

Received: 23 February 2026 • Accepted: 31 July 2026 • Published: 22 October 2026

Topic editor: Magalie Castelin • Section editor: Thierry Backeljau • Desk editor: Pepe Fernández

Research article

[urn:lsid:zoobank.org:pub:3F524A6C-84B2-40D0-BA67-27D1B08BFB16](https://zoobank.org/pub:3F524A6C-84B2-40D0-BA67-27D1B08BFB16)

Species of the genus *Gibberula* Swainson, 1840 (Gastropoda: Cystiscidae) from Namibia

Leon HOFFMAN^{1,*}  , Mayday HAULOFU²  ,
 Mildred J. JOHNSON³   & Michael L. ZETTLER⁴  

¹Leibniz Institute Senckenberg for Nature Research, Marine Research Department,
 Südstrand 40, 26382 Wilhelmshaven, Germany.

²University of Namibia, Sam Nujoma Marine and Coastal Resources
 Research Centre (SANUMARC), Henties Bay, Namibia.

³University of Namibia, Department of Environmental Sciences, Windhoek, Namibia.

⁴Leibniz Institute for Baltic Sea Research (IOW), Warnemünde, Germany.

*Corresponding author: Leon.Hoffman@Senckenberg.de

² Email: mhaulofu@unam.na

³ Email: mjohnson@unam.na

⁴ Email: Michael.Zettler@iow.de

Abstract. The marine gastropod fauna off Namibia (SW Africa) has hardly been explored. The current study on species of the genus *Gibberula* Swainson, 1840 is part of an inventory of marine gastropods from Namibia. Four species are described as new, all endemic to Namibia: *Gibberula oshishani* sp. nov., *G. evukule* sp. nov., *G. ehodhi* sp. nov., and *G. heyali* sp. nov. One additional species was also known from South Africa: *G. cf. bensoni* (Reeve, 1865). None of the species known from Angola was found in Namibia. Apparently, the Kunene River delta forms a biogeographical dividing line for species of *Gibberula* (and many others).

Keywords. SE Atlantic Ocean, Benguela Current, Mollusca, biodiversity, new species.

Hoffman L., Haulofu M., Johnson M.J. & Zettler M.L. 2026. Species of the genus *Gibberula* Swainson, 1840 (Gastropoda: Cystiscidae) from Namibia. *European Journal of Taxonomy* 1111: 1–18.
<https://doi.org/10.5852/ejt.2026.1111.3344>

Introduction

This study is part of a large biogeographic inventory of benthic, marine gastropods found off Namibia (SW Africa). An inventory of the marine bivalves of Namibia was completed in a similar recent study (Zettler & Hoffman 2025). With a reliable record of benthic fauna off Namibia, we create an assessment of the diversity of mollusks and provide input to ecological and environmental studies that can be used to improve the economic and environmental management of Namibia's offshore natural resources. This study concentrates on the marine gastropods of the genus *Gibberula* Swainson, 1840 that were found off Namibia.

For a long time, the genus *Gibberula* belonged to the family Marginellidae J. Fleming, 1828 and was only placed in the family Cystiscidae W. Stimpson, 1865 as a result of work by Coover & Coover (1995) and Fedosov *et al.* (2019). Twelve genera are currently known in Cystiscidae of which *Gibberula* contains 270 accepted extant species (MolluscaBase 2026). The majority (70%) of these 270 species were described in the years 2000–2025 in many articles, mostly concentrating on coastal areas of a large number of countries (MolluscaBase 2026). Cysticids are assumed to be active predators (Cossignani 2006).

Little is known on the occurrence of species of *Gibberula* off Namibia; a review was not yet done. In contrast, good reviews exist on the congeneric species of Angola (Gofas 1989) and South Africa (Lussi & Smith 1998). Gofas (1989) reported nine species from Angola of which five were described as new. Gofas recorded additional shells of undescribed species. Lussi & Smith (1998) reviewed the family Cystiscidae of South Africa; they reported seven species in *Gibberula* of which one was described as new. Cossignani & Lorenz (2020) described one additional new species off the NE coast of South Africa, bringing the South African species count to eight. Boyer *et al.* (2024a) described two new species of *Gibberula* from Cameroon and Boyer *et al.* (2024b) described three new species from St Helena and Ascension in the central South Atlantic. Boyer & Simbille (2025) described two new species from Gabon. Most gibberulid species from South Africa, Angola, Cameroon, Gabon, St Helena and Ascension are endemics.

Material and methods

The material included empty shells and live-collected specimens that were obtained during ten research cruises conducted between 2004 and 2022; for a listing of the sampling locations refer to Zettler & Hoffman (2025: 336–339). A comparison with known Angolan species of *Gibberula* was based on Gofas (1989); a comparison with South African species was based on Lussi & Smith (1998).

The material was predominantly collected by grabs and dredges during cruises attended by IOW staff. Benthic specimens were sampled from sublittoral depths (20 m) to the lower shelf (317 m). Biodiversity of Mollusca Linnaeus, 1758 is significantly reduced on the lower shelf off Namibia due to the presence of oxygen minimum zones (OMZ) covering large areas off central Namibia (Amorim & Zettler 2023). Cruise M122 (attended by SaM staff) investigated the palaeo-development of cold-water coral reefs in a water depth range 165–242 m and the material was obtained by grabs, box cores and gravity cores. Shells and corals were dated to Late Pleistocene or Early to Middle Holocene. The M122 material was taken in the OMZ and mostly empty shells were found.

Colour images of the shells were made using a confocal digital stacking microscope (Keyence 2000, SaM Wilhelmshaven). High resolution images of the shells were made using a scanning electron microscope (SEM) imaging (Vega 3, Tescan, SaM Wilhelmshaven). Shells were coated with gold to enhance imaging quality in the SEM. The incident electron energy was 10 keV; both secondary electron imaging as well as back-scatter electron imaging were used. The calibrated internal software of both the Keyence 2000 and Vega 3 Tescan microscopes were used to make size measurements.

For description of species we follow the terminology of Coover & Coover (1995). Spiral columellar grooves (also named folds, plaits or plica) in the aperture are named plications when they extend on the internal columella. The number of plications will be verified by removing the ultimate whorl face of one shell (only in species where many shells are available). Weaker spiral features on the parietal margin are named lirae; these lirae develop on the inner lip of adult specimens and they do not extend far on the inner whorls. The anterior or abapical channel of the aperture is herein named siphonal notch; adapically in the aperture is the posterior notch. The spire height is measured by the vertical distance between the adapical margin of the outer lip to the apex. Shell size is classified as small if height is less than 3 mm,

medium if between 3 and 6 mm and large if greater than 6 mm. The ventral view is weakly elevated when the height to width ratio is between 1.4 and 1.8 and it is regarded as (medium) elevated when the ratio exceeds 1.8. The spire is weakly elevated if the ratio of the spire height to total shell height is 5–10% and (medium) elevated when > 10%.

The great majority of our material consists of empty shells. Few specimens were sampled alive and they were initially stored in a formalin buffer and, subsequently, in ethanol. Images of living animals were not available. We did not investigate the soft parts of live-collected specimens.

Holotypes and some paratypes were deposited in the National Museum of Namibia (NMN). Some paratypes were kept in the Senckenberg Museum in Frankfurt am Main (SMF). Other material was kept in the reference collections at IOW and SaM.

Abbreviations

General

H = height of shell

W = width of shell.

Institutional

IOW = Institut für Ostseeforschung Warnemünde, Rostock, Germany

NMNWI = National Museum of Namibia, Windhoek, Namibia

SaM = Senckenberg am Meer, Wilhelmshaven, Germany

SMF = Senckenberg Museum Frankfurt, Germany

Results

Five species were identified in the material gathered off Namibia. Material of poor quality was not used in the analysis, therefore are not discussed herein.

Taxonomy

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda L.R. Cox, 1960
Order Neogastropoda Wenz, 1938
Superfamily Volutoidea Rafinesque, 1815
Family Cystiscidae W. Stimpson, 1865

Genus *Gibberula* Swainson, 1840

Type species

Gibberula zonata Swainson, 1840: 323, type by monotypy. Recent, type locality off Senegal (?).

Gibberula cf. *bensoni* (Reeve, 1865)

Figs 1–2

Marginella bensoni Reeve, 1865: pl. 27, sp. 158.

Diluculum inopinatum Barnard, 1962: 15, fig. 1.

Marginella bensoni – Barnard 1959: 7. — Kensley 1973: 188, fig. 717.

Diluculum inopinatum – Kensley 1973: 188, fig. 708.

Gibberula bensoni – Kilburn & Rippey 1982: 131.

Gibberula inopinata – Lussi & Smith 1998: 8–9, text figures.

Material examined (5 specs + 269 shells)

NAMIBIA • 8 shells; 20.7330° S, 12.8178° E; depth 232 m; 2 Jan. 2016; stn M122-GeoB20511-1; box core; SaM89133 • 26 shells; same data as for preceding; SMF 376630 • 3 shells; 20.7638° S, 12.8329° E; depth 226 m; 3 Jan. 2016; stn M122-GeoB20515-1; box core; NMNWI 259; Fig. 1A–G • 3 shells; same data as for preceding; NMNWI 260; Fig. 2A–F • 2 live-collected specs, 60 shells; same data as for preceding; SaM19134 • 57 shells; same data as for preceding; NMNWI 261 • 41 shells; 20.7636° S, 12.8313° E; depth 219 m; 3 Jan. 2016; stn M122-GeoB20516-1; box core; SMF 376631 • 10 shells; 20.7322° S, 12.8153° E; depth 232 m; 4 Jan. 2016; stn M122-GeoB20531-1 695–700 cm;

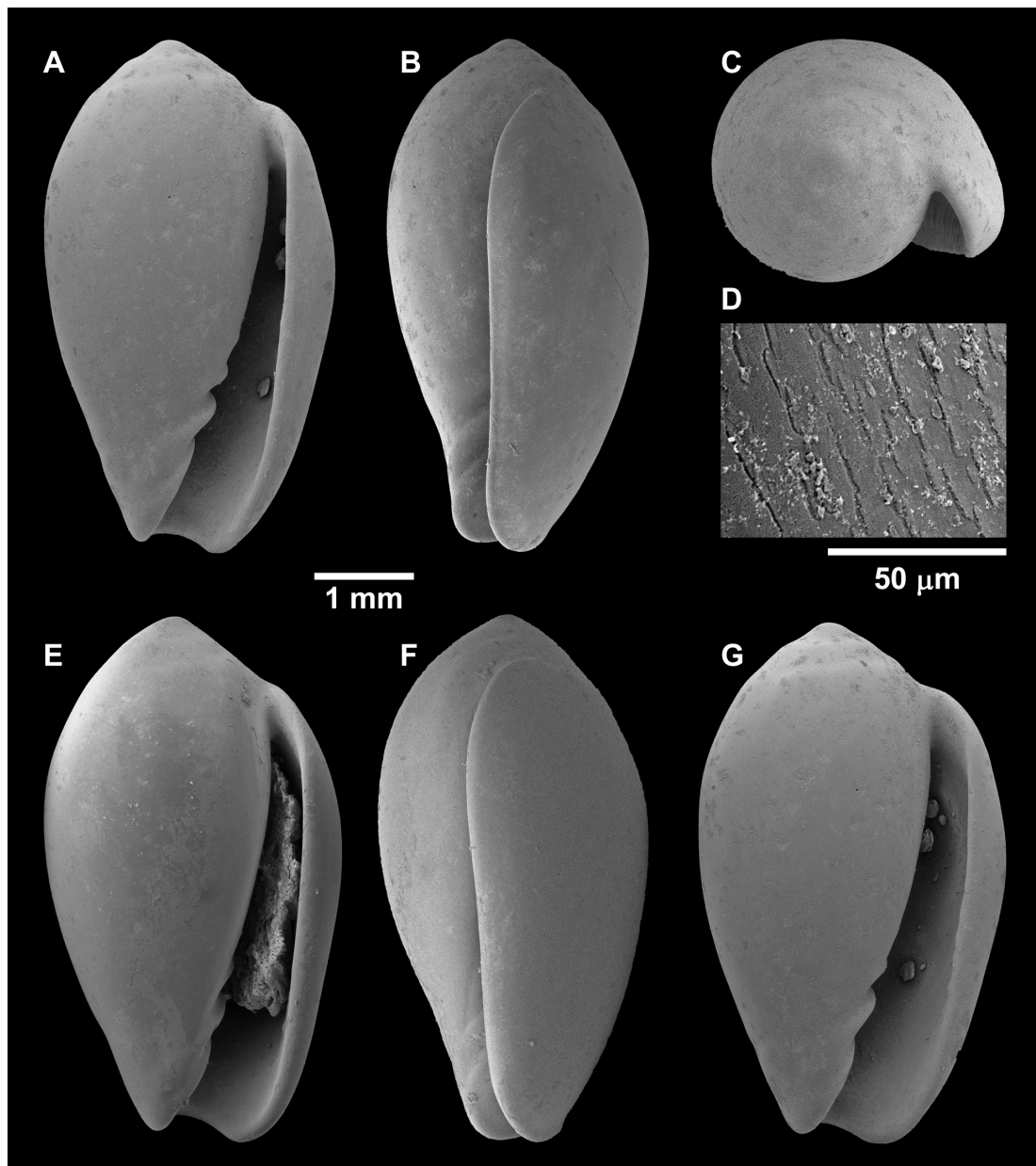


Fig. 1. *Gibberula* cf. *bensoni* (Reeve, 1865), Namibia, M122/GeoB20515-1 (NMNWI 259). A–D. H 4.8 mm, W 2.8 mm. E–F. H 4.9 mm, W 2.8 mm. G. H 4.8 mm, W 3.0 mm. A, E, G. Ventral views. B, F. Side views. C. Apical view. D. Micro-sculpture above second plication from anterior. Scale bars: A–C, E–G = 1 mm; D = 50 µm.

gravity core; Late Pleistocene; SaM89206 • 8 shells; 20.4376° S, 12.6687° E; depth 225 m; 9 Jan. 2016; stn M122-GeoB20571-1; box core; SaM8407 • 4 shells; 23.0000° S, 13.4986° E; depth 242 m; 25 Aug. 2019; stn M157-10; dredge; IOW M64.45 • 4 shells; 17.2671° S, 11.7241° E; depth 33 m; 31 Aug. 2019; stn M157-24; dredge; IOW M87.68 • 1 shell; 25.0000° S, 13.7328° E; depth 317 m; 6 Sep. 2019; stn M157-36; dredge; IOW M108.64 • 2 shells; 19.9980° S, 13.0100° E; depth 30 m; 27 Aug. 2019; stn MSM18-NAM-BE04; dredge; IOW T54.35 • 2 shells; 22.4990° S, 13.5330° E; depth 156 m; 18 Sep. 2019; stn MSM18-NAM-BE21; dredge; IOW T55.43 • 1 shell; 23.0000° S, 13.5000° E; depth 240 m; 14 Jan. 2022; stn MSM105-13; grab; IOW A64.13 • 16 shells; 23.0000° S, 13.6833° E; depth 155 m; 14 Jan. 2022; stn MSM105-14; grab; IOW A206.6 • 1 shell; 18.0000° S, 11.5167° E; depth 232.5 m; 22 Jan. 2022; stn MSM105-38; dredge; IOW A160.45 • 22 shells, 1 spec.; 27.0000° S, 15.1500° E; depth 70 m; 5 Feb. 2022; stn MSM105-97; grab; IOW A127.34, IOW A129.42 • 1 spec.; 28.2872° S, 15.7542° E; depth 115 m; 26 Nov. 2024; stn Anchor-CD/19/M/24e; grab; IOW AE9.1 • 1 spec.; 28.6599° S, 15.9653° E; depth 126 m; 20 Nov. 2024; stn Anchor-CD/19/M/24e; grab; IOW AE13.1.

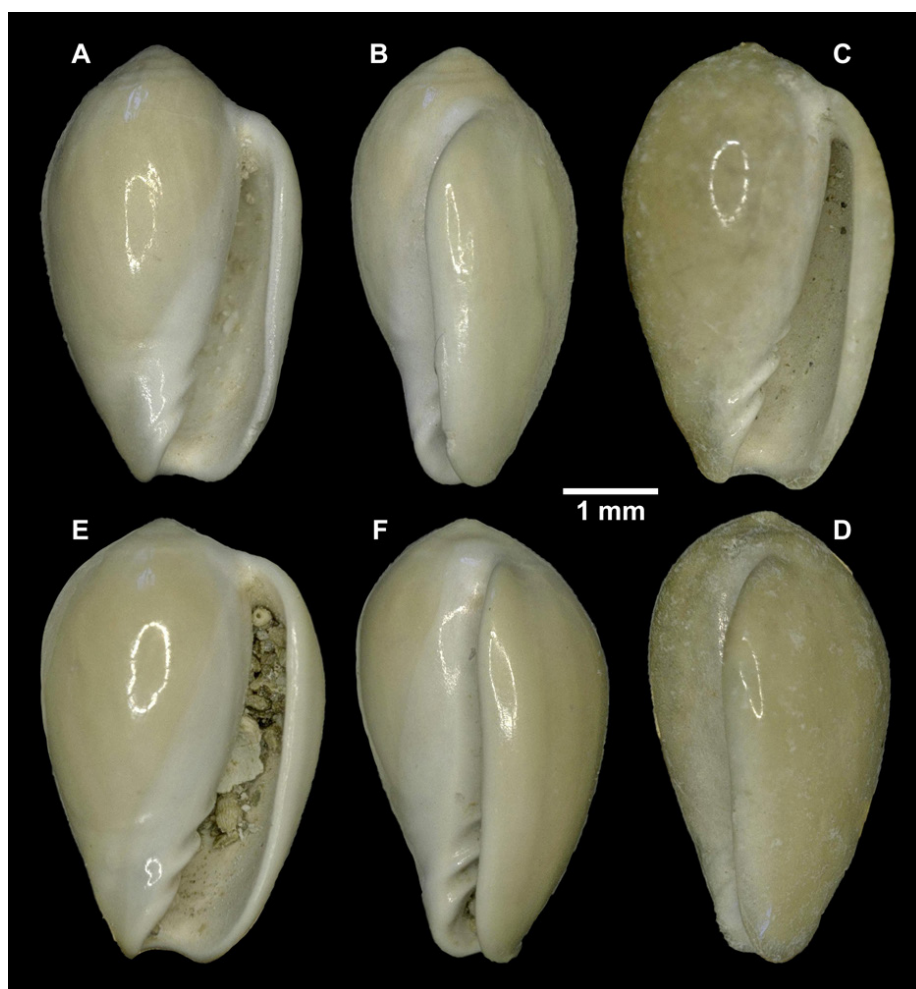


Fig. 2. *Gibberula cf. bensoni* (Reeve, 1865), M122-GeoB20515-1 (NMNWI 260). **A–B.** H 4.6 mm, W 2.7 mm. **C–D.** H 4.7 mm, W 3.0 mm. **E–F.** H 4.7 mm, W 3.0 mm. **A, C, E.** Ventral views, **B, D, F.** Side views. Scale bar = 1 mm.

Description

Marginelliform shell with medium size, ovate, weakly elongate outline, convolved, smooth, glossy; elevated, cyrtconoidal, spire, about 15% of shell height; adapically tapered, concave; apex with protoconch protruding covered in callus, weakly rounded shoulder, apical angle 100–120°; lip raised adapically at joint with penultimate whorl, slightly prosocline and straightened or weakly concave at periphery, thickened along margin, thickest at or slightly above periphery; suture obscured by callus. Aperture elongated, about 85% of shell height, narrow adapically, wider abapically; open, straight, siphonal notch and narrow posterior notch; convex columellar / parietal margin, with three oblique columellar plications that extend on the internal columella, adapical plication weaker, rarely one or two very weak parietal striae. Inside outer lip smooth or occasionally with less than five very weak denticles. Callus widely covering plications and parietal area; narrow on outer lip; micro-sculpture on callus with aligned straight margins directed towards exterior, length margins 10–60 mm. Shell white, translucent. Maximum observed height 4.9 mm, width 3.0 mm, height to width ratio 1.50–1.75.

Ecology

Uncertain. Congeners are likely predators of small invertebrates (small polychaetes, foraminiferans), or they opportunistically scavenge organic remains.

Distribution

The species is found off southern and south-western South Africa (Reeve 1865; Barnard 1959; Kensley 1973) and off Namibia (Kilburn & Rippey 1982; this study). The bathymetric depth range is 30–317 m.

Remarks

Gibberula bensoni was described from shells of Green Point, Cape Town, South Africa (Reeve 1865: pl. 27 fig. 158); it has a smooth inner lip and three plications; lirae were not reported. The type material of *G. bensoni* is considered lost (Kilburn & Rippey 1982).

Barnard (1962) ignored *G. bensoni* as a valid species and introduced a new species (*Diluculum inopinatum* Barnard, 1962) based on live-taken specimens from Saldanha Bay, North of Green Point. His description and rough sketch of the shell fits well to *G. bensoni*. He also added a sketch of its radulae but did not appoint a holotype. His genus *Diluculum* Barnard 1962 is nowadays regarded as a synonym of *Gibberula* (MolluscaBase 2026). We consider *G. inopinata* (Barnard, 1962) as a synonym of *G. bensoni*. A neotype for *G. bensoni* could be selected from Barnard's type material.

Lussi & Smith (1998: 9, top centre figure) illustrated a paratype of *Gibberula inopinata* from Saldanha Bay. This shell is most similar to our Namibian shells. They also illustrated a slender specimen labelled as *G. inopinata* (Green Point, Western Cape) and two other specimens labelled as *G. cf. inopinata*. We consider all specimens from Lussi & Smith (1998) that were named *G. inopinata* or *G. cf. inopinata* to be *G. bensoni*.

Kilburn & Rippey (1982) synonymised *G. inopinata* with *G. bensoni* and gave two sketches of the latter, one with four and another with eight plications / lirae. Hence, we believe their interpretation of *G. bensoni* to be wrong.

We are uncertain using the name of the South African *G. bensoni* for our Namibian shells because they occasionally show few weak denticles on the inside of the outer lip and occasionally have one or two weak lirae on the parietal lip.

Gibberula oshishani sp. nov.

[urn:lsid:zoobank.org:act:D7782687-71D9-4CE2-8E1D-6C87DD6CA09F](https://doi.org/10.21203/rs.3.rs-1234567/v1)

Fig. 3

Diagnosis

Large, elongated marginelliform shell with subcylindrical outline, weakly raised conoidal spire with keeled shoulder. Outer lip weakly denticulate within; about five plication/lirae. Shell beige to light orange; labial and internal callus cream white.

Etymology

‘*oshishani*’ is a crown (noun in apposition) in the Namibian language Oshiwambo; it refers to the keeled shoulder.

Type material

Holotype (Fig. 3A–C)

NAMIBIA • shell; 17.3903° S, 11.7239° E; depth 30 m; 5 Mar. 2008; stn MSM7-BE30; NMNWI 262, ex IOW K75.4b.

Paratypes (Fig. 3D–F; 10 shells)

NAMIBIA • 1 shell, for SEM; same data as for holotype; NMNWI 263, ex IOW K75.4b; Fig. 3D–F • 1 shell; same data as for holotype; IOW K75.4b • 6 shells; 18.0000° S, 11.7667° E; depth 56 m; 23 Jan. 2022; stn MSM105-42; SMF 376632, ex IOW A208.53 • 1 shell; 18.0000° S, 11.7667° E; depth 56 m; 23 Jan. 2022; stn MSM105-42; SMF 376633, ex IOW A205.2 • 1 shell; 18.0000° S, 11.7916° E; depth 20 m; 23 Jan. 2022; MSM105-43; dredge; SMF 376634, ex IOW A196.90.

Other material examined (3 live-collected specs)

NAMIBIA • 3 specs, in ethanol; 18.0000° S, 11.7667° E; depth 45 m; 2 Nov. 2016; stn M131-P4; IOW P13.22.

Description

Convolved, smooth, glossy shell; weakly elevated spire with three whorls, about 7% of shell height; subcylindrical, elongated outline with blunt, smooth, spiral keel on shoulder; convex abapical end; depressed apex with weakly protruding protoconch covered in callus, apical angle about 130°; weak spiral cord delimiting fasciole on last whorl; orthocone lip equally thickened along margin with parallel rim on outside; suture obscured by callus. Aperture elongated, about 93% of shell height, narrow adapically, wider abapically; open, straight, siphonal notch and narrow posterior notch; flexuous columellar / parietal margin, with three, oblique plications, two abapical plications strongest; three weak lirae on parietal margin. Inside of outer lip finely denticulate, 20–25 denticles. Callus narrowly covering plications, lirae, parietal area and outer lip. Observed maximum height 7.8 mm, width 4.0 mm, height to width ratio about 1.95.

Ecology

Uncertain.

Distribution

The species lives off northern Namibia (17.3–18.0° S) at depths of 20–56 m, south of the Kunene River.

Differential diagnosis

Gibberula oshishani sp. nov. is similar to *G. evukule* sp. nov. (Fig. 2), *G. cristata* Gofas, 1989 and *G. benguelensis* Jousseaume, 1875. *Gibberula evukule* has approximately the same height but the two abapical plications are much stronger and extend over the base, has an ovate as opposed to a

subcylindrical profile and lacks the shoulder keel (Fig. 4). *Gibberula cristata* has approximately the same maximum height and a shoulder keel but has a broader outline and stronger labial teeth (Gofas 1989). *Gibberula benguelensis* has approximately the same maximum height but has a blunt apex, a broader ovate outline and lacks the shoulder keel (Gofas 1989). The type locality (São Felipe de Benguela) of *G. benguelensis* is uncertain, it could be off Angola or off Namibia (Gofas 1989); we did not find the species in Namibia.

The numbers of columellar plications vs parietal lirae are uncertain because no internal check of plications was made.

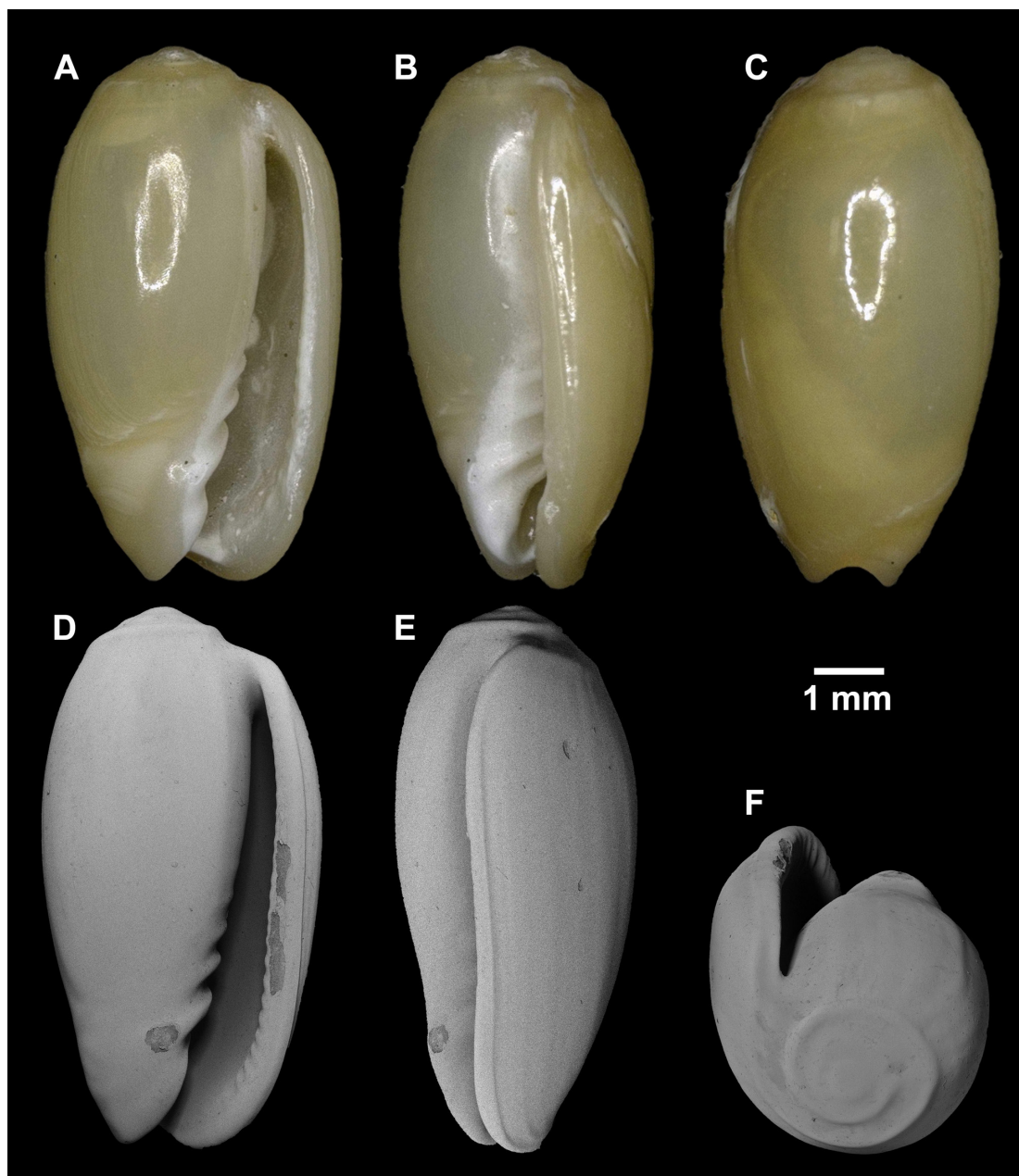


Fig. 3. *Gibberula oshishani* sp. nov., Namibia, MSM7-BE30. **A–C.** Holotype (NMNWI 262), H 7.8 mm. **D–F.** Paratype (NMNWI 263), H 7.8 mm. **A, D.** Ventral views. **B, E.** Side views. **C.** Dorsal view. **F.** Apical view. Scale bar = 1 mm.

Gibberula evukule sp. nov.

[urn:lsid:zoobank.org:act:83C55F07-E53E-4513-929C-D8A6FE4A23B5](https://zoobank.org/urn:lsid:zoobank.org:act:83C55F07-E53E-4513-929C-D8A6FE4A23B5)

Fig. 4

Diagnosis

Large, weakly elongated, marginelliform shell with ovate outline; weakly elevated, cyrtconoidal spire with pointed apex. Outer lip finely denticulate inside; about seven plication / lirae. Shell white.

Etymology

‘*evukule*’ is a giant (noun in apposition) in the Namibian language Oshiwambo; it refers to the biggest species among the Namibian congeners.

Type material

Holotype (Fig. 4E–G)

NAMIBIA • shell; 20.7638° S, 12.8329° E; depth 226 m; 3 Jan. 2016; stn M122-GeoB20515-1; box core; NMNWI 264.

Paratypes (Fig. 4A–D; 60 shells)

NAMIBIA • 1 shell for SEM; same data as for holotype; NMNWI 265 • 34 shells; same data as for holotype; NMNWI 266 • 25 shells; 20.7636° S, 12.8313° E; depth 219 m; 3 Jan. 2016; stn M122-GeoB20516-1; box core; SMF 376635.

Other material examined (33 shells)

NAMIBIA • 1 shell; 23.0000° S, 13.4986° E; depth 242 m; 25 Aug. 2019; stn M157-10; dredge; IOW M25.19 • 10 shells; 22.9998° S, 13.6832° E; depth 154 m; 26 Aug. 2019; stn M157-11; dredge; IOW M63.76 • 2 shells; 22.4990° S, 13.5330° E; depth 156 m; 18 Sep. 2019; stn MSM18-NAM-BE21; dredge; IOW T55.43 • 2 shells; 23.0000° S, 13.5000° E; depth 240 m; 18 Sep. 2011; stn MSM105-13; grab; IOW A64.13 • 7 shells; 23.0000° S, 13.6833° E; depth 155 m; 14 Jan. 2022; stn MSM105-14; grab; IOW A206.6 • 3 shells; 18.0000° S, 11.5167° E; depth 232.5 m; 22 Jan. 2022; stn MSM105-38; dredge; IOW A160.45 • 2 shells; 18.0000° S, 11.7167° E; depth 95 m; 23 Jan. 2022; stn MSM105-41; dredge; IOW A130.65 • 4 shells; 20.7186° S, 12.8174° E; depth 219 m; 3 Jan. 2016; stn M122-GeoB20522-1; grab; SaM85564 • 1 shell; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 95–100 cm; gravity core; Late Pleistocene; SaM89162 • 1 shell; 20.7322° S, 12.8153° E; depth 232 m; 4 Jan. 2016; stn M122-GeoB20531-1 695–700 cm; gravity core; Late Pleistocene; SaM89163.

Description

Convolved, smooth, glossy marginelliform shell; weakly elevated spire, 5–10% of shell height; ovate outline, abapically tapered; weakly pointed apex, weakly protruding protoconch covered by callus, apical angle about 130°; orthocline lip maximally thickened at periphery with thin parallel rim on outside of lip; suture obscured by callus (Fig. 4A–B, E–F). Aperture wide abapically, narrow adapically, 90% of shell height; open, straight siphonal notch; narrowly curved posterior notch; convex columellar / parietal margin, three abapical columellar plications, the second plication strongest, flattened; four parietal lirae, weaker adapically. Outer lip finely denticulate inside (about 27 denticles in holotype, Fig. 4E). Callus widely covering plications, lirae and parietal area; narrow on lip; callus micro-sculpture with misaligned straight margins directed towards exterior, length margins 10–60 mm (Fig. 4C). Observed maximum height 8.2 mm, width 4.8 mm, height to width ratio about 1.7.

Ecology

Uncertain.

Distribution

Empty shells were found off northern Namibia (18–23° S) at depths of 95–242 m.

Differential diagnosis

The present species is similar to *Gibberula oshishani* sp. nov. (Fig. 3, see remarks under that species), *G. gruveli* (Bavay, 1913), and *G. benguelensis* Jousseaume, 1875. *Gibberula gruveli* has approximately the same maximum height but it has a broader outline, a more elevated apex and five plications/lirae

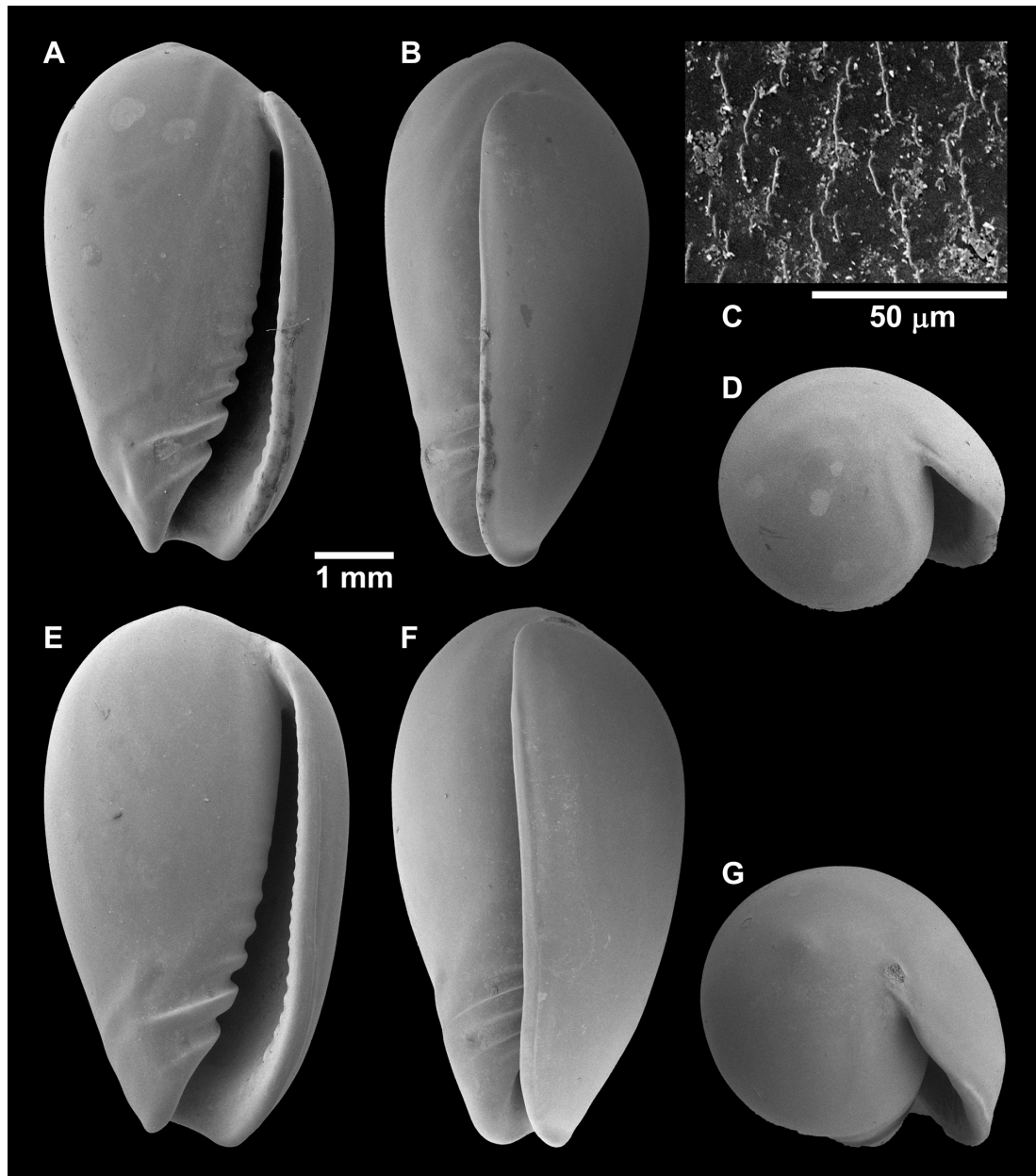


Fig. 4. *Gibberula evukule* sp. nov., Namibia, M122-GeoB20515-1. **A–D.** Paratype (NMNWI 265), H 7.9 mm, W 4.5 mm. **E–G.** Holotype (NMNWI 264), H 8.2 mm, W 4.8 mm. **A, E.** Ventral views. **B, F.** Side view. **C.** Micro-sculpture above second plication from anterior. **D, G.** Apical views. Scale bars: A–B, D–G = 1 mm; C = 50 µm.

(Gofas 1989), as opposed to seven in *Gibberula evukule* sp. nov. *Gibberula benguelensis* has approximately the same height but it has a blunt apex with more tapered abapical outline and five plications/lirae (Gofas 1989). In contrast to both these species, *G. evukule* is more ovate-elongated with pointed apex and has three plications and about four lirae.

Note that the number of plications (3) was checked on the internal columella by removing the outer whorl face of a shell.

***Gibberula ehodhi* sp. nov.**

[urn:lsid:zoobank.org:act:B2672A5D-B834-4A8B-8CD5-AF761EBEDC42](https://zoobank.org/urn:lsid:zoobank.org:act:B2672A5D-B834-4A8B-8CD5-AF761EBEDC42)

Fig. 5

Diagnosis

Medium-sized, weakly elongated, marginelliform shell with biconoidal outline, tapered abapically; elevated, cyrtconoidal spire with blunt apex. Outer lip denticulate inside; three columellar plications, no lirae. Shell white, translucent.

Etymology

‘*ehodhi*’ is a tear (noun in apposition) in the Namibian language Oshiwambo; it refers to the shell shape.

Type material

Holotype (Fig. 5H–I)

NAMIBIA • shell; 22.9998° S, 13.6832° E; depth 154 m; 26 Aug. 2019; stn M157-11; box core; NMNWI 267, ex IOW M63.39.

Paratypes (Fig. 5A–G; 101 shells)

NAMIBIA • 2 shells for SEM; same data as for holotype; NMNWI 268 (Fig. 5A–C), NMNWI 269 (Fig. 5D–G) • 99 shells; same data as for holotype; NMNWI 270.

Other material examined (8 specs, 1155 shells)

NAMIBIA • 1 shell; 18.0000° S, 11.7167° E; depth 95 m; 23 Jan. 2022; stn MSM105-41; dredge; IOW A130.65 • 1 spec.; 18.0000° S, 11.7916° E; depth 20 m; 23 Jan. 2022; stn MSM105-43; IOW A196.6 • 3 specs, in ethanol; 27.0000° S, 14.7167° E; depth 245 m; 4 Feb. 2022; stn MSM105-92; grab; IOW A163.16 • 1 spec., in ethanol; 27.0000° S, 14.8167° E; depth 207 m; 4 Feb. 2022; stn MSM105-93; grab; IOW A113.16 • 1 spec., in ethanol; 18.0000° S, 11.7667° E; depth 45 m; 2 Nov. 2016; stn M131-P4; grab; IOW P12.27 • 10 shells; 25.0001° S, 13.9168° E; depth 187 m; 7 Sep. 2019; stn M157-38; dredge; IOW M99.62; Fig. 5J • 2 specs, 99 shells; 20.7330° S, 12.8178° E; depth 232 m; 2 Jan. 2016; stn M122-GeoB20511-1; box core; SaM85559 • 585 shells; 20.7638° S, 12.8329° E; depth 226 m; 3 Jan. 2016; stn M122-GeoB20515-1; box core; SaM85560 • 405 shells; 20.7636° S, 12.8313° E; depth 219 m; 3 Jan. 2016; stn M122-GeoB20516-1; box core; SaM85561 • 8 shells; 20.6902° S, 12.8532° E; depth 182 m; 4 Jan. 2016; stn M122-GeoB20527-1; gravity core; Late Pleistocene; SaM89189 • 4 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 90–95 cm; gravity core; Late Pleistocene; SaM89303 • 7 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 95–100 cm; gravity core; Late Pleistocene; SaM89304 • 3 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 105–110 cm; gravity core; Late Pleistocene; SaM89305 • 6 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 115–120 cm; gravity core; Late Pleistocene; SaM89306 • 3 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 135–140 cm; gravity core; Late Pleistocene; SaM898307 • 2 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 175–180 cm; gravity core; Late Pleistocene; SaM89308 • 4 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-

GeoB20528-1 205–210 cm; gravity core; Late Pleistocene; SaM89309 • 2 shells; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 225–230 cm; gravity core; Late Pleistocene; SaM89310 • 1 shell; 20.7055° S, 12.8768° E; depth 187 m; 4 Jan. 2016; stn M122-GeoB20528-1 245–250 cm; gravity core; Late Pleistocene; SaM89311 • 3 shells; 20.7322° S, 12.8153° E; depth 232 m; 4 Jan. 2016; stn M122-GeoB20531-1 695–700 cm; gravity core; Late Pleistocene; SaM89312 • 33 shells; 20.7503° S, 12.8622° E; depth 166 m; 5 Jan. 2016; stn M122-GeoB20539-1; box core; Late Pleistocene; SaM8364 • 1 spec., 16 shells; 20.5031° S, 12.6678° E; depth 224 m; 5 Jan. 2016; stn M122-GeoB20545-1; box core; Holocene; SaM89181 • 25 shells; 20.7504° S, 12.8619° E; depth 162 m; 6 Jan. 2016; stn M122-GeoB20548-1; grab; Holocene; SaM8431 • 25 shells; 20.7376° S, 12.6687° E; depth 225 m; 9 Jan. 2016; stn M122-GeoB20571-1; box core; Holocene; SaM8406.

Description

Medium-sized, weakly elongated, convolved, smooth, glossy, marginelliform shell; elevated spire about 10–12% of shell height, apical angle 110–120°; apex with weakly protruding protoconch covered by callus; three whorls; margin ultimate whorl slightly raised, partly covering penultimate whorl; orthocline lip, weakly concave below periphery, reclining adapically, thickness maximum at periphery, thinner below; suture obscured by callus. Elongated aperture, about 88% of shell height, widening anteriorly; open, straight, posterior notch; wide siphonal notch; weakly convex columellar/parietal margin with three, oblique, columellar plications, two abapical plications strongest, 0–1 weak parietal lirae. Inside outer lip with about 11 denticles, strongest denticles anteriorly. Callus widely covering plications, narrow on parietal area and outer lip; micro-sculpture of columellar callus with regular straight margins directed towards exterior, length margins 10–60 mm. Maximum observed shell height 4.1 mm, width 2.5 mm; height to width ratio 1.6–1.7.

Ecology

Uncertain.

Distribution

The species is known off Namibia (18–27° S) at depths of 20–245 m.

Differential diagnosis

The present species is similar to *Gibberula bensoni*, *G. benguelensis*, *G. aurata* (Bavay, 1913), *G. atlantidea* (Knudsen, 1956), *G. mimetica*, *G. rufanensis* (W.H. Turton, 1932), *G. almo* (Bartsch, 1915) and *G. jeanae* Lussi & G. Smith, 1998. *Gibberula bensoni* is of similar size but is more elongated, with a sloping outer lip, inner lip without denticulations and a more pointed apex. The Angolan *G. benguelensis* is larger with five plications/lirae (Gofas 1989); *Gibberula ehodhi* sp. nov. is wider with pointed apex and has 3–4 plications/lirae. The Angolan *G. aurata* has a similar outline but is smaller (up to 3 mm) with strong denticles and is light orange (Gofas 1989); *Gibberula ehodhi* is about 4 mm, with weaker denticles and is white. *Gibberula atlantidea* is very similar but has 4–5 plications/lirae and is about 3 mm (Gofas 1989); *Gibberula ehodhi* has less plications/lirae and is larger. The Angolan *G. mimetica* is about 2.5 mm and has 5–6 plications/lirae (Gofas 1989); *Gibberula ehodhi* is larger (4 mm) and has 3–4 plications/lirae. The South African *G. rufanensis* has a similar outline and size but is more conical apically and has more parietal plications/lirae (Lussi & Smith 1998). The South African *G. almo* has a similar outline and size but is more ovate-oblong abapically and has more parietal plications/lirae (Lussi & Smith 1998). The South African *G. jeanae* has a similar size but is more ovate abapically, with a fasciole and more parietal plications/lirae (Lussi & Smith 1998).

Note that the number of plications on the internal columellar plications (3) was checked by removing the outer whorl face of a paratype shell.

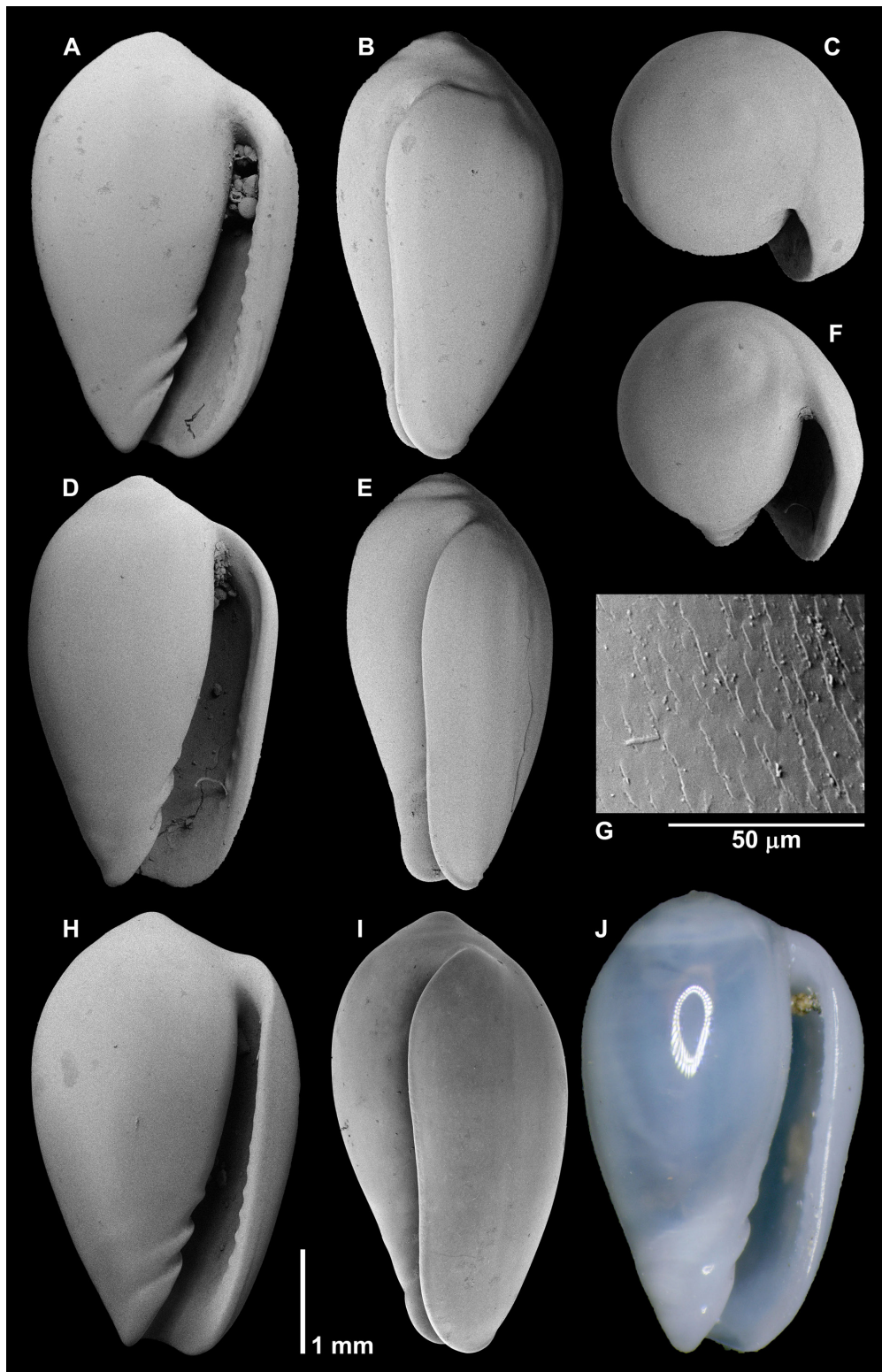


Fig. 5. *Gibberula ehodhi* sp. nov., Namibia. **A–C.** Paratype (NMNWI 268), M157-11, H 3.7 mm. **D–G.** Paratype (NMNWI 269), same locality, H 3.6 mm. **H–I.** Holotype (NMNWI 267), same locality, H 3.9 mm. **J.** M157-38, H 4.1 mm (IOW M99.62). **A, D, H, J.** Ventral views. **B, E, I.** Side views. **C, F.** Apical views. **G.** Micro-sculpture above 2nd plication from anterior. Scale bars: A–F, H–J = 1 mm; G = 50 µm.

Gibberula heyali sp. nov.

[urn:lsid:zoobank.org:act:0D8648FE-69E0-432E-8104-BDB2FD4C4C89](https://zoobank.org/urn:lsid:zoobank.org:act:0D8648FE-69E0-432E-8104-BDB2FD4C4C89)

Fig. 6

Diagnosis

Small, marginelliform shell with elongated, ovate outline; weakly elevated cyrtconoidal spire with blunt apex. Outer lip finely denticulate inside; seven plications/lirae. Shell white.

Etymology

‘*heyali*’ (noun in apposition) means seven in the Namibian language Oshiwambo; it refers to the seven plications/lirae.

Type material

Holotype (Fig. 6A–D)

NAMIBIA • shell; 18.0000° S, 11.7667° E; depth 56 m; 23 Jan. 2022; stn MSM105-42; dredge; NMNWI 271, ex IOW A205.2.

Description

Small, convolved, smooth, glossy shell; weakly elevated spire about 8% of shell height; ovate-elongated outline, abapically weakly tapered; apex with weakly protruding protoconch covered by callus; apical angle about 120°; two whorls; outer lip slightly raised adapically, partly covering penultimate whorl; orthocline lip, weakly concave below periphery, reclining adapically, thickness maximum at periphery, thinner below; lip blunt and bevelled at periphery; suture obscured by callus. Elongated aperture, 92%

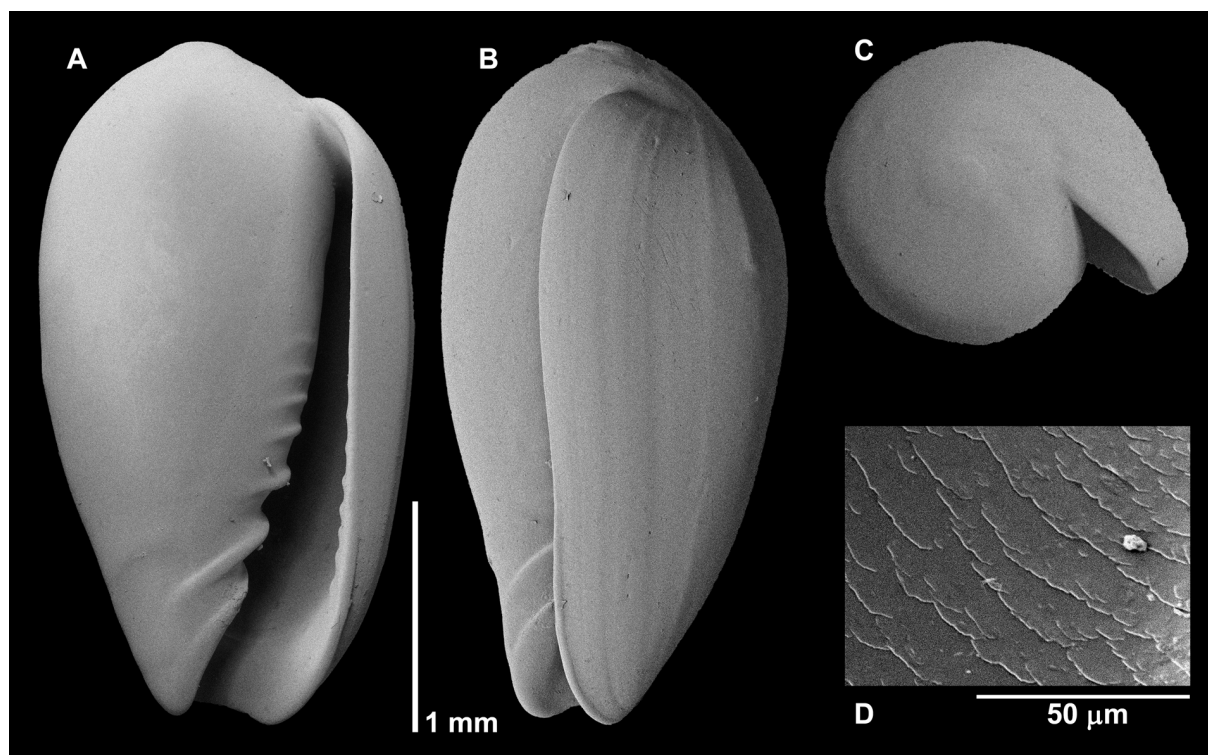


Fig. 6. *Gibberula heyali* sp. nov., holotype (NMNWI 271), Namibia, MSM105-42, H 2.8 mm, W 1.5 mm. A. Ventral view. B. Side view. C. Apical view. D. Micro-sculpture above 2nd plication from the anterior. Scale bars: A–C = 1 mm; D = 50 µm.

of shell height, widening anteriorly; open, curved, posterior notch; wide siphonal notch; weakly convex columellar/parietal margin, with two strong abapical, highly-oblique plications, five weaker adapical slightly-oblique lirae. About 12 denticles inside outer lip, strongest denticles anteriorly. Callus covering plications/lirae and parietal area, narrow on outer lip; micro-sculpture of callus with weakly convex margins directed towards exterior, length margins 5–40 mm. Observed height 2.8 mm, width 1.5 mm; height to width ratio about 1.9.

Ecology

Uncertain.

Distribution

The species is known from a single specimen off Namibia (18° S) at a depth of 56 m.

Differential diagnosis

Gibberula heyali sp. nov. differs from all known congeners from Angola or South Africa by the combination of a small size (2.8 mm) and seven plications/lirae. The high number of plications/lirae is encountered in larger congeneric species like *G. oshishani* sp. nov. and *G. evukule* sp. nov. Both are about 8 mm whereas the present species is 2.8 mm. *Gibberula oshishani* is more elongated and has a shoulder keel whereas *G. evukule* has a weakly elevated, pointed apex. The South African *G. almo* has a similar outline but is larger (4.4–5.4 mm) and has less parietal lirae, which are more obliquely placed (Lussi & Smith 1998).

The numbers of plications vs lirae are uncertain because no internal check of plications was made.

Key to Namibian species of *Gibberula*

1. Inside outer lip smooth, no or few very weak denticles *G. cf. bensoni* (Reeve, 1865)
 - Inner lip denticulate 2
2. Only 3 plications, no lirae *G. ehodhi* sp. nov.
 - Lirae present 3
3. With cord on shoulder *G. oshishani* sp. nov.
 - Smooth shoulder 4
4. Shell height less than 5 mm *G. heyali* sp. nov.
 - Shell height more than 5 mm *G. evukule* sp. nov.

Discussion

This study identified four new species of *Gibberula* off Namibia. All newly described species can be considered as endemic to the continental shelf off Namibia. The continental slope off the mouth of the Kunene River forms a dividing line between the species of Cystiscidae of Namibia and those of Angola. *Gibberula cf. bensoni* was also found off Namibia; a very similar *G. bensoni* is known from western South Africa.

Three species were sampled alive: *G. oshishani* sp. nov., *G. ehodhi* sp. nov. and *G. cf. bensoni*. It is uncertain whether *G. evukule* sp. nov. and *G. heyali* sp. nov. currently live off Namibia as their shells may be remains of the Late Pleistocene period when sea water temperatures dropped in the Atlantic Ocean and cold water species might have migrated north along the continental slope of SW Africa (van den Hoek 1975; John & Lawson 1991; Kirkman & Nsengi 2019).

Gofas (1989) reported nine existing or newly-described species off Angola. He also reported four unnamed additional species from Angola. We include *G. benguelensis* in the Angolan fauna because none were found off Namibia despite the fact that the northern Namibian region, south of the Kunene River, was well sampled; we hereby assume that the uncertain type locality (Côte de Benguela) of *G. benguelensis* was off Angola, possibly near the central Angolan city of Benguela (12.55° S).

Nine species of *Gibberula* were reported from South Africa (Reeve 1865; Barnard 1962; Lussi & Smith 1998; Cossignani & Lorenz 2020). This number suggests that South Africa has a higher diversity of *Gibberula* than Namibia. This may be explained by a wider variety of habitats that are influenced by warm currents of the Indian Ocean (Agulhas Current, Mozambique Current) as well as the colder Benguela Current along the western coast. Additionally, South Africa has a diverse cystiscid fauna of the genera *Canalispira* Jousseaume, 1875, *Plesiocystiscus* Covert & Covert, 1995, *Crithe* Gould, 1860 and *Cystiscus* Stimpson, 1865 (Lussi & Smith 1998). Congeners of these genera were not found off Namibia or Angola.

A high endemism of species of *Gibberula* was found off Namibia; this is in line with the high endemism of congeners from South Africa (Lussi & Smith 1998; Cossignani & Lorenz 2020), Angola (Gofas 1989), Gabon (Boyer & Simbille 2025), Cameroon (Boyer *et al.* 2024a), St Helena and Ascension (Boyer *et al.* 2024b). A recent review of the bivalves of Namibia showed a high endemism of Nuculidae Gray, 1824, Condylardiidae Lamarck, 1809, Lasaeidae Gray, 1842 and Neoleptonidae Thiele, 1934 (Zettler & Hoffman 2025). Most likely, endemism off SW Africa is influenced by the habitats created by the Benguela Current off western South Africa and Namibia (Zettler *et al.* 2013), the south-flowing Angola Current off Angola (Kirkman & Nsingi 2019) and the south-east-flowing Guinea Current off Cameroon and Gabon. The north-flowing Benguela Current off Namibia has cold water, which is influenced by upwellings and associated oxygen minimum zones along the coast (Zettler *et al.* 2013). The south-flowing Angola Current has warm tropical waters and is also influenced by upwellings (John & Lawson 1991; Sakko 1998; Kirkman & Nsingi 2019). The south-flowing Guinea Current off Cameroon and Gabon has warm tropical waters that are influenced by the influx of fresh waters, organic remains and sediments from the major rivers (Niger, Congo and Zambesi) of equatorial Africa (John & Lawson 1991).

The micro-sculpture of the columellar callus was studied using SEM images. Unfortunately, we have no information on the microstructures of other species of *Gibberula* outside Namibia. However, there appear to be clear differences, at least between the species presented herein. Our studies did not yield additional specific characters related to the micro-sculpture that proved helpful in differentiating species of *Gibberula*.

Gibberula cf. *bensoni*, *G. evukule* sp. nov., and *G. ehodhi* sp. nov. have three plications on the internal columella. It is likely that all Namibian congeners share this trait and that the number of plications is not a distinctive character. In contrast, the number of lirae varies between species and proved to be a useful morphological character (amongst other characters) to distinguish species.

Future studies will benefit from images of living gibberulids from Namibia because the body of different congeneric species have different pigmentation patterns (Gofas 1989). Molecular analyses of DNA will provide valuable evidence for distinct species and for their interrelationships.

Conclusions

There are clear differences between the gibberulids from Namibia and those from Angola or South Africa; this is probably caused by different environmental conditions. Four endemic species were confirmed on the continental shelf of Namibia. One Namibian species is also known from western South Africa.

Funding

The ship time of the cruises was sponsored by the Deutsche Forschungsgemeinschaft. MSM105 was part of the EVAR project funded by the Federal Ministry of Education and Research (grant no.03V01279).

Data availability

Not applicable.

Author contribution

Conceptualization: LH, MH, MJ, MZ. Data curation: LH, MJ, MZ. Formal analysis: LH, MH, MZ. Investigation & Validation: LH, MH, MZ. Methodology: LH, MZ. Project administration: MZ. Supervision: LH, MZ. Visualization: LH. Writing - original draft: LH, MH. Writing - review and editing: LH, MH, MJ, MZ.

Acknowledgements

We thank captains, crews and scientific staff on board of the research vessels *Meteor* (cruises M122, M131, M157) and *MS Merian* (cruises MSM7, MSM18, MSM105) that enabled sampling the material studied herein. We acknowledge André Freiwald, department head at SaM, for allowing the first author to join on a cruise M122 offshore Namibia, providing access to material and facilities to execute these studies; including access to the SEM and Keyence microscopes. NMN and SMF staff facilitated the registration and conservation of the type material. Bernard Landau (Naturalis, Leiden, Netherlands) and one anonymous reviewer improved the quality of the manuscript.

References

- Amorim K. & Zettler M.L. 2023. Gradients and instability: Macrozoobenthic communities in the Benguela Upwelling System off Namibia. *Estuarine, Coastal and Shelf Science* 291: e108421. <https://doi.org/10.1016/j.ecss.2023.108421>
- Barnard K.H. 1959. Contributions to the knowledge of South African marine Mollusca. Part. II. Gastropoda: Prosobranchiata: Rhachiglossa. *Annals of the South African Museum* 45: 1–237.
- Barnard K.H. 1962. A new genus in the family Marginellidae. *Proceedings of the Malacological Society of London* 35 (1): 14–15.
- Boyer F. & Simbille C. 2025. Description de deux espèces nouvelles du Gabon dans le genre *Gibberula* Swainson, 1840 (Mollusca: Volutacea: Cystiscidae). *Revue suisse de Zoologie* 132 (1): 115–121. <https://doi.org/10.35929/rsz.0144>
- Boyer F., Renda W. & Swinnen F. 2024a. Description de deux *Gibberula* nouvelles du Cameroun (Mollusca: Volutacea: Cystiscidae). *Revue suisse de Zoologie* 131 (1): 139–143. <https://doi.org/10.35929/rsz.0117>
- Boyer F., Renda W. & Swinnen F. 2024b. Revision of the cystiscid fauna (Neogastropoda Volutacea) from Ascension and St. Helena Islands, Southern Atlantic. *Biodiversity Journal* 15 (4): 829–844. <https://doi.org/10.31396/Biodiv.Jour.2024.15.4.829.844>
- Coover G.A. & Coover H.K. 1995. Revision of the supraspecific classification of the marginelliform Gastropods. *The Nautilus* 109: 43–110. Available from <https://www.biodiversitylibrary.org/page/8274195> [accessed 18 Jun. 2026].
- Cossignani V. 2006. *Marginellidae and Cystiscidae of the World*. Ancona. L'Informatore Piceno.

- Cossignani T. & Lorenz F. 2020. Quattro nuove marginelle dal Sud Africa. *Malacologia Mostra Mondiale* 106: 12–16.
- Fedosov A.E., Caballer Gutierrez M., Buge B., Sorokin P.V., Puillandre N. & Bouchet P. 2019. Mapping the missing branch on the neogastropod tree of life: molecular phylogeny of marginelliform gastropods. *Journal of Molluscan Studies* 85 (4): 439–451. <https://doi.org/10.1093/mollus/eyz028>
- Gofas S. 1989. The Marginellidae of Angola: the genus *Gibberula*. *Journal of Conchology* 33 (3): 109–139. <https://doi.org/10.5962/p.407941>
- John D.M. & Lawson G.W. 1991. Littoral ecosystems of tropical western Africa. In: Mathieson A.C. & Nienhuis P.H. (eds) *Ecosystems of the World, Vol. 24*: 297–321. London. New York, Tokyo.
- Kensley B. 1973. *Sea-Shells of Southern Africa. Gastropods*. Maskew Miller Ltd., Cape Town.
- Kilburn R.N. & Rippey E. 1982. *Sea Shells of Southern Africa*. Macmillan South Africa, Johannesburg.
- Kirkman S.P. & Nsingi K.K. 2019. Marine biodiversity of Angola: Biogeography and conservation part 1 (3): 42–53. In: Huntley B.J., Russo V., Lage F. & Ferrand F. (eds) *Biodiversity of Angola. Science & Conservation: A Modern Synthesis*: 43–52. Springer Open, Cham, Switzerland. https://doi.org/10.1007/978-3-030-03083-4_3
- Lussi M. & Smith G. 1998. Family Cystiscidae Stimpson, 1865. Revision of the family Cystiscidae in South Africa with the introduction of three genera and the description of eight new species. *Malacologia Mostra Mondiale* 27: 3–23.
- MolluscaBase 2026. MolluscaBase. *Gibberula* Swainson, 1840. Available from <https://www.marinespecies.org/aphia.php?p=taxdetails&id=137881> [accessed 18 Jun. 2026].
- Reeve L.A. 1864–1865. Monograph of the genus *Marginella*. In: *Conchologia Iconica, or, Illustrations of the Shells of Molluscous Animals, vol. 15*: pls 1–27 and unpaginated text. L. Reeve & Co., London [stated dates: pls 1, 14–27, January 1865; pls 2–13, August 1864]. <https://doi.org/10.5962/bhl.title.8129>
- Sakko A.L. 1998. The influence of the Benguela upwelling system on Namibia's marine biodiversity. *Biodiversity and Conservation* 7: 419–433. <https://doi.org/10.1023/A:1008867310010>
- Swainson W. 1840. *A Treatise on Malacology; or the Natural Classification of Shells and Shell-fish*. Longman, London. <https://doi.org/10.5962/bhl.title.8027>
- Van den Hoek C. 1975. Phytogeographic provinces along the coast of the northern Atlantic Ocean. *Phycologia* 14: 317–330. <https://doi.org/10.2216/i0031-8884-14-4-317.1>
- Zettler M.L. & Hoffman L. 2025. *Marine Bivalves of Namibia*. Conchbooks, Harxheim, Germany.
- Zettler M.L., Bochert R. & Pollehne F. 2013. Macrozoobenthic biodiversity patterns in the northern province of the Benguela upwelling system. *African Journal of Marine Science* 35 (2): 283–290. <https://doi.org/10.2989/1814232X.2013.798592>

The members of the *EJT* consortium are: Muséum national d'Histoire naturelle, Paris, France; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Meise Botanic Garden, Meise, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israel.