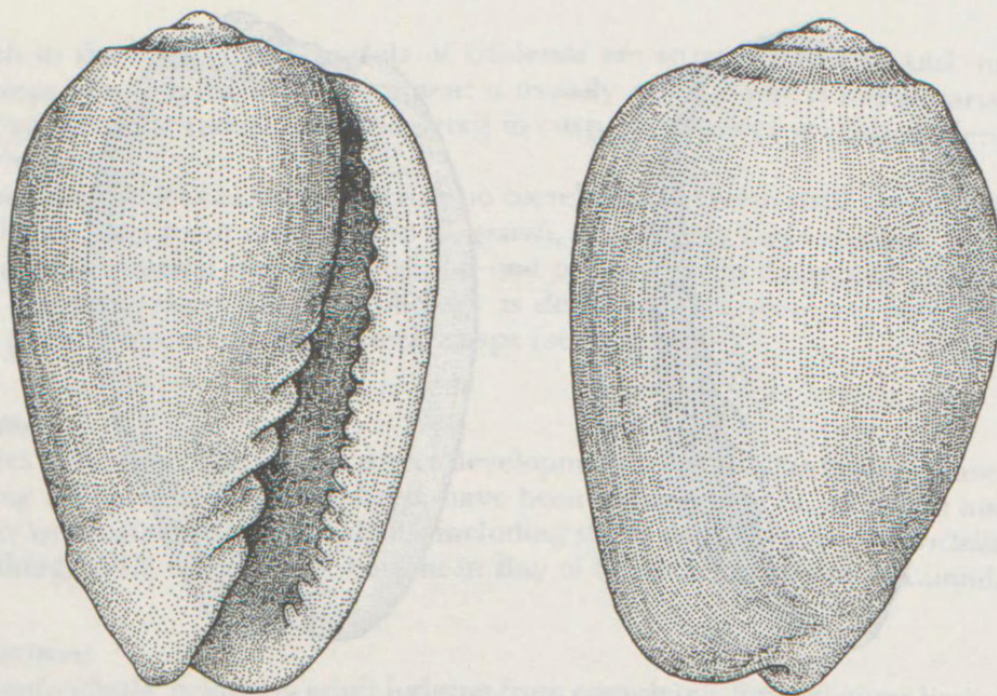


Fig. 4. *Gibberula cristata* n. sp.: specimen from off Ilha de Luanda, 50 m. Actual size: 6.2 mm.

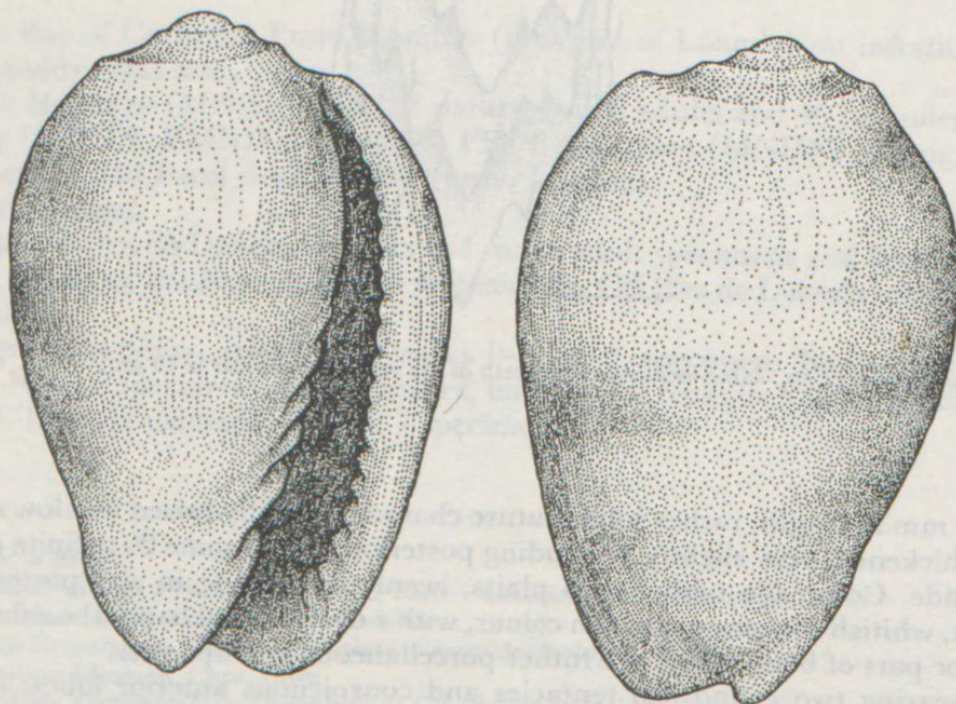


Fig. 5. *Gibberula cristata* n. sp.: specimen from Bay of Lucira (Praia do Cesar), dredging on calcareous algae 10 m, showing confuse banding on the shell. Actual size: 6.0 mm.

Foot conspicuously raised in parapodia, bearing evenly distributed orange and pale yellow spots.

Inner mantle with a variable combination of orange spots on dark grey and whitish background.

Radular teeth (Fig. 3) arched, with a strong triangular axial cusp flanked by one or two small denticles. There is on each side another large cusp building with the central cusp a rather flattened tricuspid structure, then two or three smaller lateral cusps.

Remarks

This species is most similar to *G. oryza* (Lamarck, 1822), from which it differs conchologically by a broader spire and a more conspicuously raised suture. The animal differs by the attitude of the foot, which crawls flat on the substrate in *G. oryza*.

Specimens dredged from deeper water, in 40–50 m off Ilha de Luanda on rocks and gravel, differ from littoral populations of Cacucaco and Corimba by a deeper orange hue of the shell. No essential difference has otherwise been noted, and they are considered conspecific. Populations of *G. pallata* found alongside show the same trend in shell colour.

Specimens found in Southern Angola on infralittoral rocks differ from those of Luanda by presence of obscure spiral bands on the shell (Fig. 5), by burnt carmine stains on siphon and behind eyes, and by apparently stiffer parapodia. They are also considered conspecific.

Some specimens found in dredging of Lucira and Santa Maria are larger, with a more slender anterior part of shell. One of them, observed alive, has a predominantly burnt carmine siphon, and very scarce orange and burnt carmine dots on the foot, also raised in parapodia. Material seen is not sufficient to ascertain if these should represent another species.

Habitat

In algal mat with agglomerated sediment or among muddy gravel, usually on hard substrates, low water mark to 50 m.

Gibberula pallata (Bavay, 1913) (Figs. 6–10, 48–51)

Original reference: *Marginella pallata* Bavay, in Dautzenberg, 1913, p. 24, Pl. 1, figs. 27–28

Type locality: Praia Amelia and Bay of Moçâmedes, prov. Namibe

Type material: Figured specimen, here designated as lectotype, in MNHN

Other material examined

Northern Angola: Bay of Corimba, dredging 5–20 m: numerous specimens. Off Ilha de Luanda, dredging 40–50 m: 11 specimens.

Southern Angola: Santo Antonio, dredging on mud 10 m: numerous specimens. Bay of Santa Maria, beach 1 m: 5 specimens. Bay of Lucira, dredging 15–30 m in front of fisheries, numerous specimens. Santa Marta, dredging 40 m: 4 specimens. Praia Amelia, dredging 40–60 m: 16 specimens. Baía dos Tigres, dredging 5–6 m within bay: 15 specimens.

Description

Shell 4.5 to 6 mm, inflated posteriorly and narrowing anteriorly, with a distinctly conical, low spire. Suture flush. Outer lip with some 20 definite denticles. Shell material somewhat translucent, usually whitish with a dark sutural band and a brown spiral band to the anterior third. Some shells are plain white.

Head with pale yellow spots, some clusters of orange and dark brown spots, and a large brown area behind the eyes. There are also some pale yellow spots and an occasional orange spot on the tentacles.

Foot crawling flat, with a pattern of alternating pale yellow patches and clusters of

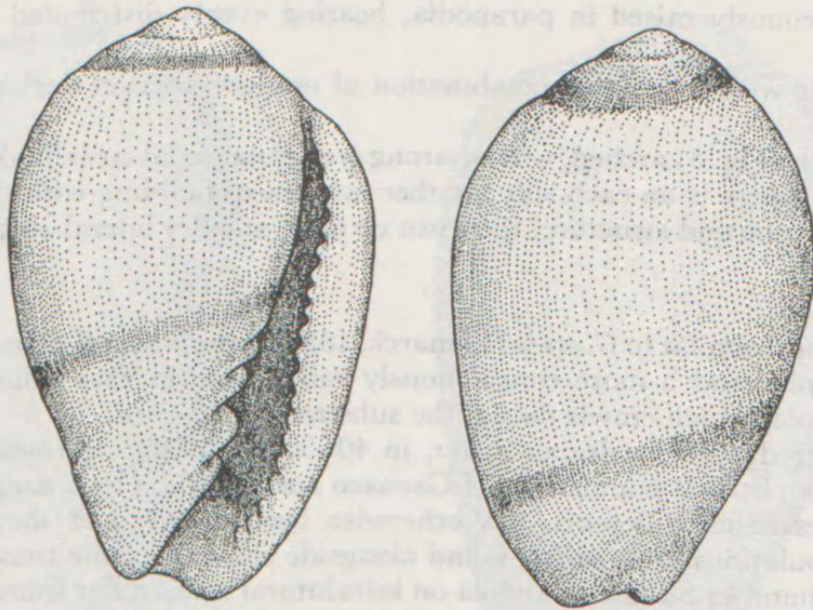


Fig. 6. *Gibberula pallata*: specimen from Bay of Corimba, 20 m. Actual size: 5.3 mm.

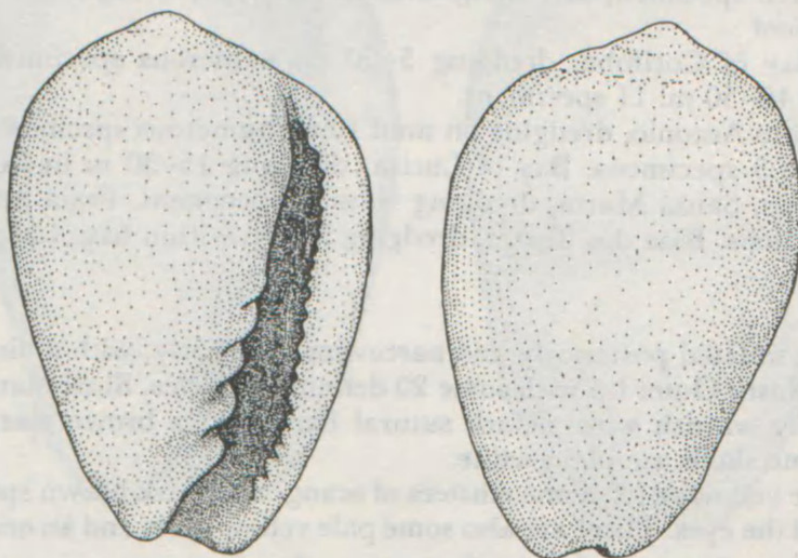


Fig. 7. *Gibberula pallata*: same locality, specimen with white shell. Actual size: 4.8 mm.

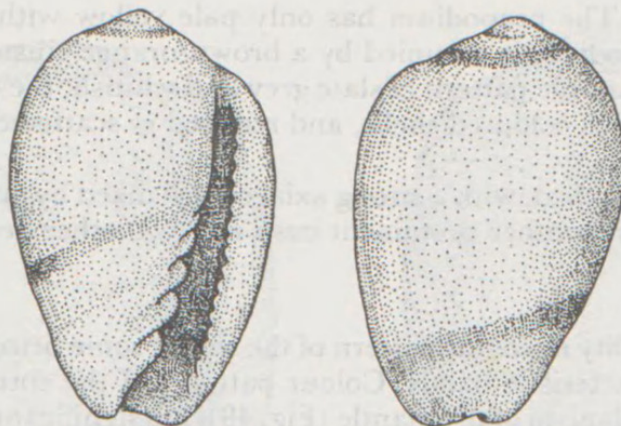


Fig. 8. *Gibberula pallata*: same locality, 'dwarf' specimen. Actual size: 3.7 mm.



Fig. 9. *Gibberula pallata*: same locality, three teeth of the radula. Scale bar is 10 μ m.

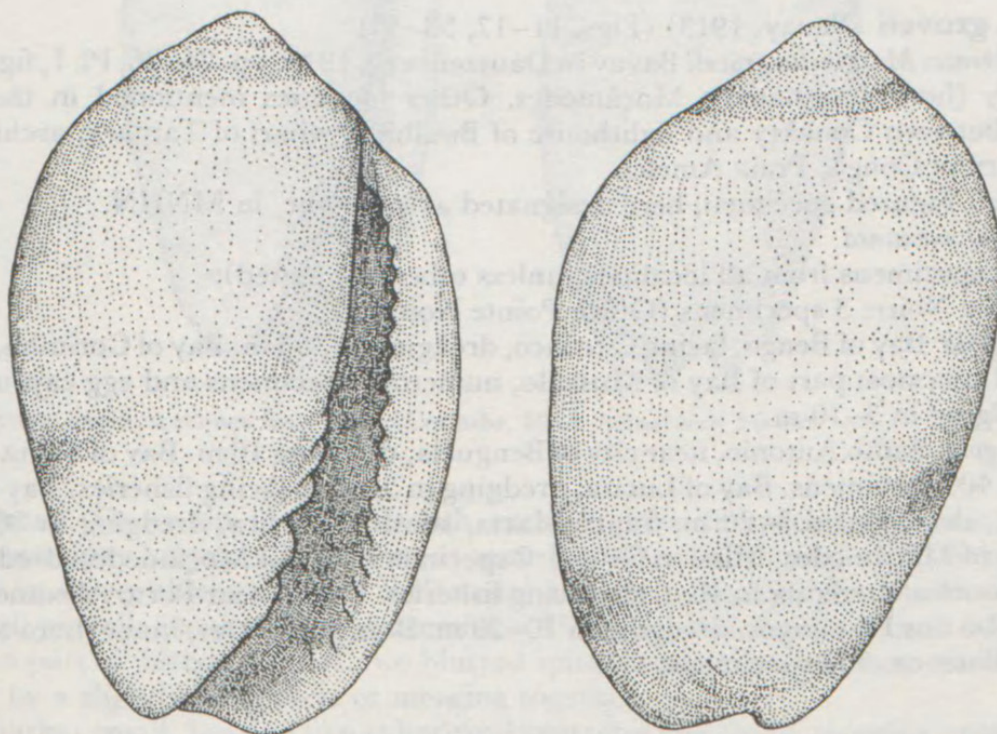


Fig. 10. *Gibberula pallata*: specimen from Baia dos Tigres, 5 m. Actual size: 6.5 mm.

orange and brown spots. The propodium has only pale yellow with some orange spots, whereas the axis of metapodium is occupied by a brown/orange cluster.

Inner mantle with a variable pattern of slate grey and whitish, the dark element usually dominant in individuals with coloured shells, and reduced to scattered spots in individuals with white shell.

Radular teeth (Fig. 9) arched, with a strong axial cusp flanked by one or two small cusps. On each side, there is then another prominent cusp and two other decreasing in size.

Remarks

There is a discrete variability in colour pattern of the shells, some being plain white (Fig. 7) and others with the characteristic bands. Colour patterns of the corresponding soft parts differ only by reducing melanism of the mantle (Fig. 49). No significant difference in habitat has been found for these phenotypes, which occur together wherever the species is found.

Numerous dwarfed individuals, hardly 3.5 mm in length but definitely adult with thickened outer lip (Fig. 8), have been found in a restricted area of Bay of Corimba, Luanda. Their polychromatism is similar to that of normal sized populations (Fig. 50), and normal sized individuals were found nearby. There is no argument for giving any taxonomic value to this difference, but their significance is not explained.

Specimens from deeper water, off Ilha de Luanda, 40–60 m, have a more intensely coloured shell, yellowish to pale orange. Colour pattern of the soft parts is not appreciably different.

Specimens from Baía dos Tigres (Fig. 10) are definitely larger than those from Benguela or Luanda, to the same extent as observed for *G. gruveli*.

Habitat

This species has been found on soft bottoms, usually muddy sand or gravel, in 5 to 50 m depth. It is usually common where present.

Gibberula gruveli (Bavay, 1913) (Figs. 11–17, 53–54)

Original reference: *Marginella gruveli* Bavay in Dautzenberg, 1913, pp. 24–26, Pl. 1, figs. 29–30.

Type locality (here designated): Moçâmedes. Other localities mentioned in the original reference: between Conakry and lighthouse of Boulbiné; wharf of Tamara; archipelago of Los; Estuary of Congo; Praia Amelia.

Type material: Figured specimen, here designated as lectotype, in MNHN.

Other material examined

(numerous specimens from all localities, unless otherwise stated):

Congo: Pointe Noire: 3 specimens (Office Pointe Noire).

Northern Angola: Bay of Bengo, facing Cacuaco, dredging in 3–5 m. Bay of Corimba, dredging 10–20 m. Innermost part of Bay of Mussulo, numerous specimens and egg capsules. Cabo Ledo, dredging in 5–10 m.

Southern Angola: Santo Antonio, near city of Benguela, dredging 10 m. Bay of Santa Maria, in 1–2 m: ca. 400 specimens. Bay of Lucira, dredging in 5–10 m facing fisheries. Bay of Lucira, (Bissonga), dredging in 5–20 m. Santa Marta, south of Lucira, dredging in 30–40 m: 7 shells. Bay of Moçâmedes, Mission Gruvel: 2 specimens. Bay of Moçâmedes, dredging in 10 m. Praia Amelia, dredging in 40–60 m facing fisheries. Pinda, near Porto Alexandre, facing mouth of Rio dos Flamings, dredging in 10–20 m. Baía dos Tigres, inner shore of the sand bar, tidal flats: ca. 300 specimens.

Description

Shell 4 to 7 mm in length, oblong, with a bluntly rounded spire. Suture flush; obscured by

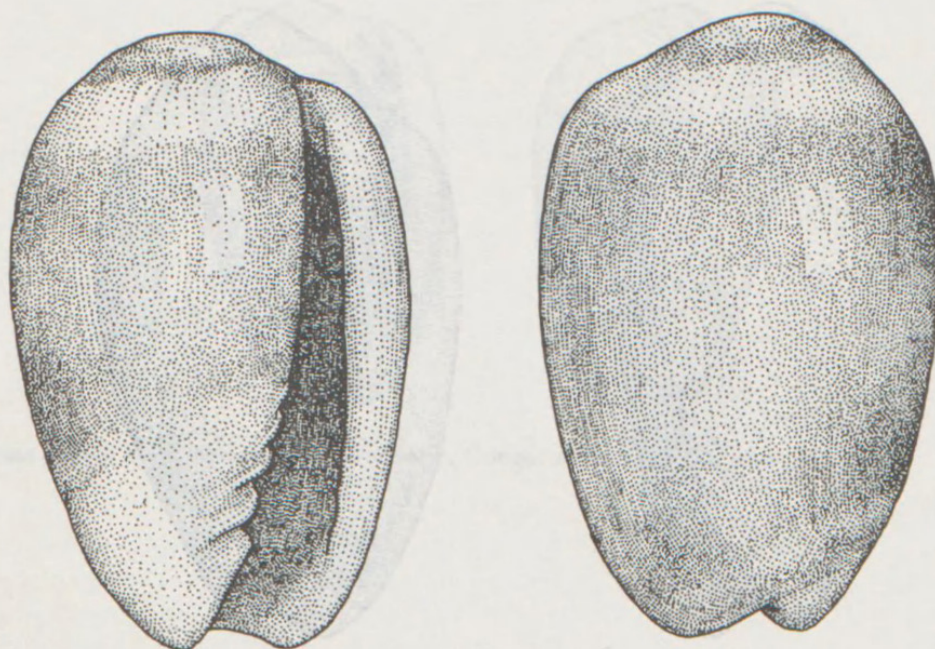


Fig. 11. *Gibberula gruveli*: specimen from Bay of Moçâmedes, 10 m. Actual size: 5.6 mm.

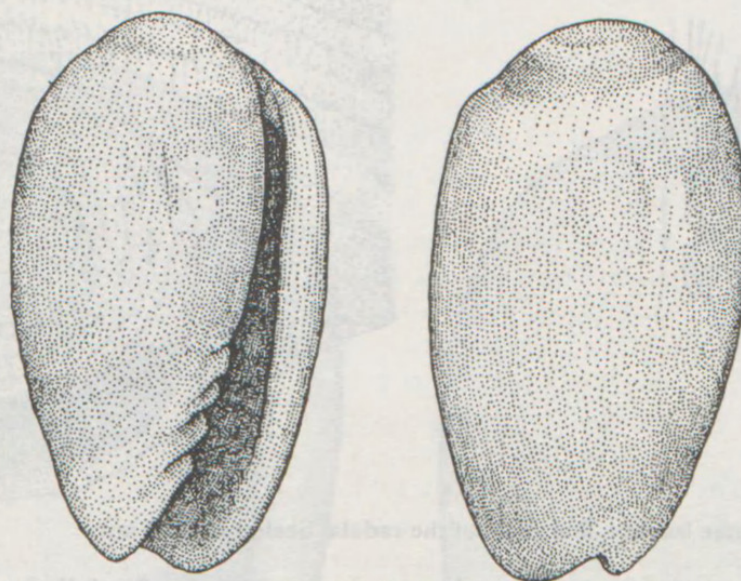


Fig. 12. *Gibberula gruveli*: specimen from Bay of Corimba, 10 m. Actual size: 5.0 mm.

glassy deposit. Outer lip usually smooth even in gerontic specimens; some very faint denticulations may occasionally be seen at some distance inside aperture. Columella with 4 to 5 plaits on a very thickened rim. Shell material rather translucent in the median part of body whorl, porcellaneous towards extremities. There is a dark brown sutural band and, on the median part of the body whorl, two blurred spiral bands of pale brown, often indistinct, separated by a slightly paler zone or merging together.

Head rather small, bearing two cylindrical tentacles and small, tapering anterior lobes. There is a burnt carmine area around the eyes, and some yellow on tentacles and lobes.

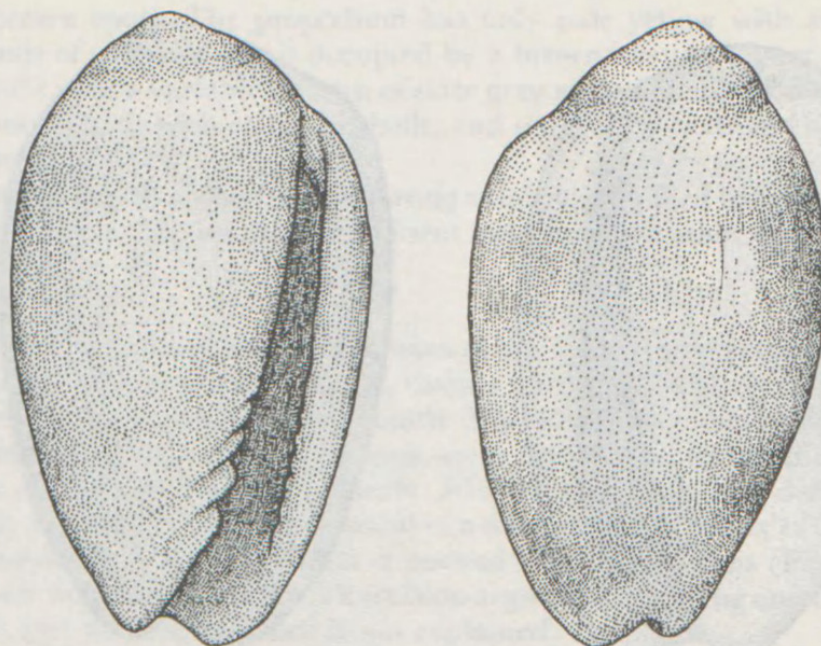


Fig. 13. *Gibberula gruveli*: same locality, specimen with higher spire. Actual size: 5.8 mm.

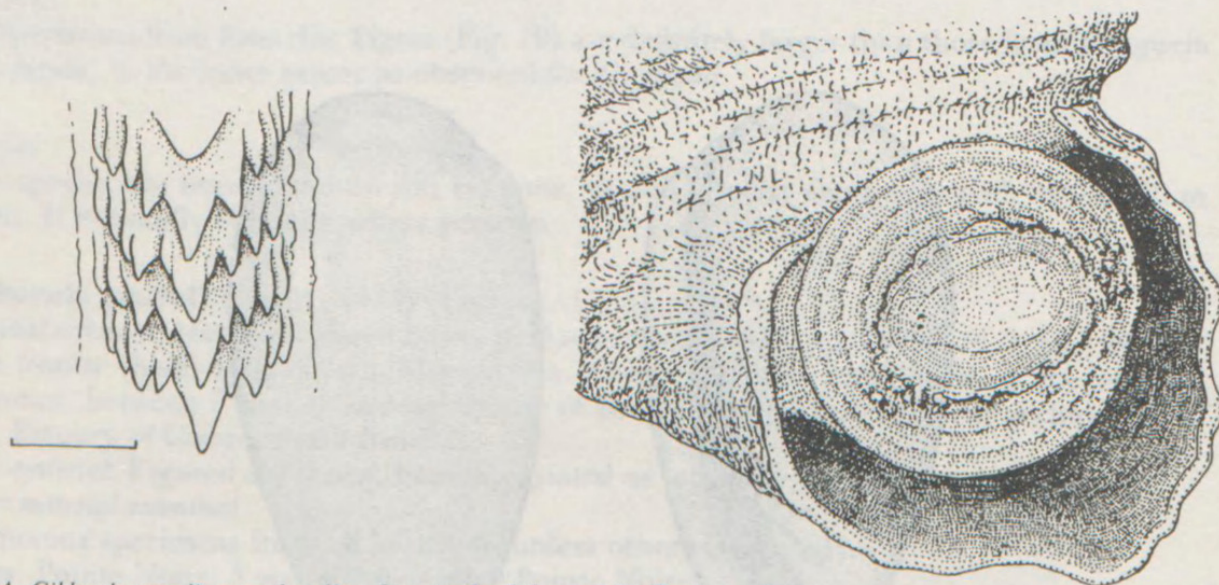


Fig. 14. *Gibberula gruveli*: same locality, four teeth of the radula. Scale bar is 10 μ m.

Fig. 15. *Gibberula gruveli*: egg capsule with single embryo on the operculum of a *Turritella*; bay of Mussulo, dredged 10 m.

Foot broad and ovate in outline, conspicuously raised in parapodia, colourless with only some opaque white patches increasing in size towards metapodium; occasionally, some burnt carmine spots are also present. The siphon is small, with a burnt carmine band and yellow patches. It is bordered by a distinct pad, of the same colour.

The inner mantle is not very apparent through the shell; it has a variable pattern of dark grey reticulation and pale areas.

Radular teeth (Fig. 14) arched, with a very prominent, triangular axial cusp, and four other smaller cusps on each side; the cusps next to the axial are strong on some teeth, reduced on others in which case it is the next one which is well developed.

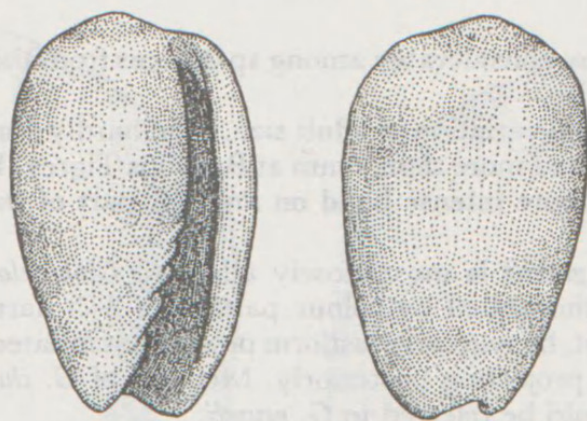


Fig. 16. *Gibberula gruveli*: specimen from Pointe Noire, Congo. Actual size 3.7 mm.

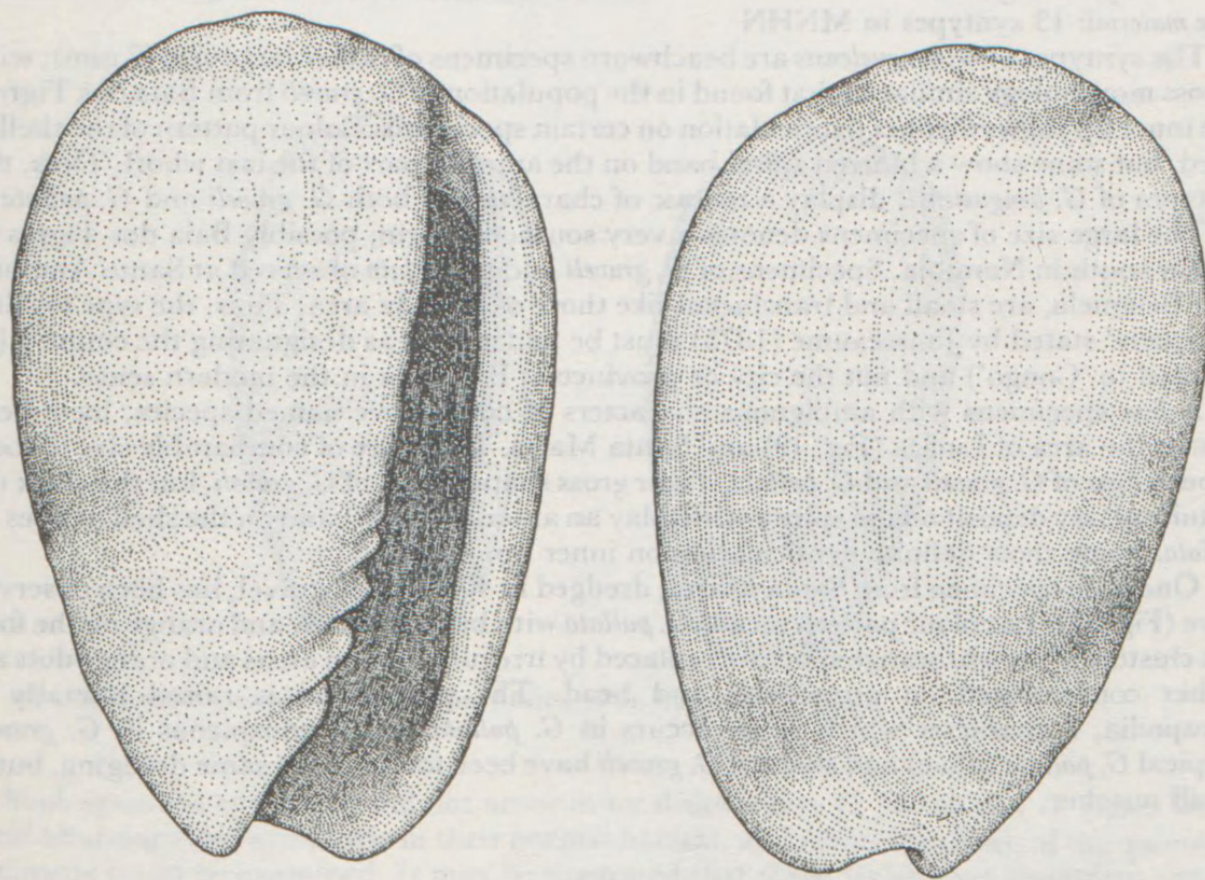


Fig. 17. *Gibberula gruveli*: specimen from Baia dos Tigres, tidal flat. Actual size: 7.0 mm.

Remarks

The angle of spire can vary considerably among specimens from the same locality (Figs. 12, 13).

There is a definite clinal variation in adult size, from hardly 4 mm in Congo (Fig. 16) to 5–6 mm around Luanda and more than 7 mm at Baia dos Tigres (Fig. 17). Specimens from Baia dos Tigres show a more intense band on anterior part of shell (see discussion of *G. benguelensis*).

Conchologically, *G. gruveli* is most closely allied to *Gibberula chudeaui* (Dautzenberg, 1910). The latter is distinguished by colour pattern of 3–5 narrow spiral bands evenly distributed on body whorl, by regularly fusiform profile, not inflated posteriorly, by outer lip denticulated inside and projecting posteriorly. Mention of *G. chudeaui* at Moçâmedes by Dautzenberg (1913) should be referred to *G. gruveli*.

Habitat

This species is found on soft bottoms, mostly on mud or muddy sand. It is locally very abundant to the point of being a major component of the molluscan fauna.

There is a shift in the upper bathymetric limit, from North to South. In the Luanda area, *G. gruveli* is found in 5 to 20 m water depth; it has been collected by hand-dredging very close to the beach in 1–2 m at Santa Maria and Lucira, and has been found intertidally on muddy tidal flats at Baia dos Tigres.

***Gibberula benguelensis* Jousseaume, 1875 (Fig. 18)**

Original reference: *Gibberula Benguelensis* Jousseaume, 1875, pp. 82–83, Pl. 8, fig. 8.

Type locality: 'Benguela'

Type material: 13 syntypes in MNHN

The syntypes of *G. benguelensis* are beachworn specimens of rather large size (7 mm), with a gross morphology similar to that found in the population of *G. gruveli* from Baia dos Tigres. The inner lip shows distinct denticulation on certain specimens. Colour pattern of the shell is faded, but some show a blurred spiral band on the anterior part of the last whorl. Thus, the syntypes of *G. benguelensis* display a mosaic of characters of both *G. gruveli* and *G. pallata*.

The large size of specimens denotes a very southern origin, possibly Baia dos Tigres or further south in Namibia. Specimens of *G. gruveli* and *G. pallata* observed at Santo Antonio, near Benguela, are small and translucent like those of Luanda area. Thus, the type locality 'Benguela' stated by Jousseaume (1875) must be understood as designating the country (as opposed to 'Congo') and not the city or province of Benguela in the modern sense.

A few specimens with ambiguous characters of both above named species, have been seen in the area of Lucira (Fig. 19) and Santa Maria. These are of comparable size to local populations of *G. gruveli* and *G. pallata*. Their gross shape is that of *G. gruveli*, but they lack the definite glassy deposit on the spire and display an anterior spiral band on the shell as does *G. pallata*. Some show definite denticulation on inner lip.

One such specimen from Santa Marta, dredged in 40 m sandy gravel, has been observed alive (Fig. 52). Its colour pattern recalls *G. pallata* with brown, yellow and orange on the foot, but clusters of brown/orange spots are replaced by irregular brown areas and orange dots are rather concentrated on propodium and head. The propodium is raised laterally in parapodia, a character which never occurs in *G. pallata* and is conspicuous in *G. gruveli*. Typical *G. pallata* (alive) and shells of *G. gruveli* have been found in the same dredging, but in small number.

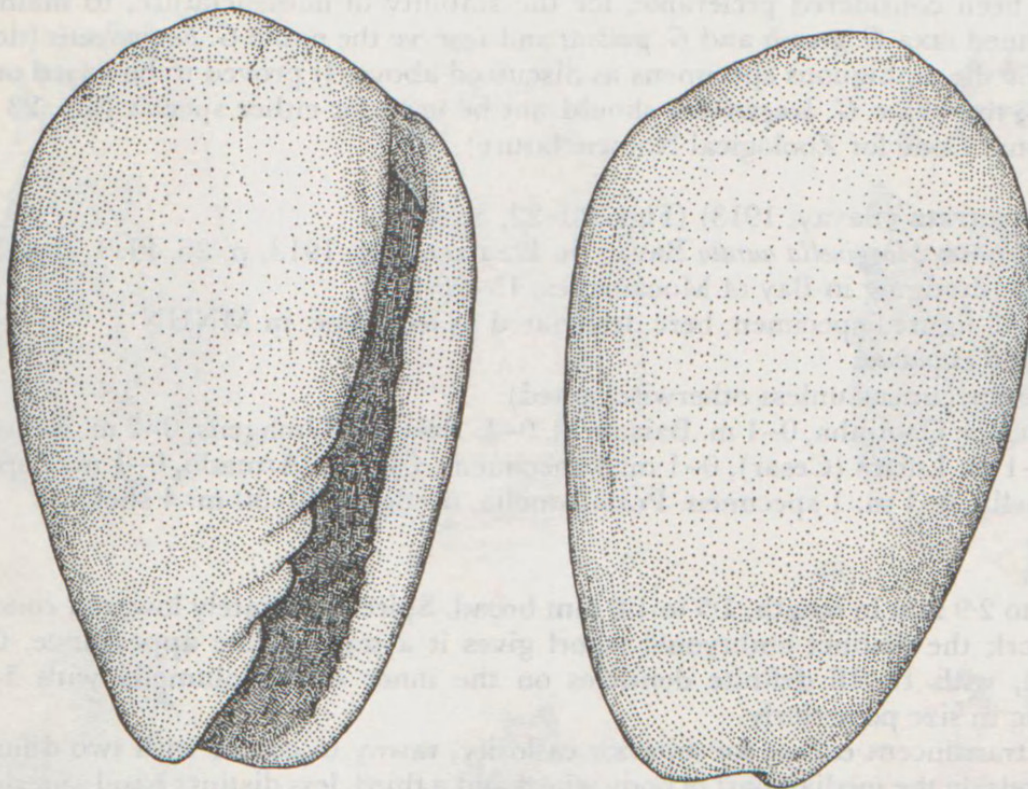


Fig. 18. *Gibberula benguelensis*: syntype. Actual size: 6-8 mm.

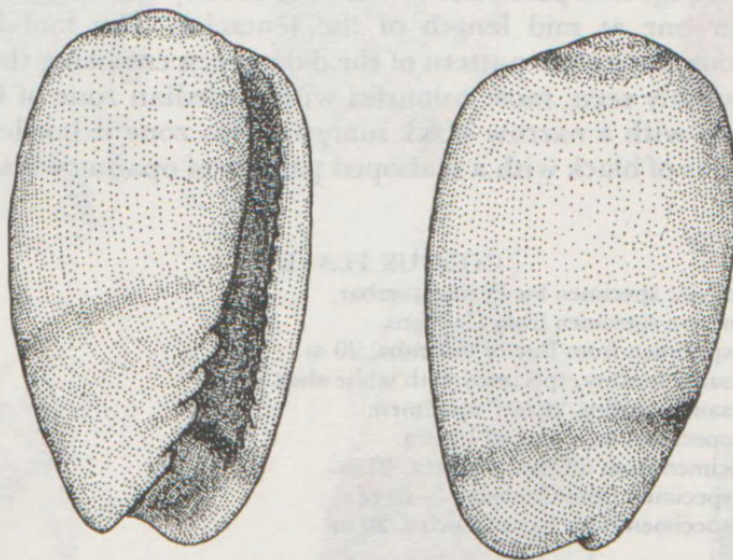


Fig. 19. *Gibberula* sp.: specimen from off Santa Marta, 40 m. Actual size: 4-9 mm.

Such spurious specimens did not occur in localities where *G. pallata* and *G. gruvelli* were found abundant and sympatric in their normal habitat, and where hundreds of unequivocal specimens could be examined. It may be suggested that these ambiguous specimens result from hybridization, occurring in marginal habitats where normal mating becomes problematic.

It has been considered preferable, for the stability of nomenclature, to maintain the clearly defined taxa *G. gruveli* and *G. pallata* and reserve the name *G. benguelensis* (despite its priority) for the ambiguous specimens as discussed above. If proved to be based on hybrid specimens, the name *G. benguelensis* should not be used for either species (art. 23 h of the International Code for Zoological Nomenclature).

Gibberula aurata (Bavay, 1913) (Figs. 20–22, 56–57)

Original reference: *Marginella aurata* Bavay, in Dautzenberg, 1913, p. 26, Pl. 1, figs. 33–34

Type locality: dredging in Bay of Moçâmedes, 15–20 m

Type material: figured specimen, here designated as lectotype, in MNHN

Other material examined:

(numerous specimens unless otherwise stated)

Southern Angola: Caotinha, 0–1 m. Baia Azul, 0–1. Baia dos Limagens, 0–2 m. Baia de Santa Maria, 0–1 m. Lucira (Cesar), 0–1 m: 4 specimens. Chapeu Armado, 0–1 m: 2 specimens. Praia Amelia, 0–1 m: 1 specimen. Praia Amelia, dredging 40–50 m: 4 shells.

Description

Shell 2.5 to 2.9 mm in length, 1.5 to 1.8 mm broad. Spire moderately low, not concealed by body whorl; the distinct embryonic whorl gives it a mammillate appearance. Outer lip thickened, with 16–18 definite denticles on the inner side. Columella with 5–6 plaits decreasing in size posteriorly.

Shell translucent except for anterior callosity, tawny in colour with two diffuse darker spiral bands on the median part of body whorl and a third, less distinct band anteriorly, next to the opaque anterior callus. The internal suture and soft parts are distinctly seen by transparency.

Head and foot with a colourful pattern of dark green (grading to black in some populations), bright orange and pale yellow. There is usually a dark green blotch in front of the eyes and another one at mid length of the tentacles. The foot has a pale yellow background, with a loose reticulate pattern of the dark green enclosing the orange blotches.

Inner mantle distinctly seen, most colourful with a median zone of bright orange with rounded spots of green with a narrow black margin. This zone is bordered anteriorly and posteriorly by two zones of black with a scalloped pattern of opaque white loops, each white

COLOUR PLATE 1

- Fig. 46. *Gibberula cristata* n. sp.: specimen for Praia Etambar.
- Fig. 47. *Gibberula cristata* n. sp.: specimen from Cacuaco.
- Fig. 48. *Gibberula pallata*: specimen from Bay of Corimba, 20 m.
- Fig. 49. *Gibberula pallata*: same locality, specimen with white shell.
- Fig. 50. *Gibberula pallata*: same locality, 'dwarf' specimen.
- Fig. 51. *Gibberula pallata*: specimen from bay of Lucira.
- Fig. 52. *Gibberula* sp.: specimen from off Santa Marta, 40 m.
- Fig. 53. *Gibberula gruveli*: specimen from Cacuaco, 5–10 m
- Fig. 54. *Gibberula gruveli*: specimen from bay of Lucira, 20 m.

COLOUR PLATE 2

- Fig. 55. *Gibberula atlantidea*: specimen from off Ilha de Luanda, 90 m.
- Fig. 56. *Gibberula aurata*: specimen from bay of Limagens, 0–2 m.
- Fig. 57. *Gibberula aurata*: specimen from bay of Lucira (praia do Cesar).
- Fig. 58. *Gibberula mimetica* n. sp.: 'dwarf' specimens from Chapeu Armado.
- Fig. 59. *Gibberula mimetica*: same locality, specimen of normal size.
- Fig. 60. *Gibberula tantula* n. sp.: specimen from Chapeu Armado.
- Fig. 61. *Gibberula confusa* n. sp.: specimen from Praia Etambar.
- Fig. 62. *Gibberula mendacis* n. sp.: specimen from Bay of Corimba, 20 m.
- Fig. 63. *Gibberula columnella*: specimen from Praia Amelia, rocks 2–5 m.

GOFAS : MARGINELLIDS OF ANGOLA



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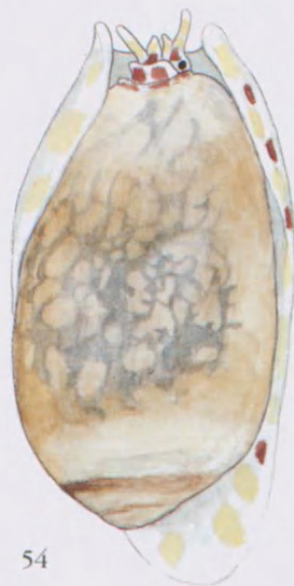
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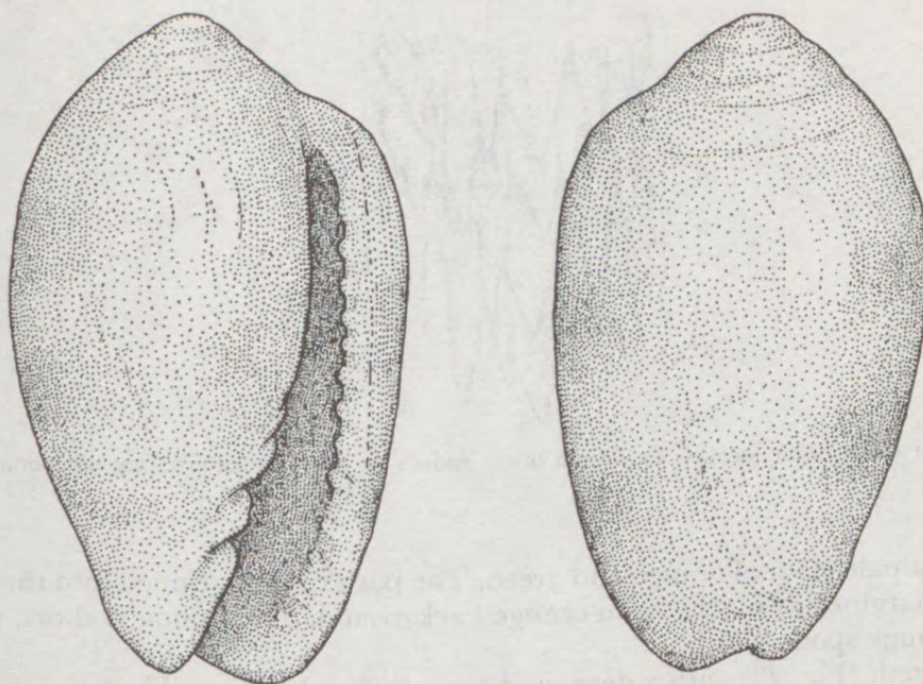


Fig. 20. *Gibberula aurata*: specimen from Santa Maria, infralittoral rocks 0–2 m Actual size: 3.0 mm.

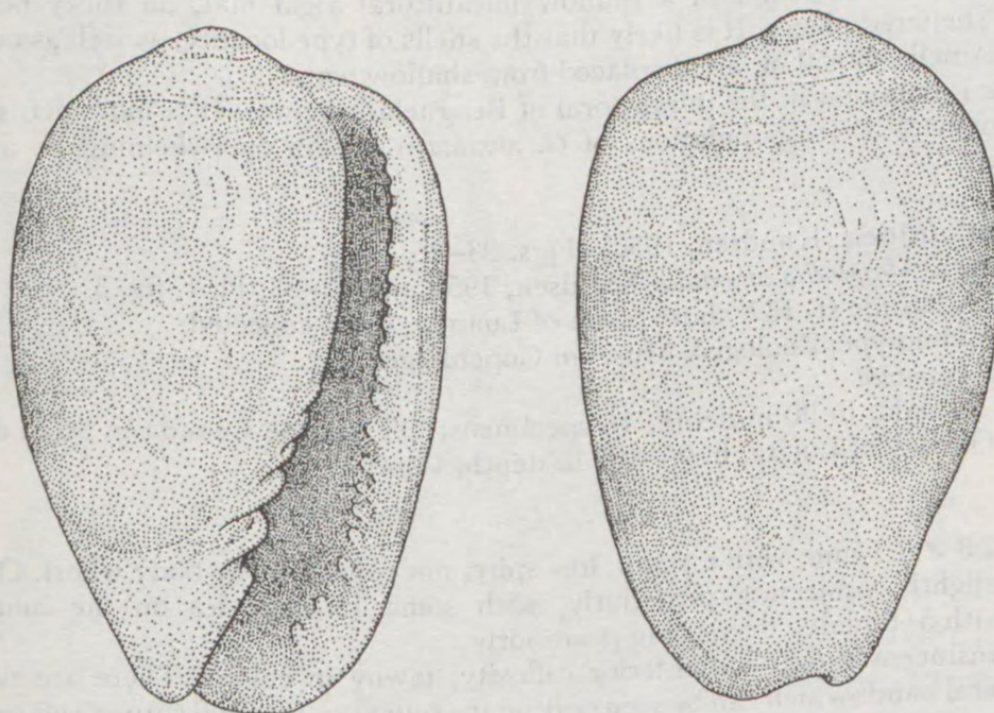


Fig. 21. *Gibberula aurata*: same locality, specimen with lower spire. Actual size: 2.9 mm.

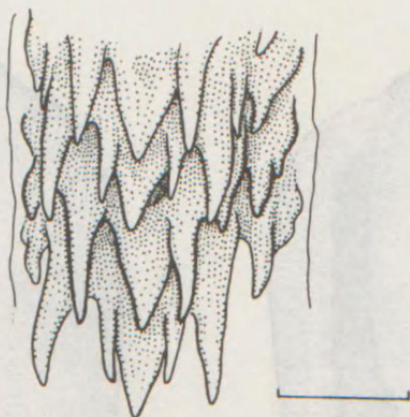


Fig. 22. *Gibberula aurata*: same locality, four teeth of the radula, to show the alternating morphology. Scale bar is 10 μ m.

area bearing a pale stain of orange and green. The pattern is continued into the spire, with green loops margined of black, on an orange background. The siphon is short, tinged with green and orange spots.

Radular teeth (Fig. 22) with a depressed axial triangular cusp. The cusps next to it are extremely long and pointed in one of every two teeth; in every other tooth, these are reduced and it is the second cusp next to the central which is extremely developed. Next to this structure, there is a smaller cusp on the outer side.

Remarks

The pattern of foot is dark green in populations from Caotinha and Limagens (province of Benguela) (Fig. 56), rather black in populations from Lucira and Chapeu Armado (Fig. 57).

Habitat

This species has been found in a shallow infralittoral algal mat, on rocky bottom in moderately sheltered places. It is likely that the shells of type locality, as well as our shells from Praia Amelia 40–50 m, are displaced from shallow water.

G. aurata is common in the infralittoral of Benguela province. It is more occasional in Namibe province, where populations of *G. miniata* n.sp. are overwhelming in a similar environment.

Gibberula atlantidea (Knudsen, 1956) (Figs. 23–26, 55)

Original reference: *Marginella atlantidea* Knudsen, 1956, pp. 82–83, Pl. 1, fig. 3

Type locality: Atlantide st. 137, shore north of Luanda, hand collected.

Type material: Holotype, Zoologisk Museum Copenhagen.

Other material examined

Off Ilha de Luanda, in 90 m depth, 16 specimens; Off Ilha de Luanda in 50 m depth, 2 specimens. Off Bay of Lucira, in 90–100 m depth, 1 specimen.

Description

Shell up to 2.8×1.7 mm, with a small, low spire, not concealed by body whorl. Outer lip thickened, slightly projecting posteriorly, with some 15 denticles on the inner side. Columella with 5–6 plaits, decreasing posteriorly.

Shell translucent except for anterior callosity, tawny in colour. There are two very indistinct spiral bands which can be seen only on the outer lip. Internal suture, soft parts and prolongation of labial denticles are clearly seen by transparency.

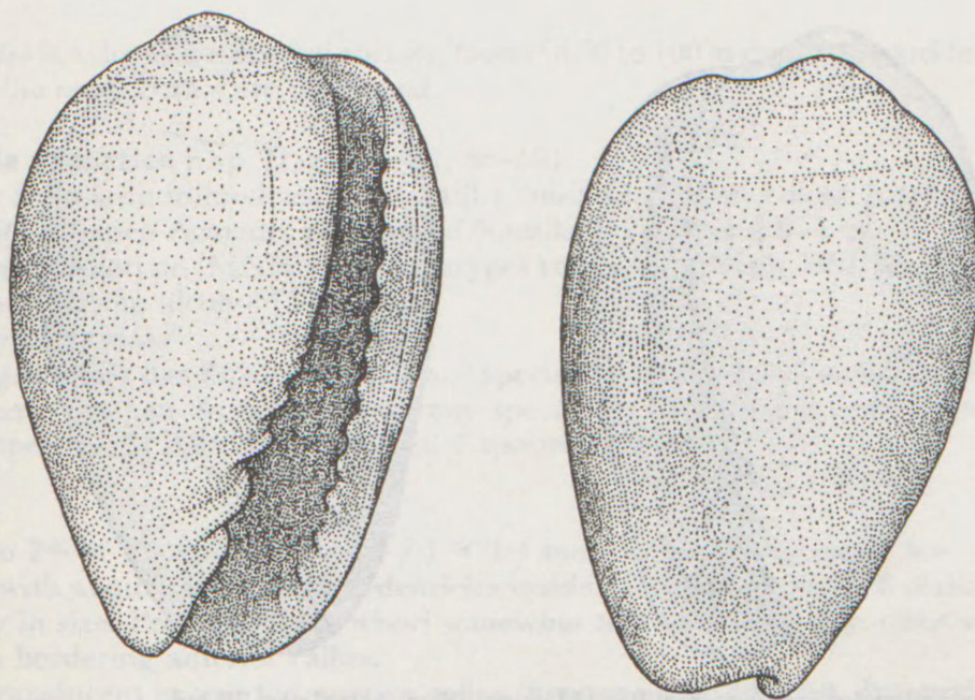


Fig. 23. *Gibberula atlantidea*: specimen from off Ilha de Luanda, 90 m. Actual size: 2.8 mm.

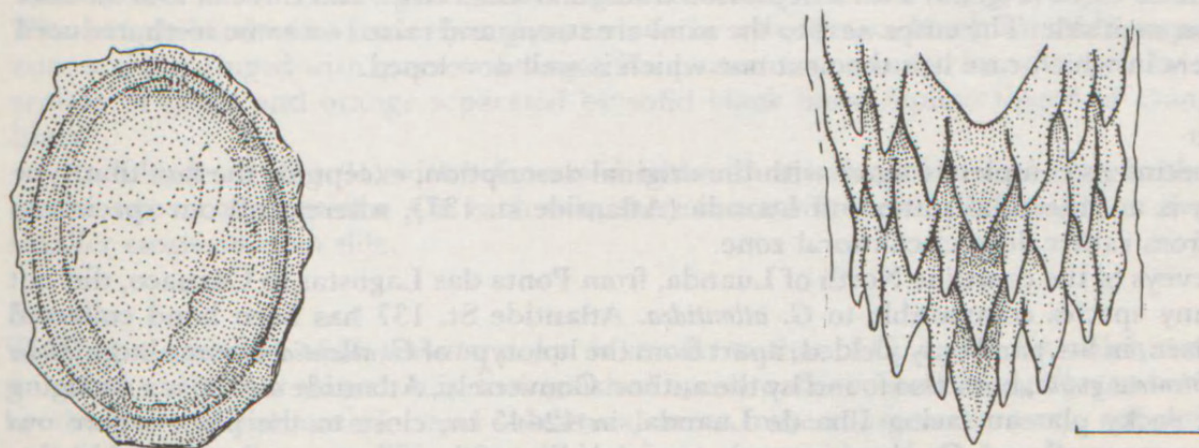


Fig. 24. *Gibberula atlantidea*: same locality, egg capsule. actual size: 1.1 mm.

Fig. 25. *Gibberula atlantidea*: same locality, three teeth of the radula. Scale bar is 10 μ m.

Head and foot with a pattern of dark green, pale yellow and orange. There is usually a large dark green area behind the eyes, an orange spot in front of them, and some yellow or dark spots on the tentacles. The foot is bordered by alternating dark green areas and clusters of yellow and orange blotches.

The internal mantle is covered with a blackish, amoeboid pattern with few large orange spots, on a pale greenish background. A lobe of external mantle, translucent, has been seen extended on the left side of a specimen. The siphon is short, tinged with dark green and orange.

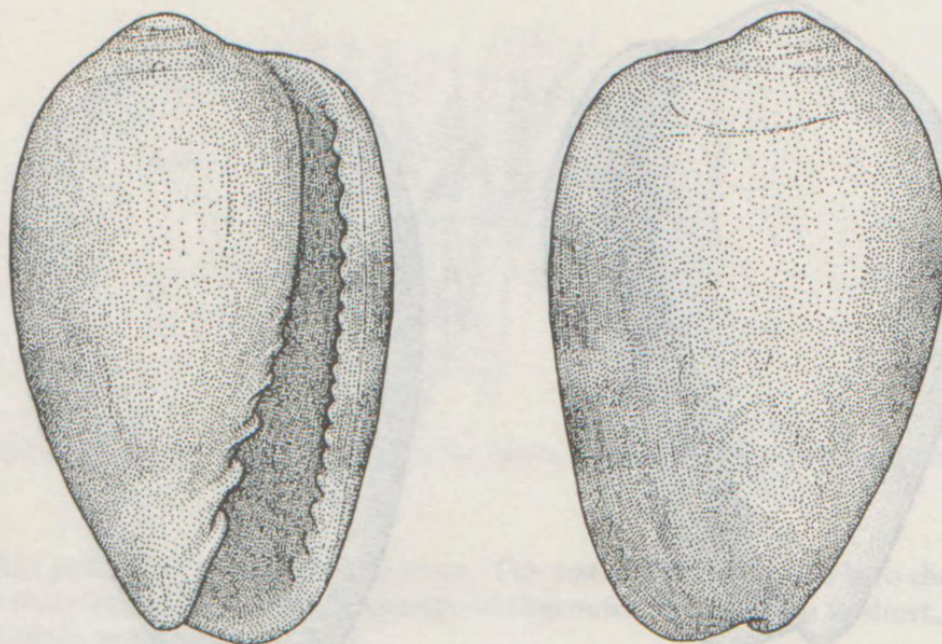


Fig. 26. *Gibberula atlantidea*: specimen from Bay of Lucira, 100 m. Actual size: 2.8 mm.

Radular teeth (Fig. 25) with a depressed triangular axial cusp, and three or four smaller cusps on each side. The cusps next to the axial are strong and raised on some teeth, reduced on others in which case it is the next one which is well developed.

Remarks

Our specimens completely agree with the original description, except for the fact that type locality is an intertidal station off Luanda (Atlantide st. 137), whereas all our specimens come from rather deep circalittoral zone.

Surveys of the coastline North of Luanda, from Ponta das Lagostas to Cacuaco, did not yield any species comparable to *G. atlantidea*. Atlantide St. 137 has been hand collected (Knudsen, in litt.) and only yielded, apart from the holotype of *G. atlantidea*, some large *Thais* and *Chicoreus gubbi*, both also found by the author. Conversely, Atlantide st. 136 is a dredging on the rocky plateau facing Ilha de Luanda, in 42–45 m, close to the place where our specimens were found. On these grounds, a mislabeling of the holotype is considered likely.

The holotype of *G. atlantidea* is presently badly damaged by acidic alcohol. The shell has lost transparency, colour pattern and shows signs of desquamation.

G. atlantidea is difficult to distinguish from *G. aurata* on the basis of the shell only. It differs by a more uniformly tawny colour, less distinct spiral bands which are seen only on the outer lip, lower spire and distinct notch at posterior insertion of outer lip.

It is readily distinguished by the colour pattern of the mantle, characteristic in either species although obviously derived from the same stock. *G. atlantidea* and *G. aurata* have been found sympatric at Lucira, each one within its characteristic depth zone.

An egg capsule with a well developed embryo, presumed to be conspecific from observation of the enclosed larval shell, has been collected with the specimens off Ilha de Luanda (Fig. 24).

Habitat

G. atlantidea is a deep circalittoral species, found in 50 to 100 m depth on hard bottoms where *Dendrophyllia ramea* corals are developed.

***Gibberula mimetica* n.sp.** (Figs. 27–32, 58–59)

Etymology: from latin mimeticus, a, um (adj.), 'imitator' [of the colour pattern of *G. aurata*]

Type locality: Chapeu Armado, province of Namibe, infralittoral 0–1 m.

Type material: Holotype (MNHN), 44 paratypes kept dry (MNHN, BMNH, IIT, UAN, FF) and 19 paratypes in alcohol (MNHN).

Other material examined

Souther Angola: Baia das Pipas, tidal pools, 7 specimens. Praia das Conchas, by Moçâmedes, 3 specimens. Chapeu Armado, numerous specimens including juveniles. Bay of Santa Maria, 5 specimens. Baia dos Limagens, 1 specimen.

Description

Shell up to 2.6×1.5 mm (holotype: 2.5×1.4 mm), with a moderately low, small spire. Outer lip with about 14–15 definite denticles inside. Columella with 5–6 plaits decreasing posteriorly in size. Profile of body whorl somewhat tapering anteriorly, often with a slight depression bordering anterior callus.

Shell translucent except for anterior callus, hyaline and colourless. Internal suture and soft parts are clearly visible through the shell.

Head/foot brightly coloured of orange, black and yellow in the type locality, of orange, black and green elsewhere. The head has black solid lines in front of the eyes, across each tentacle and on anterior lobules, these separating orange and yellow (or green) areas. The foot has a similar pattern of thick black lines separating orange and yellow (or green) areas.

Internal mantle very brightly coloured. There is a broad median band, with round, amoeboid or vermiculated green areas bordered with black, on a bright orange background. This zone is bordered anteriorly and posteriorly by a thick wavy black line and opaque white zone vaguely tinged with green or orange. The pattern is continued into the spire by definite sectors of green and orange separated by solid black lines. Siphon tinged of orange and black.

Radular teeth (Fig. 31) with a depressed, rather short, triangular axial cusp, flanked with one or two small denticles. On each side, there is a stout, raised cusp and then two other smaller cusps on each side.

Remarks

The mantle pattern of *G. mimetica* n. sp. is similar to that of *G. aurata*, for which it may be mistaken at the first glance. It is distinguished by a broader central orange/green band, and by the pale whitish anterior and subsutural areas more continuous, wavy, not definitely scalloped as in *G. aurata*. The green designs in the central band are usually contorted, not rounded or ovate. The foot is distinctive with black separations between green (or yellow) and orange areas, which do not exist in *G. aurata*. The shell is anyway readily distinguished, being smaller, more slender and completely hyaline.

All specimens seen at Chapeu Armado (Figs. 58, 59) have an orange, black and yellow foot and head, whereas specimens collected further south at Baia das Pipas and Praia das Conchas are orange, black and green. The mantle areas are consistently green in any case.

A sinistral specimen was collected at Chapeu Armado (Fig. 29).

Several dwarfed specimens (1.5×0.9 mm) (Fig. 30) were collected at Chapeu Armado, not differing otherwise from the remainder of the population. These cannot be distinguished, conchologically, from *G. tantula*.

All specimens from Limagens and Santa Maria, tentatively referred to this species, are

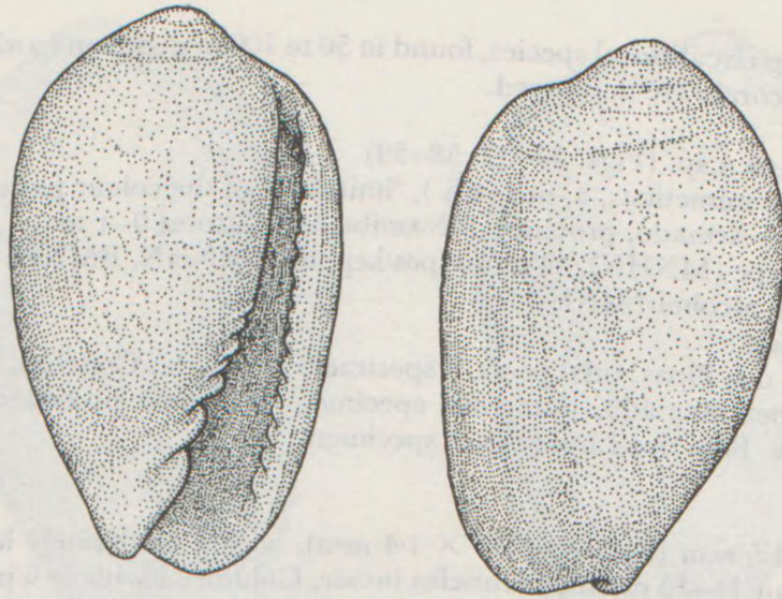


Fig. 27. *Gibberula mimetica* n. sp.: holotype from Chapeu Armado. Actual size: 2.5 mm.

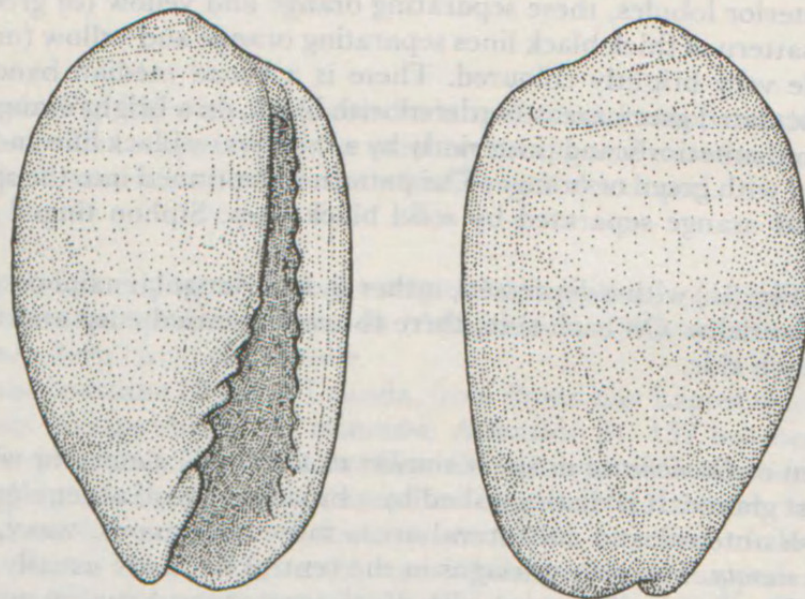


Fig. 28. *Gibberula mimetica* n. sp.: paratype, same locality. Actual size: 2.5 mm.

within the size of *G. tantula*. There were not enough adequately observed specimens to decide of their taxonomic treatment. The species is surprisingly absent from Bay of Lucira, in an apparently favourable environment.

Habitat

Within algal mat with agglutinated sediment in moderately exposed infralittoral localities, also in larger tidal pools.

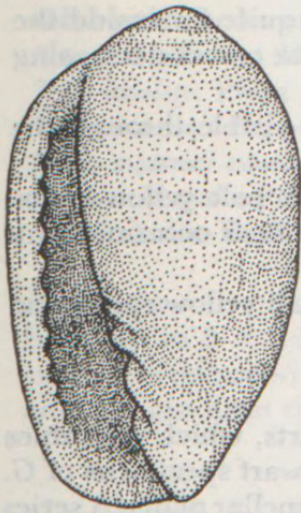


Fig. 29. *Gibberula mimetica* n. sp.: same locality, sinistral specimen. Actual size: 2.1 mm.



Fig. 30. *Gibberula mimetica* n. sp.: same locality, 'dwarf' specimen. Actual size: 1.5 mm.

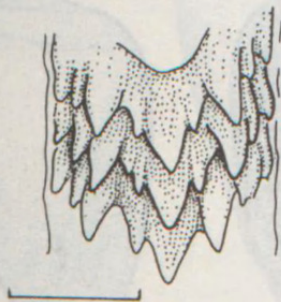
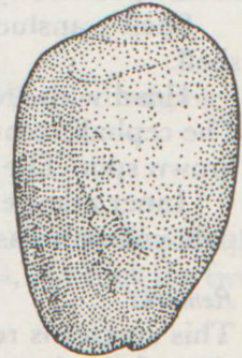
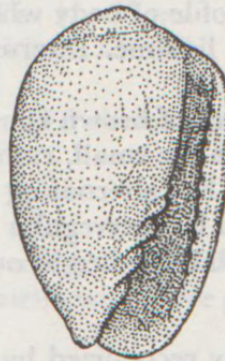


Fig. 31. *Gibberula mimetica* n. sp.: same locality, three teeth of the radula. Scale bar is 10 μ m.

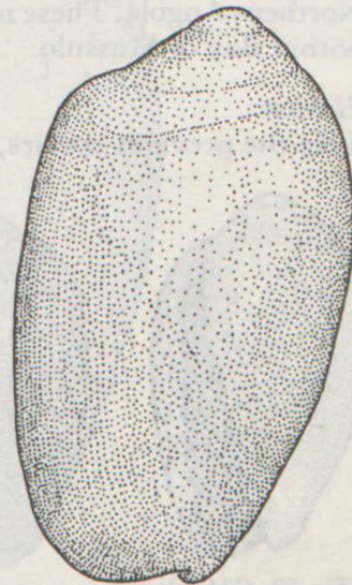
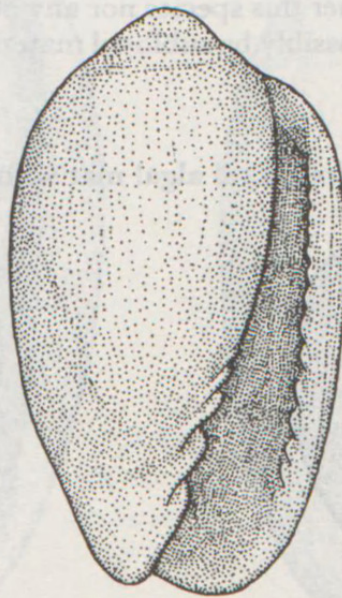


Fig. 32. *Gibberula mimetica* n. sp.: specimen from Praia das Conchas, tidal pools. Actual size 2.6 mm.

***Gibberula tantula* n.sp. (Figs. 33–35, 60)**

Etymology: from latin tantulus, a, um: 'so small'.

Type locality: Chapeu Armado, province of Namibe.

Type material: Holotype (MNHN), 66 paratypes kept dry (MNHN, BMNH, IIT, UAN, FF) and 9 paratypes in alcohol (MNHN).

Other material examined

Southern Angola: Praia Amelia, 10 specimens. Baia das Pipas: 1 specimen. Baia de Santa Maria, numerous specimens.

Description

Shell up to 1.6×0.9 mm (dimension of holotype), with a moderately low spire. Outer lip

thickened, with internally a dozen poorly defined denticles reaching quite far inside the aperture. Columella with four plaits, the foremost distinctly stronger, the others decreasing in size posteriorly. Profile of body whorl rather tapering anteriorly.

Shell translucent, hyaline. Internal sutures and soft parts clearly visible through the shell.

Head with a cluster of brown spots around the eyes, elsewhere with pale yellow spots. The cephalic tentacles are small, rather club shaped and flattened and bear occasionally a brown spot. The foot has alternating orange and pale yellow spots.

Inner mantle with large irregular areas of brownish black with small yellow spots, and pale yellow areas with large bright orange spots. Siphon pale yellow.

Remarks

This species is readily recognized by the colour pattern of the soft parts, which resembles that of *G. columnella*. Otherwise, shells cannot be distinguished from dwarf specimens of *G. mimetica* n.sp. (although a clue may be given by the strong foremost columellar plait). A series of specimens from Limagens, which were not observed for colour patterns when alive, possibly belong to this species but their identity cannot be ascertained.

Shells from Corimba, near Luanda, have been found to resemble this species. This occurrence is confusing, as neither this species nor any other similar has been found alive in Northern Angola. These may possibly be subfossil material, as are most of dead shells found within Bay of Mussulo.

Habitat

Like the previous species, in infralittoral algal mat with agglutinated sediment.



Fig. 33. *Gibberula tantula* n. sp.: holotype from Chapeu Armado. Actual size: 1.6 mm.

Fig. 34. *Gibberula tantula* n. sp.: paratype, same locality. Actual size: 1.5 mm.

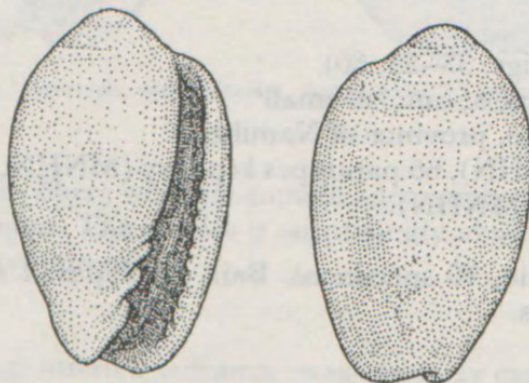


Fig. 35. *Gibberula tantula* n. sp.: specimen from Santa Maria. Actual size: 1.6 mm.

Gibberula columnella (Bavay, 1913) (Figs. 36–37, 63)

Original reference: *Marginella columnella* Bavay, in Dautzenberg, 1913, p. 26, Pl. 1, figs. 31–32.

Type locality: Praia Amelia (prov. Namibe), dredged in 15–35 m.

Type material: Holotype (figured in Dautzenberg, 1913) in MNHN.

Other material examined

Southern Angola: Praia Amelia, 3–5 m: 18 specimens and 6 shells. Santa Marta, dredging 40 m: 23 shells. Bay of Lucira (Bissonga), 1 m: 1 shell.

Description

Shell up to 3×1.5 mm, subcylindrical in shape, with a low spire. Outer lip thickened, smooth inside or with poorly defined denticles. Columella with three plaits, of which the two anterior are most distinct.

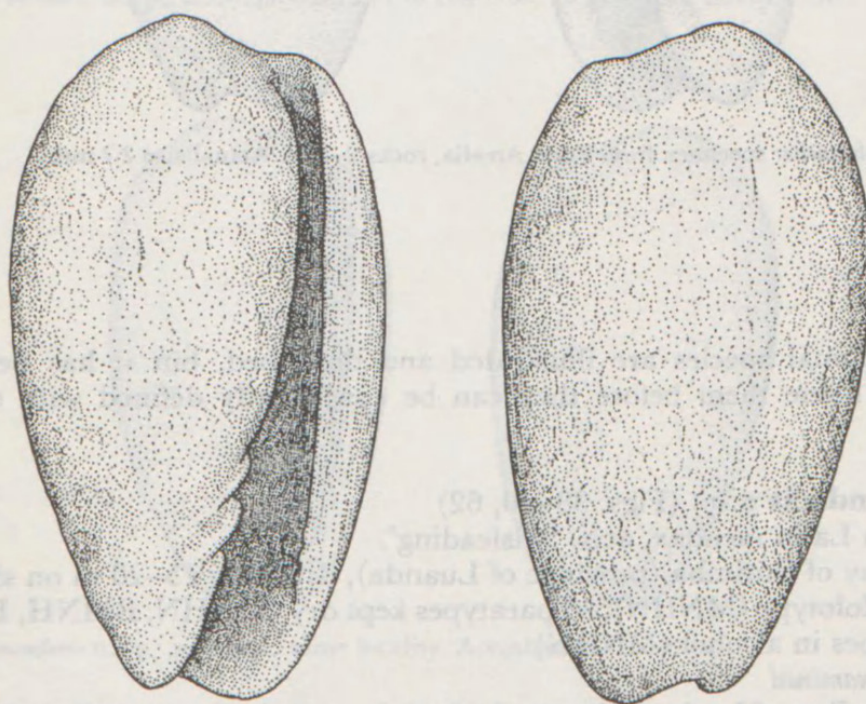


Fig. 36. *Gibberula columnella*: holotype from Praia Amelia. Actual size: 3.0 mm.

Shell translucent, hyaline. Internal sutures and soft parts clearly seen by transparency.

Head and foot coloured orange, yellow and black. The foot has alternating areas of yellow, and of black with yellow and orange spots; one large such black area covers axially the metapodium. The foot has not been seen to raise as parapodia.

Internal mantle mostly black, mixed with pale areas, entirely covered with numerous yellow spots and some orange spots. The same pattern extends to the siphon.

Remarks

This description is based on a living specimen observed close to the type locality, and conchologically compared to the holotype (here refigured, Fig. 36).

The list of observed occurrences is very conservative, as there are several similar species related to *Gibberula columnella*. Two new taxa (*G. mendacis* n. sp. and *G. confusa* n. sp.) observed on numerous living specimens, are introduced herein. Some shells which most probably

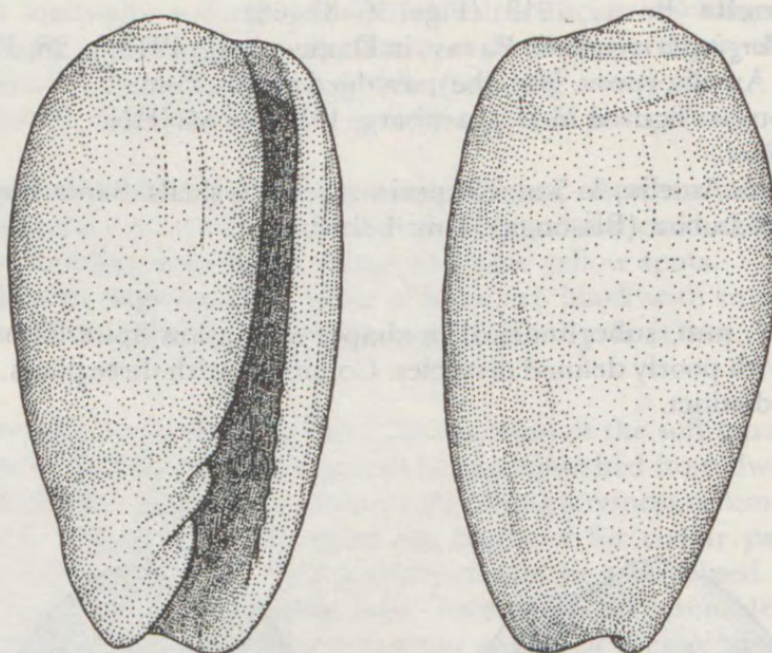


Fig. 37. *Gibberula columnella*: specimen from Praia Amelia, rocks 2–5 m. Actual size 2.7 mm.

represent additional species are illustrated and described, but it has been considered inadequate to name them before they can be consistently defined with data on living animals.

***Gibberula mendacis* n.sp.** (Figs. 38–40, 62)

Etymology: from Latin mendax, acis, 'misleading'.

Type locality: Bay of Corimba (province of Luanda), dredging 15–20 m on shell gravel.

Type material: Holotype (MNHN), 31 paratypes kept dry (MNHN, BMNH, IIT, UAN, FF) and 25 paratypes in alcohol (MNHN).

Other material examined

Southern Angola: Bay of Lucira (Bissonga), dredging on algal gravel 10 m: 14 shells. Santa Marta, dredging 40 m on shell sand: numerous specimens and shells.

Description

Shell up to 2.1×1.2 mm (Holotype 2.1×1.15), subcylindrical in shape, with a low spire. Outer lip thickened, rather straight with an abrupt posterior termination, minutely and distinctly denticulated inside. Columella with four thick plaits, decreasing posteriorly in size.

Shell translucent, tawny in colour. Internal sutures and soft parts may be seen by transparency.

Head with orange and yellow spots, and a crescentic brown mark to the inner side of each eye. Foot crawling flat, with the edge slightly curled upwards but not forming parapodia. It has broad radiating areas of yellow, a few orange spots anteriorly and posteriorly, and one or several broad brown patches on the metapodium.

Internal mantle with a reticulation of pale brown, including scattered small orange spots. The brown hue is denser along the anterior area.

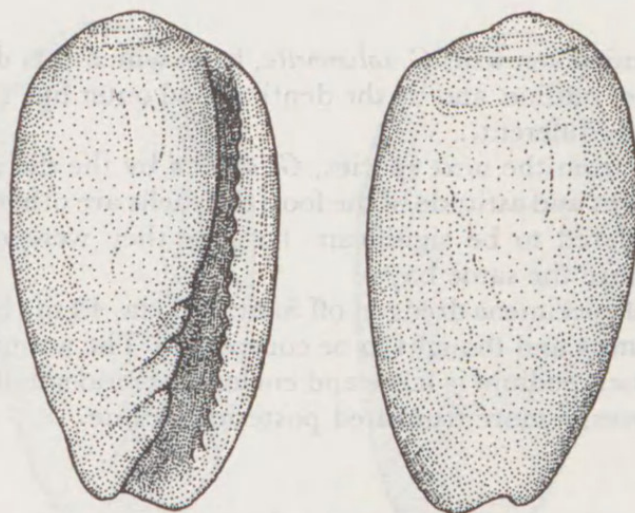


Fig. 38. *Gibberula mendacis* n. sp.: holotype from Bay of Corimba, 20 m. Actual size: 2.1 mm.

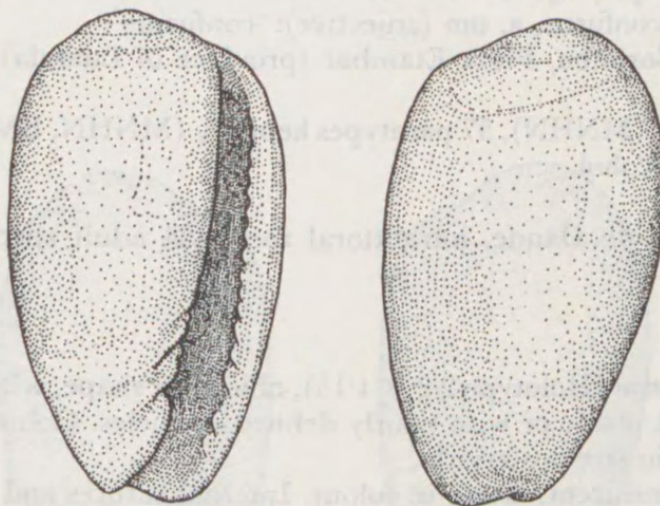


Fig. 39. *Gibberula mendacis* n. sp.: paratype, same locality. Actual size: 2.1 mm.

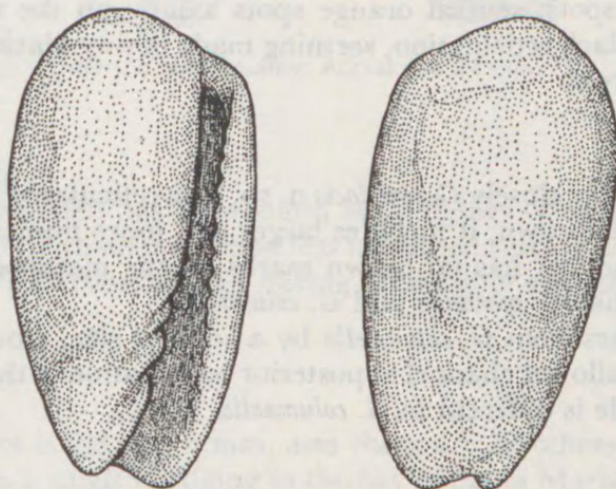


Fig. 40. *Gibberula mendacis* n. sp.: specimen from off Santa Marta, 40 m. Actual size 2.0 mm.

Remarks

This species may be mistaken with *G. columnella*, from which it is distinguished by slightly smaller size and stouter outline, and by the denticulated outer lip. The pattern on head/foot and mantle is also very different.

G. mendacis differs from the next species, *G. confusa* by the distinct denticulation of the outer lip, mantle pattern and attitude of the foot; the shells are otherwise very similar. These differences are considered to be significant because they were observed in populations distant less than 2 km in the same bay.

A large number of specimens dredged off Santa Marta, 40 m (Fig. 40) are similar to the specimens from Corimba and thought to be conspecific. The animal differs only in that the brown mark on the metapodium is large and encloses several small yellow spots. The shells have, in some instances, a more truncated posterior outline.

Habitat

This species has been found on bottoms of shell grit and sand devoid of mud, in 20 to 40 m depth.

***Gibberula confusa* n.sp.** (Figs. 41–42, 61)

Etymology: from Latin *confusus*, a, um (adjective): 'confusing'.

Type locality: Bay of Corimba, Praia Etambar (province of Luanda), on muddy rocks in 0–1 m.

Type material: Holotype (MNHN), 57 paratypes kept dry (MNHN, BMNH, IIT, UAN, FF) and 16 paratypes in alcohol.

Other material examined

Northern Angola: Barra do Dande, infralittoral rocks: 34 adult specimens and juveniles. Cacucaco, 1 shell.

Description

Shell up to 2.2×1.2 mm (Holotype 2.2×1.15), oblong in shape, with a blunt spire. Outer lip thickened, smooth inside or with poorly defined denticles. Columella with four plaits, decreasing regularly in size posteriorly.

Shell material translucent, tawny in colour. Internal sutures and soft parts clearly seen by transparency.

Head with orange and yellow spots, and a crescentic mark of crowded tiny black dots behind each eye. Foot raised laterally in parapodia, with large radiating spots of yellow, and few alternating orange spots; several orange spots axially on the metapodium. Internal mantle with a tenuous black reticulation, seeming made of tiny black dots, inserting orange spots and pale yellow areas.

Remarks

This species resembles very closely *G. mendacis* n. sp. The reticulated pattern of the mantle is definitely black, not pale brown; it includes larger and more numerous orange spots on a yellow background. The foot has no brown marks on the metapodium, and is distinctly folded in parapodia unlike *G. mendacis* and *G. columnella*.

G. confusa n.sp. differs from *G. columnella* by a smaller size, stouter and less truncated outline of the shell, a shallower channel at posterior termination of the aperture. The pattern on head/foot and mantle is different in *G. columnella*.

Habitat

G. confusa has been found in an algal mat infilled with mud, on infralittoral rocks 0–1 m.

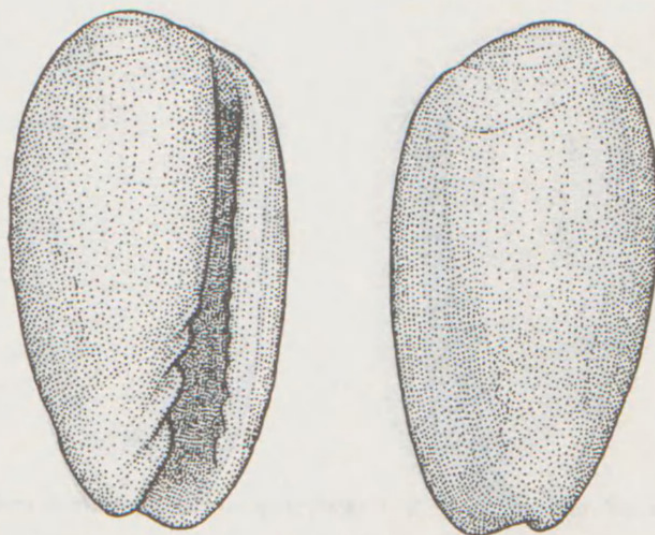


Fig. 41. *Gibberula confusa* n. sp.: holotype from Praia Etambar. Actual size: 2.2 mm.

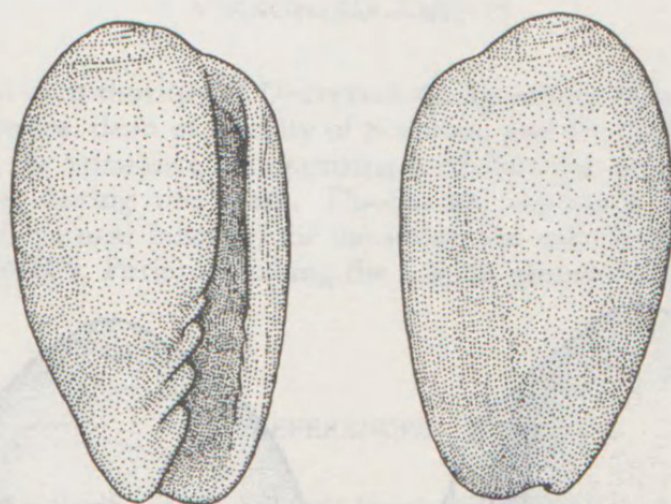


Fig. 42. *Gibberula confusa* n. sp.: paratype, same locality. Actual size 2.1 mm.

Gibberula sp. 1 (Fig. 43)

This kind of very slender shell has been found in dredgings of many southern localities. It differs from *G. columnella* by smaller size and less truncated spire. The outline of the posterior end of the outer lip is evenly rounded, not flaring. The rather smooth outer lip recalls that of *G. confusa* n. sp.

Gibberula sp. 2 (Fig. 44)

The specimen illustrated is 2.8×1.5 mm, and there are 22 others all live-taken (but not observed at that time) in a single dredging in the bay of Santa Maria. They look like a large and fat *G. mendacis*, with a very thick anterior end.

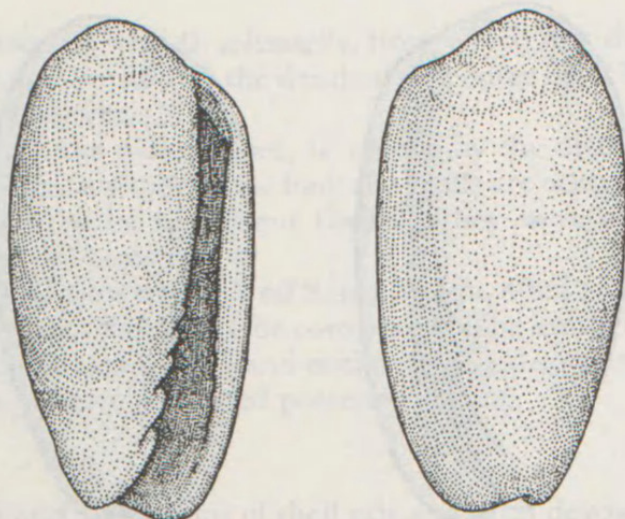


Fig. 43. *Gibberula* sp.: specimen from Bay of Lucira (Bissonga), 15 m. Actual size: 2.2 mm.

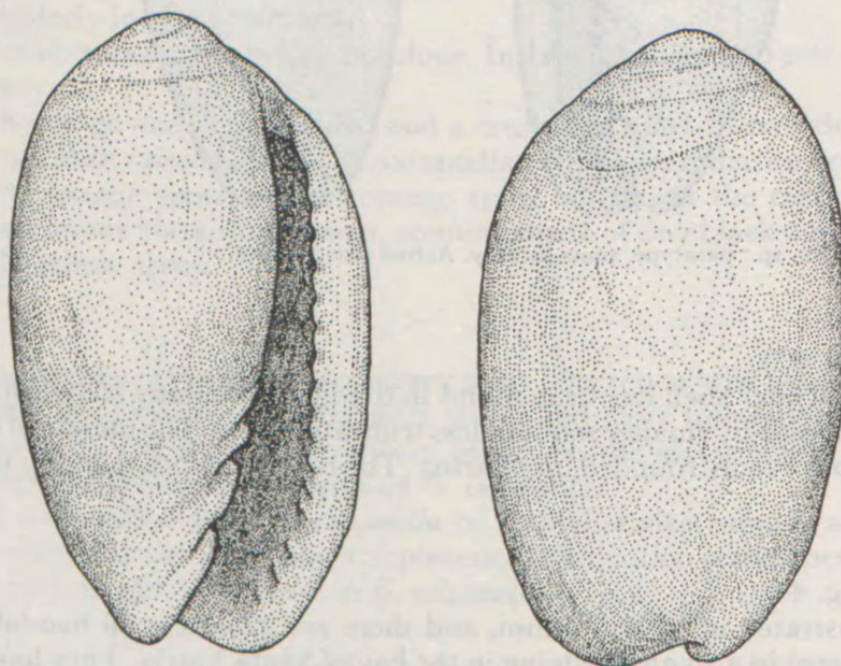


Fig. 44. *Gibberula* sp.: specimen from Bay of Santa Maria, 8–10 m. Actual size: 2.8 mm.

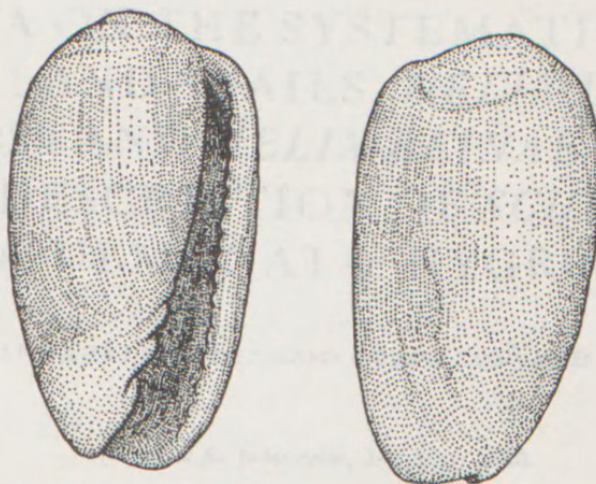


Fig. 45. *Gibberula* sp.: specimen from bay of Limagem, rocks 1–2 m. Actual size: 1.9 mm.

Gibberula sp. 3 (Fig. 45)

This is a very small species (2×1 mm) found alive in the infralittoral algal mat of the bays of Limagens and Santa Maria, alongside with *G. aurata*. The outer lip is minutely denticulated. The growth lines give the surface of body whorl a characteristic frosty appearance.

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REFERENCES

- COAN, E., 1965. A proposed reclassification of the family Marginellidae. *Veliger*, **7**: 184–194.
- DAUTZENBERG, P., ('1912') 1913. Mission Gruvel sur la côte occidentale d'Afrique (1909–1910): Mollusques marins. *Ann. Inst. Oceanogr.*, **5**: 1–111, pls. 1–3.
- GOFAS, S., in press. Le genre *Gibberula* (Marginellidae) en Méditerranée. *Lavori Soc. Ital. Malac.* **23** (2^o congresso, Sorrento, 1987).
- JOUSSEAUME, F. P., 1875. Coquilles de la famille des Marginelles. *Rev. Mag. Zool.*, **3**: 164–271, pls. 7–8.
- KNUDSEN, J., 1956. Marine Prosobranchs of tropical West Africa (Stenoglossa). *Atlantide Rep.*, **4**: 7–110, pls. 1–4.
- ODHNER, N., 1923. Contribution to the marine Molluscan faunas of south and west Africa. *Gbgs. K. Vet. Vitt. Samh. Handl.*, **26**: 1–39, 1 pl.
- REEVE, L. A., 1864–65. *Conchologia iconica, or illustrations of the shells of Molluscos animals. Monograph of the genus Marginella*. Vol. 15, 27 pls.
- TOMLIN, J. R. le B., 1917. A systematic list of the Marginellidae. *Proc. Malac. Soc., Lond.* **12**: 242–306.



Gofas, Serge. 1989. "The Marginellidae of Angola: the Genus *Gibberula*." *Journal of Conchology* 33(3), 109–139. <https://doi.org/10.5962/p.407941>.

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