

Research article

urn:lsid:zoobank.org:pub:7EC5E08C-7E6C-4C06-A0C6-1346A4A30A10

***Varadia*, a new helicarionoidean semi-slug genus from India's Western Ghats (Stylommatophora: Helicarionoidea)**Amrut R. BHOSALE^{1,*}, Ahmed J. SAADI², Christopher M. WADE³,
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Abstract. We here describe a new Indian helicarionoidean genus, *Varadia* Bhosale & Raheem gen. nov., containing the single species *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. This new semi-slug is endemic to the northern and central Western Ghats and is primarily a forest-

living species. We describe and figure the shell, reproductive system, radula, spermatophore and external morphology of this new species, and detail its known distribution. We explore its relationships to other helicarionoideans using phylogenetic analyses of DNA sequence data for part of the ribosomal RNA gene cluster and discuss the morphology of the new genus in relation to other, primarily South Indian, helicarionoidean taxa. Based on characters of the reproductive system, particularly the male genitalia and the gametolytic sac, we provisionally place *Varadia* gen. nov. in the Macrochlamydiae (Ariophantidae). This is consistent with the results of our molecular phylogenetic analyses. The combination of large size, broad, densely tuberculated shell lobes and a shell with ca 4 whorls and a disproportionately large body whorl makes *V. amboliensis* gen. et sp. nov. unique among the helicarionoidean taxa of the Western Ghats. The new semi-slug is also highly distinctive in the morphology of its male genitalia.

Keywords. *Varadia amboliensis* gen. et sp. nov., Macrochlamydiae, taxonomy, phylogenetics, ribosomal RNA gene cluster.

Bhosale A.R., Saadi A.J., Wade C.M., Thackeray T.U., Tamboli A.S., Kadam S.K., Muley D.V. & Raheem D.C. 2021. *Varadia*, a new helicarionoidean semi-slug genus from India's Western Ghats (Stylommatophora: Helicarionoidea). *European Journal of Taxonomy* 757: 50–79. <https://doi.org/10.5852/ejt.2021.757.1413>

Introduction

The stylommatophoran superfamily Helicarionoidea Bourguignat, 1877 is particularly diverse in the tropics and subtropics of Asia, Africa and Australia (Blanford & Godwin-Austen 1908; Hausdorf 2000). South Asia is a major centre of diversity with at least 21 genera and more than 400 described species (Blanford & Godwin-Austen 1908), representing two of three currently recognized helicarionoidean families (Helicarionidae Bourguignat, 1877 and Ariophantidae Godwin-Austen, 1888; Bouchet *et al.* 2017). A substantial part of this diversity is restricted to the Western Ghats–Sri Lanka (WGSL) hotspot, which has a taxonomically diverse helicarionoidean fauna (123 species in 15 genera; Naggs & Raheem 2000; Raheem *et al.* 2014). This fauna is dominated by species belonging to the ariophantid subfamily Ariophantinae, a group that in its strictest sense is restricted to Peninsular India and Sri Lanka and is characterized by distinctive reproductive anatomy (Blanford & Godwin-Austen 1908; but see Zilch 1959 and Bank 2017). The WGSL fauna also includes taxa belonging to other helicarionoidean genera, such as *Eurychlamys* Godwin-Austen, 1899 (Helicarionidae: Helicarioninae), *Macrochlamys* sensu Godwin-Austen (1883) (Ariophantidae: Macrochlamydiae Godwin-Austen, 1888), *Pseudaustenia* Cockerell, 1891 (Helicarionidae: Helicarioninae), *Satiella* Blanford & Godwin-Austen, 1908 (Helicarionidae: Durgellinae Godwin-Austen, 1888) and *Sitala* Adams, 1865 (Helicarionidae: Durgellinae). The helicarionoideans of the WGSL hotspot are diverse in external morphology (Blanford & Godwin-Austen 1908). They range from snails, such as *Ariophanta* Desmoulins, 1829, *Euplecta* Semper, 1870, *Eurychlamys* and *Sitala*, with well-developed, robust or heavy shells into which the body can be fully withdrawn, to taxa with greatly reduced external or internal shells (semi-slugs and slugs, respectively, sensu Cameron 2016). Semi-slug taxa include *Indrella ampulla* (Benson, 1850), in which the shell is globose, fragile and not covered by the mantle; *Satiella* and *Ratnadvipia karui* Raheem & Naggs, 2006, both characterized by flexible and mostly proteinaceous shells that are largely covered by the mantle; and *Pseudaustenia*, which has an auriform shell that is almost entirely exposed.

Our current understanding of this taxonomically and morphologically diverse fauna has many gaps and is largely based on publications and collections from the British colonial period (see monographs by Blanford & Godwin-Austen 1908; Raheem *et al.* 2014). Many taxa were poorly described/defined and/or were not illustrated in the original literature, hence making their identification problematic. The genus-level placement of some taxa is uncertain and questionable (e.g., at least some of the western and southern Indian species assigned to the genus *Macrochlamys* may belong to *Eurychlamys*; Blanford &

Godwin-Austen 1908; Raheem *et al.* 2014). Data on the reproductive anatomy, external morphology and radula are scarce or lacking for most species. Knowledge of species' distributions is poor; while many species are known only from single localities and have not been recorded for over a century, the snail fauna of substantial parts of the Western Ghats remains to be explored (Raheem *et al.* 2014). To date, although South Asian taxa have been included in molecular phylogenetic analyses of deep-level pulmonate relationships (e.g., Wade *et al.* 2001, 2006; Herbert & Mitchell 2009; Ramirez *et al.* 2012), studies focussing on the molecular systematics and diversification of South Asian helicarionoideans have yet to be carried out. With the exception of the substantial work done on Australian helicarionids (e.g., Hyman *et al.* 2007, 2017; Hyman & Ponder 2010; Hyman & Köhler 2019), this reflects the general scarcity of such studies globally (but see Schilthuizen *et al.* 2019; Pholyotha *et al.* 2020a).

The taxonomic study of the WGSL land-snail fauna has seen a renewed interest in recent years (e.g., Raheem & Naggs 2006; Raheem *et al.* 2014; Aravind & Páll-Gergely 2018; Bhosale *et al.* 2019, in press; Páll-Gergely *et al.* 2020). This includes the first modern surveys of the land-snail fauna of the northern Western Ghats by one of us (Bhosale *et al.* 2016, 2019, in press; Bhosale 2018). Begun as PhD fieldwork, these surveys focussed initially on Kolhapur District, Maharashtra, a 7685-km² area in the extreme south of the northern Western Ghats, which had not been previously explored by malacologists. It was during these surveys that a large, forest-living semi-slug with a *Macrochlamys*-like shell and broad, conspicuously tuberculate shell lobes was encountered. Based on comparative morphological study and molecular phylogenetic analyses of part of the ribosomal RNA (rRNA) gene cluster, we here describe this semi-slug as a new Indian helicarionoidean genus, *Varadia* Bhosale & Raheem gen. nov., containing the single species *V. amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. We discuss the morphology of this new genus in relation to other, primarily South Indian, taxa and explore its phylogenetic relationships to other helicarionoideans, provisionally placing it in the subfamily Macrochlamyinae (Ariophantidae).

Material and methods

Living snails and shells of *Varadia amboliensis* gen. et sp. nov. were collected and/or observed by A. Bhosale at 5 localities in the state of Maharashtra, India in September 2017, November 2019 (during the autumn) and in September 2020, towards the end of the monsoon rains (Fig. 1). After sampling of foot tissue for DNA analysis, snails were euthanized following the guidelines of the American Veterinary Medical Association (2020) and preserved in 80% ethanol for anatomical study. The whole radulae were prepared following Bhosale *et al.* (2019) and SEM images were taken on a TESCAN VEGA3 SEM. All radula counts were carried out in the area of greatest width. Morphological studies of collected material were carried out at the Department of Zoology, Shivaji University, Kolhapur, India, with type and other material being deposited in the collections of the Bombay Natural History Society (BNHS), Mumbai and Zoological Survey of India (ZSI), Western Regional Centre (WRC), Pune, India. Unless stated otherwise, we follow the morphological terminology of Raheem & Naggs (2006) and Bhosale *et al.* (2019) for the mantle and reproductive system (the terms 'proximate' and 'distal' are used with reference to the genital orifice); Hyman & Köhler (2019) for the spermatophore; and Cox (1960) for the shell (including shell sculpture). Shell whorl counts (to the nearest quarter whorl) are based on the approach of Kerney & Cameron (1979). Shell height and width were measured as shown in Fig. 2. Unless stated otherwise, all photographic images are by A. Bhosale.

For the molecular phylogenetic study, our ingroup consisted of 30 taxa belonging to the order Limacoidea Batsch, 1789 (Table 1). The outgroup comprised three species of Arionoidea Gray, 1840; a recent study has shown that the orders Arionoidea and Limacoidea are sister groups (Saadi & Wade 2019). Unless stated otherwise, we have followed the higher-level classification of Bouchet *et al.* (2017). Phylogenetic analyses were based on the region of the rRNA gene cluster described by Wade & Mordan (2000). DNA sequence data for eight of the 33 taxa were generated during the course of the present study; data for

the remainder were generated in previous studies by Wade *et al.* (2001, 2006). For the newly sequenced samples, DNA was extracted from a 1–2-mm³ piece of foot tissue using a CTAB DNA extraction protocol (Goodacre & Wade 2001). PCR amplifications were done by adding 2.5 µl of DNA extract to a reaction mix containing 1× PCR reaction buffer (including 1.5 mm MgCl₂), 0.2 mm each dNTP (Sigma-Aldrich, USA), 0.2 µM each primer and 1 unit Taq DNA polymerase (Sigma-Aldrich, USA) in a final volume of 25 µl. The PCR conditions were as follows: 96°C for 1 min; 30 cycles of 94°C for 30 s, 50°C for 30 s

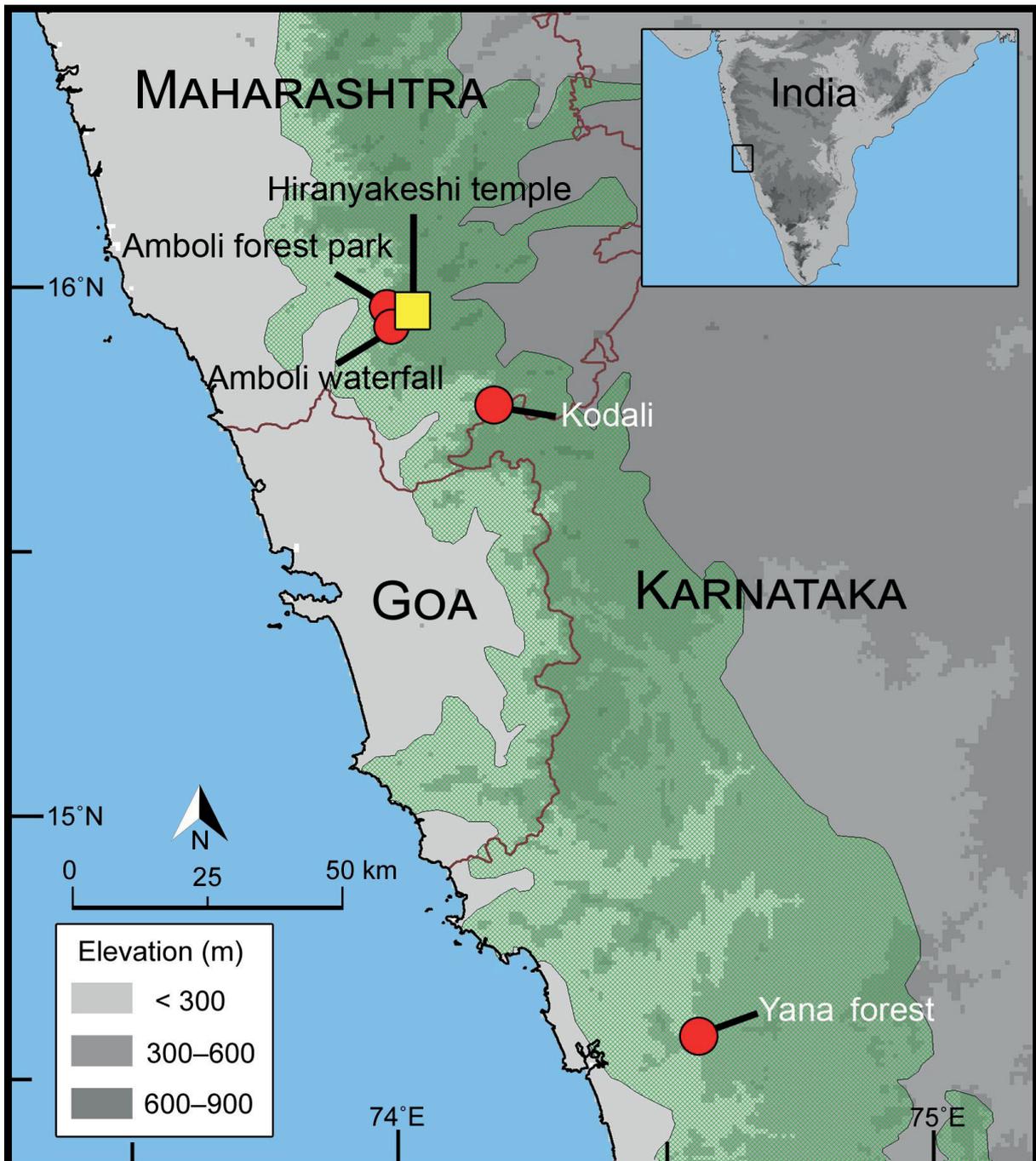


Fig. 1. Distribution of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. (coloured symbols) in the Western Ghats (green shading; sensu Irfan-Ullah & Davande 2008). The yellow square indicates the type locality of the new species and the red circles are the other localities.

and 72°C for 1 min; and a final extension step of 72°C for 5 min. Amplified products were purified using the HiPurA™ Quick Gel Purification Kit. Sequencing was carried out using a BigDye Terminator ver. 3.1 Cycle Sequencing Kit (Applied Biosystems, USA) with both DNA strands sequenced on a 3500 Genetic Analyzer (Applied Biosystems, USA); sequencing was done at the Department of Biochemistry, Shivaji University, Kolhapur. DNA sequences were assembled using STADEN ver. 1.5.3 (Staden *et al.* 2000). Subsequently, the sequences were manually aligned using the Genetic Data Environment ver. 2.2 package (Smith *et al.* 1994).

Phylogenetic analyses were based on a dataset of 874 unambiguously aligned nucleotide sites for 33 taxa. We used maximum likelihood (ML; Felsenstein 1981), neighbour joining (NJ; Saitou & Nei 1987) and Bayesian (Larget & Simon 1999) approaches, with the nucleotide substitution model being GTR+ Γ (Lanave *et al.* 1984; Gu *et al.* 1995). ML analyses were carried out using RAxMLHPC2 (Stamatakis 2014). Each RAxML analysis involved a single programme run and consisted of a rapid bootstrap analysis with the extended majority rule bootstopping criterion, followed by a search for the best-scoring ML tree (Stamatakis 2014); analyses were run on the CIPRES Science Gateway ver. 3.3 (<http://www.phylo.org/index.php>, Miller *et al.* 2010) and each run was repeated at least once. NJ analysis was performed using PAUP* ver. 4.0b10 (Swofford 2002) with model parameters estimated following an iteration process; for each tree the parameters were estimated and used to build the next tree until there was no further improvement of the likelihood score. Bootstrap resampling (Felsenstein 1985) with 1000 replicates was undertaken for the NJ trees. Bayesian analyses were done using MrBayes ver. 3.1.2 (Ronquist & Huelsenbeck 2003). Each MrBayes analysis involved two independent MCMC runs (with four chains per run) for 5 million generations, sampling every 100 generations; each analysis was repeated at least once. To ensure adequate chain swapping, a range of heating parameters were tested with the optimal parameter used to construct the final trees. Only after the Bayesian MCMC searches had reached a stationary phase (indicating convergence of the chains onto the target distribution) was the run ended. A consensus tree was built using the last 75% of trees (burnin = 5001). Trees were rooted on a composite outgroup comprising three members of the Arionoidea, *Arion hortensis* Férussac, 1819, *Meghimatium bilineatum* (Benson, 1842) and *Philomycus carolinianus* (Bosc, 1802). Branches with bootstrap support (BS) values $\geq 70\%$ and posterior probabilities (PP) ≥ 0.95 were considered to be well/strongly supported (Hillis & Bull 1993; Alfaro & Holder 2006). The frequency of all bipartitions in the bootstrap trees used for computing the NJ and ML consensus (50% majority-rule) trees were estimated using PAUP*.

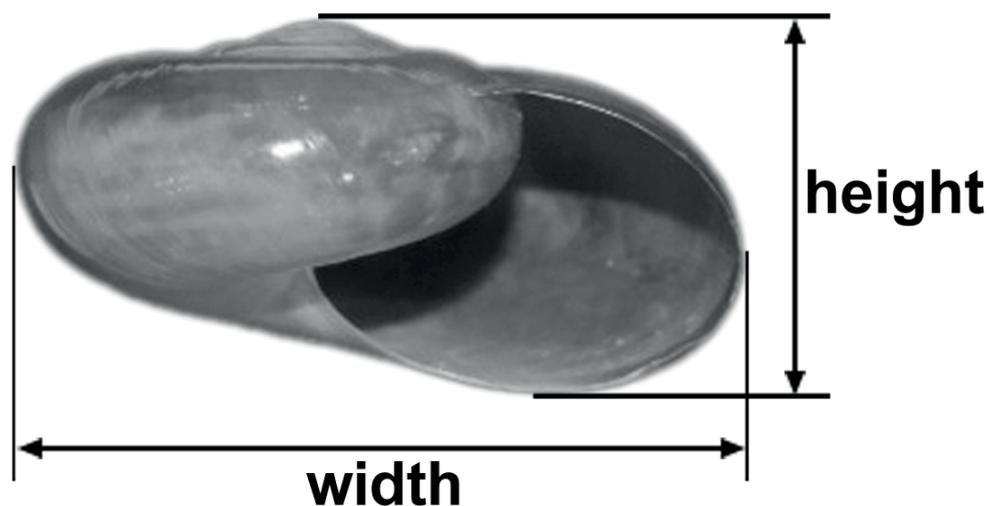


Fig. 2. Shell height and width, as measured for this study. The shell axis is parallel to the height and perpendicular to the width.

Table 1 (continued on next two pages). Taxa used in the DNA analyses with locality data, GenBank accession numbers and source. Subfamily-level placements are shown only for helicarioideoan genera. Superfamily-level classification follows Bouchet *et al.* (2017). Genus- and species-level names follow Wade *et al.* (2006), Raheem *et al.* (2014) and Bank & Neubert (2017).

Taxa	Sources for family- and subfamily-level placement	Locality	DNA sequence data	
			GenBank acc. nos	Source
INGROUP				
LIMACOIDEA				
Agriolimacidae				
1. <i>Deroceras reticulatum</i> (Müller, 1774)	Bouchet <i>et al.</i> (2017)	Kirkdale, Derbyshire, UK	AY014118, AY014119	Wade <i>et al.</i> (2001)
Vitrinidae				
2. <i>Vitrina pellucida</i> (Müller, 1774)	Bouchet <i>et al.</i> (2017)	Kirkdale, Derbyshire, UK	AY014113	Wade <i>et al.</i> (2001)
3. <i>Azorivitrina laxata</i> (Morelet, 1860)	Bank & Neubert (2017)	São Miguel, Azores	AY014112	Wade <i>et al.</i> (2001)
GASTRODONTOIDEA				
Oxychilidae				
4. <i>Oxychilus alliarius</i> (Miller, 1822)	Bouchet <i>et al.</i> (2017)	Deepdale, Derbyshire, UK	AY014114	Wade <i>et al.</i> (2001)
5. <i>Oxychilus cellarius</i> (Müller, 1774)	Bouchet <i>et al.</i> (2017)	Co. Kerry, Ireland	AY014116	Wade <i>et al.</i> (2001)
6. <i>Oxychilus navarricus</i> <i>helveticus</i> (Blum, 1881)	Bouchet <i>et al.</i> (2017)	Kirkdale, Derbyshire, UK	AY014115	Wade <i>et al.</i> (2001)
Pristilomatidae				
7. <i>Vitrea crystallina</i> (Müller, 1774)	Bouchet <i>et al.</i> (2017)	New Forest, Hampshire, UK	AY014113	Wade <i>et al.</i> (2001)
PARMACELLOIDEA				
Milacidae				
8. <i>Tandonia budapestensis</i> (Hazay, 1881)	Bank & Neubert (2017)	Kirkdale, Derbyshire, UK	AY014117	Wade <i>et al.</i> (2001)
TROCHOMORPHOIDEA				
Trochomorphidae				
9. <i>Trochomorpha pallens</i> Pease, 1870	Bouchet <i>et al.</i> (2017)	Faatoai Valley, Moorea	AY014109, AY014110	Wade <i>et al.</i> (2001)
10. <i>Videna gouldiana</i> (Pilsbry, 1901)	Hyman & Ponder (2010)	Amami Island, Ryukyu, Japan	AY841313, AY841314	Wade <i>et al.</i> (2006)
Dyakiidae				
11. <i>Asperitas inquinata</i> (v.d. Busch, 1842)	Hausdorf (1995)	Java	AY014108	Wade <i>et al.</i> (2001)

Table 1 (continued). Taxa used in the DNA analyses with locality data, GenBank accession numbers and source. Subfamily-level placements are shown only for helicarionoidean genera. Superfamily-level classification follows Bouchet *et al.* (2017). Genus- and species-level names follow Wade *et al.* (2006), Raheem *et al.* (2014) and Bank & Neubert (2017).

Taxa	Sources for family- and subfamily-level placement	Locality	DNA sequence data	
			GenBank acc. nos	Source
12. <i>Craterodiscus pricei</i> McMichael, 1959	Wade <i>et al.</i> (2006)	Ravenshoe, NE Queensland, Australia	AY014123	Wade <i>et al.</i> (2001)
Euconulidae				
13. <i>Euconulus fulvus</i> (Müller, 1774)		New Forest, Hampshire, UK	AY014098	Wade <i>et al.</i> (2001)
14. <i>Louisia barclayi</i> (Benson, 1850)	Hyman & Ponder (2010); Wade <i>et al.</i> (2006)	Mauritius	AY014102	Wade <i>et al.</i> (2001)
15. <i>Hiona</i> sp.	Hyman & Ponder (2010); Wade <i>et al.</i> (2006)	Moorea	AY014104, AY014105	Wade <i>et al.</i> (2001)
HELICARIONOIDEA				
Helicarionidae				
Helicarioninae				
16. <i>Fastosarion brazieri</i> (Cox, 1873)	Bouchet <i>et al.</i> (2017); Hyman & Ponder (2010); Zilch (1959)	Mossman, Queensland, Australia	AY014099	Wade <i>et al.</i> (2001)
17. <i>Harmogenanina argentea</i> (Reeve, 1852)	Bouchet <i>et al.</i> (2017); Wade <i>et al.</i> (2006); Zilch (1959)	Réunion	AY014101	Wade <i>et al.</i> (2001)
18. <i>Plegma caelatura</i> (Férussac, 1821)	Bouchet <i>et al.</i> (2017); Wade <i>et al.</i> (2006); Zilch (1959)	Réunion	AY014103	Wade <i>et al.</i> (2001)
19. <i>Eurychlamys platychlamys</i> (Blanford, 1880)	Blanford & Godwin-Austen (1908)	Sagar Upavan, Mumbai, Maharashtra, India	MW583029	This study
20. <i>Mariaella dussumieri</i> Gray, 1855	Blanford & Godwin-Austen (1908)	Ramling Temple, Kolhapur, Maharashtra, India	MW583030	This study
Durgellinae				
21. <i>Satiella</i> sp.	Bouchet <i>et al.</i> (2017)	Jawali, Kolhapur, Maharashtra, India	MW583028	This study

Table 1 (continued). Taxa used in the DNA analyses with locality data, GenBank accession numbers and source. Subfamily-level placements are shown only for helicarionoidean genera. Superfamily-level classification follows Bouchet *et al.* (2017). Genus- and species-level names follow Wade *et al.* (2006), Raheem *et al.* (2014) and Bank & Neubert (2017).

Taxa	Sources for family- and subfamily-level placement	Locality	DNA sequence data	
			GenBank acc. nos	Source
Ariophantidae				
Ariophantinae				
22. <i>Ariophanta belangeri</i> (Deshayes, 1834)	Bouchet <i>et al.</i> (2017)	Kagal, Kolhapur, Maharashtra, India	MW583023	This study
23. <i>Ariophanta intumescens</i> (Blanford, 1866)	Bouchet <i>et al.</i> (2017)	Mhalunge, Kolhapur, Maharashtra, India	MW583024	This study
24. <i>Ariophanta bistrialis</i> (Beck, 1837)	Bouchet <i>et al.</i> (2017)	Sri Lanka	AY014106, AY014107	Wade <i>et al.</i> (2001)
25. <i>Euplecta gardeneri</i> (Pfeiffer, 1846)	Bouchet <i>et al.</i> (2017); Blanford & Godwin- Austen (1908)	Sri Lanka	AY841310, AY841311	Wade <i>et al.</i> (2006)
26. <i>Ratnadvipia</i> sp.	Bouchet <i>et al.</i> (2017); Blanford & Godwin- Austen (1908)	Sri Lanka	AY841312	Wade <i>et al.</i> (2006)
Macrochlamydinae				
27. <i>Macrochlamys indica</i> Benson in Godwin- Austen, 1883	Bouchet <i>et al.</i> 2017)	Shivaji University, Kolhapur, Maharashtra, India	MW583025	This study
28. <i>Macrochlamys pedina</i> (Benson, 1865)	Bouchet <i>et al.</i> 2017)	Khandala, Maharashtra, India	MW583026	This study
29. <i>Varadia amboliensis</i> gen. et sp. nov.	this study	Amboli, Maharashtra, India	MW583027	This study
Urocyclidae				
30. <i>Rhysotina heptazion</i> (Gould, 1848)	Bouchet <i>et al.</i> (2017)	São Tomé	AY014100	Wade <i>et al.</i> (2001)
OUTGROUP				
ARIONOIDEA				
Arionidae				
31. <i>Arion hortensis</i> Férussac, 1819	Bouchet <i>et al.</i> (2017)	Kirkdale, Derbyshire, UK	AY014143	Wade <i>et al.</i> (2006)
Philomycidae				
32. <i>Philomycus carolinianus</i> (Bosc, 1802)	Bouchet <i>et al.</i> (2017)	Wake Co., USA	AY841349	Wade <i>et al.</i> (2006)
33. <i>Meghimatium bilineatum</i> (Benson, 1842)	Tsai <i>et al.</i> (2011); Saadi & Wade (2019)	Mauritius	AY841348	Wade <i>et al.</i> (2006)

Results

Systematic descriptions

Phylum Mollusca Linnaeus, 1758
Class Gastropoda Cuvier, 1795
Subclass Heterobranchia sensu Bouchet *et al.*, 2017
Order Stylommatophora sensu Bouchet *et al.*, 2017
Superfamily Helicarionoidea Bourguignat, 1877
Family Ariophantidae Godwin-Austen, 1888
Subfamily Macrochlamydiae Godwin-Austen, 1888

Varadia Bhosale & Raheem gen. nov.

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Type species

Varadia amboliensis Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. (here designated).

Diagnosis

Only known large semi-slug species from the Western Ghats having broad shell lobes (covering nearly all of the dorsal shell surface when fully extended) and a depressed, discoid shell with a large body whorl. Shell thin, glossy golden brown, with 4–4½ rapidly increasing whorls and barely raised spire. Extensive, largely free penial sheath enclosing substantial part of male genitalia. When sheath is in situ and penis in relaxed state, male genitalia constitute a single elongate, irregularly-shaped mass, with all of penis and epiphallic caecum, most of epiphallus and part of flagellum enclosed by sheath; only vas deferens and most of flagellum is visible outside intact sheath. Penial sheath divisible into thick proximal part and thin distal part, with transition between these two parts occurring between distal penis and epiphallic caecum. With penial sheath removed, following evident: region extending from penis to epiphallic caecum long and cylindrical, with distinctive S-shaped bend in penis and associated band of muscle running along length of penis; proximal ¾ of epiphallus held in long, conspicuous loop; and penial retractor muscle with two branches, one inserting subterminally on epiphallic caecum and one inserting on apex of loop of epiphallus. Inner wall of penis divisible into three regions: proximal penis (one major and several minor longitudinal pilasters), mid-penis (several minor longitudinal pilasters) and distal penis (a few minor pilasters with associated regular transverse ridges in interspaces). Inner wall of epiphallic caecum shows one long major longitudinal pilaster, a large mass of reticulate ridges proximally and several minor longitudinal pilasters distally. Gametolytic gland elongated and long; gametolytic sac 3–3.5 times as long as gametolytic duct. Amatorial organ absent. Spermatophore consists of elongated, soft capsule and long tail-pipe, with U-shaped bend at capsule–tail-pipe junction and funnel-like opening at tip of tail-pipe; surface smooth apart from four ribs running obliquely along length of tail-pipe and short spines near end of tail-pipe.

Etymology

The new genus is named in honour of the herpetologist Dr Varad Giri, who has made a major contribution to the modern study and conservation of the Indian herpetofauna; masculine.

Varadia amboliensis Bhosale, Thackeray, Muley & Raheem gen. et sp. nov.

urn:lsid:zoobank.org:act:5C93F719-2DEF-4A9A-8973-06B7FE6E6528

Figs 3–12

Diagnosis

As genus-level diagnosis.

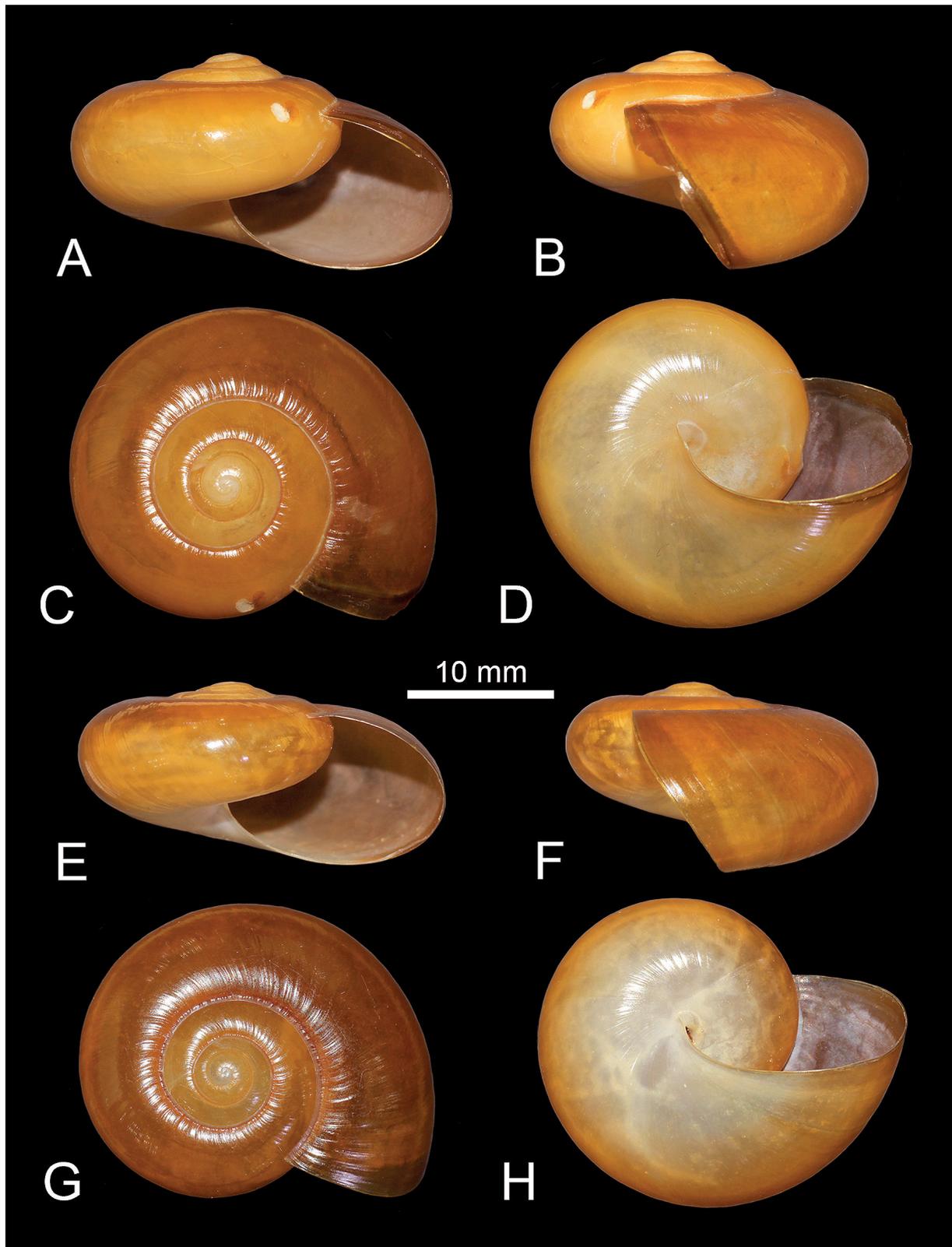


Fig. 3. Apertural, lateral, apical and umbilical views of the shell of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A–D.** Holotype (BNHS GAS 113). **E–H.** Paratype (BNHS GAS 116).

Etymology

Named after the type locality, Amboli, in the Sindhudurg District of southern Maharashtra, India. In recent years, Amboli has emerged as a hotspot for the discovery of new species (particularly reptiles and amphibians) in the northern Western Ghats.

Type material

Holotype

INDIA • Maharashtra State, Sindhudurg District, Amboli, Hiranyakeshi temple; 15°57'17.8" N, 74°01'39.1" E; 839 m a.s.l.; 2019; A. Bhosale leg.; BNHS GAS 113.

Paratypes

INDIA • 21 specimens (17 whole preserved specimens and 4 shells); same locality data as for holotype; 2019; A. Bhosale leg.; BNHS GAS 114–127, ZSI Moll/1820–1826 • 3 preserved specimens; same locality data as for holotype; 2020; A. Bhosale leg.; BNHS GAS 136–138.

Other material examined

INDIA – **Maharashtra State** • 1 specimen (sampled for DNA analysis); Sindhudurg District, Amboli Forest Park; 15°57'37.4" N, 73°59'58.1" E; 724 m a.s.l.; 2017; A. Bhosale leg.; BNHS GAS 129 • 9 preserved specimens; Sindhudurg District, near Amboli waterfall; 15°56'26.9" N, 73°59'41.2" E; 645 m a.s.l.; 2020; A. Bhosale leg.; BNHS GAS 130–135, BNHS GAS 139–141 • 1 shell; Kolhapur District, Kodali; 15°46'42.4" N, 74°10'40.0" E; 620 m a.s.l.; 2019; A. Bhosale leg.; BNHS GAS 128.

Description

SHELL. Adult shell thin, depressed, glossy and appearing non-umbilicate, with ca 4–4.5 rapidly increasing whorls and colour ranging from golden-brown to reddish yellow (Fig. 3). Shell measurements ($n = 35$): width 20.2–26.3 mm; height 10.2–15.0 mm. Spire only slightly raised with flat apex and suture only slightly impressed. Body whorl disproportionately large, rounded at periphery, gently convex beneath. Aperture large, crescent-shaped, with width greater than height (Fig. 3A, E). Apertural margin simple, thin and delicate; in lateral view angled forward, with upper apertural margin noticeably anterior to the lower margin. When shell is viewed from below, basal margin curved (not straight) and expanded columellar margin reflected over, covering umbilical region. Shell surface smooth and glossy to naked eye, with irregular, faint collabral striae; under SEM, seen to be finely and closely sculptured with well-defined spiral lines on protoconch (first 1.5–2 whorls) and indistinct and irregular oblique lines on teleoconch (Fig. 4).

BODY AND MANTLE. Total adult body length, excluding extended tentacles, ranges from 4.8 to 6.9 cm ($n = 5$). Living snail glossy grey or greyish white with irregular dark mottling; head and tail dark grey or blackish with tentacles tending to be paler at their tips (Fig. 5–6). Surface of mantle densely and conspicuously covered by small, irregular tubercles that appear lighter on top. Sole tripartite with well-defined sole furrows dividing it into three distinct longitudinal tracts; central tract paler than lateral ones. Tail with large slit-like caudal pit (sensu Hausdorf 1998: 51); caudal horn prominent when extended (Fig. 6A) but when retracted gives tail truncated and blunt appearance (Fig. 6B). Mantle consists of two broad shell lobes (right and left) and two dorsal lobes (right and left) (Fig. 7). Shell lobes may cover nearly all of dorsal surface of shell (Fig. 5), but individuals have also been observed with shell lobes largely retracted and much of shell exposed (Fig. 6). Left dorsal lobe extends as far as base of tentacles when snail is resting (i.e., body not fully extended) and tentacles are retracted.

REPRODUCTIVE SYSTEM. Male genitalia consist of proximally penis and distally epiphallic caecum (= epiphallic retractor caecum of Hyman & Ponder 2010: 139) and epiphallus. These three regions are

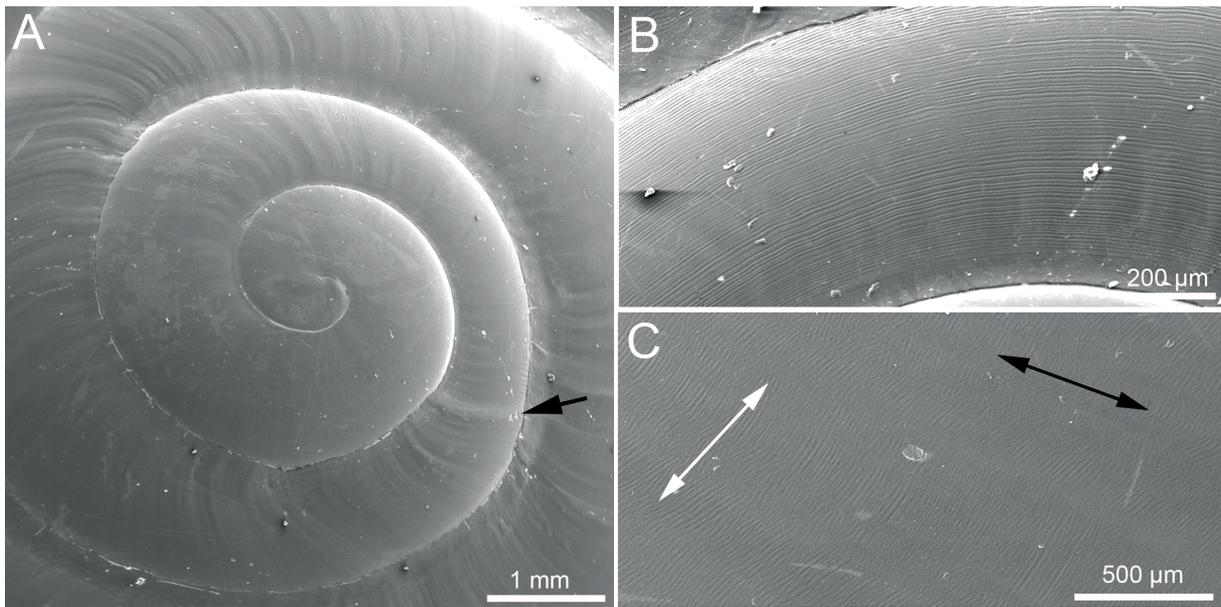


Fig. 4. Shell sculpture of a paratype (BNHS GAS 119) of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A.** Protoconch showing irregular collabral lines; black arrow indicates the approximate point of transition from the protoconch to the teleoconch. **B–C.** Close longitudinal striae of protoconch (B) and teleoconch (C). The direction of the longitudinal striae and the faint collabral striae (barely evident) are shown, respectively, by the white and black arrows in C.



Fig. 5. Live individual of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. from the site near Amboli waterfall. Image: O. Yadav.

held together by a penial sheath (= penial tunica of Hausdorf 1998), which is largely independent of wall of penis, epiphallic caecum and epiphallus (Figs 8A, 9A–C). Penial sheath encloses all of penis, all of epiphallic caecum, much of epiphallus and part of flagellum; it holds proximal three quarters of epiphallus in a loop against epiphallic caecum, with remaining part of epiphallus (i.e., part closest to vas deferens and flagellum) lying outside sheath, along with a substantial part of flagellum (Fig. 9A). Proximal part of penial sheath is thick and covers penis; distal half of this sheath is thin and covers epiphallus and epiphallic caecum. Thick penial sheath attached to proximal end of penis, close to genital atrium. Thin penial sheath attached to distal end of epiphallic caecum and is open where penial retractor muscle inserts on epiphallic caecum (Fig. 9A–C); an extension of the thin penial sheath also encloses a sizeable section of flagellum (this section located about halfway along length of flagellum). Epiphallus passes through and is attached to penial sheath in region where thick penial sheath transitions into thin penial sheath.

With penial sheath dissected open, penis seen to have noticeable S-shaped bend midway; this bend is associated with a band of muscle that extends for some distance along penis, on either side of bend (Fig. 9D–E). Distally, penis branches into wider-lumened epiphallic caecum and narrower-lumened epiphallus. Epiphallus passes into much narrower-lumened vas deferens; junction between these two regions marked by long, bluntly pointed flagellum, which is similar in length to epiphallus. Penial retractor muscle, which originates on inner lung wall, inserts in two places (Fig. 9E): subterminally on epiphallic caecum, and on apex of loop of epiphallus (i.e., about three quarters of distance from vas deferens to penis). Junction between two branches of penial retractor muscle located near most distal part of epiphallic caecum. Irregular small holes/pores visible on inner surface of thin part of penial sheath (i.e., with sheath cut open and pinned out).

On the basis of the morphology of its inner wall, penis divisible into three morphologically distinct regions, proximal penis, mid-penis and distal penis, with S-shaped bend of penis including all of mid- and



Fig. 6. Live individuals of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. from Hiranyakeshi Temple, Amboli, showing shell lobes in retracted state. **A.** Right lateral view. **B.** Left lateral view. Note that the caudal horn is extended in A and fully retracted in B.

distal penial regions (Fig. 10). Proximal penis shows one major and several minor longitudinal pilasters; close study at low magnification ($4\times$) of holotype and one paratype (BNHS GAS 114) showed that pilasters are interspersed by fine, obliquely longitudinal ridges that are close and irregular. Mid-penis ornamented by several thin longitudinal pilasters. Distal penis also with thin longitudinal pilasters, but here they are fewer in number and are contiguous with uniform, widely spaced transverse ridges that

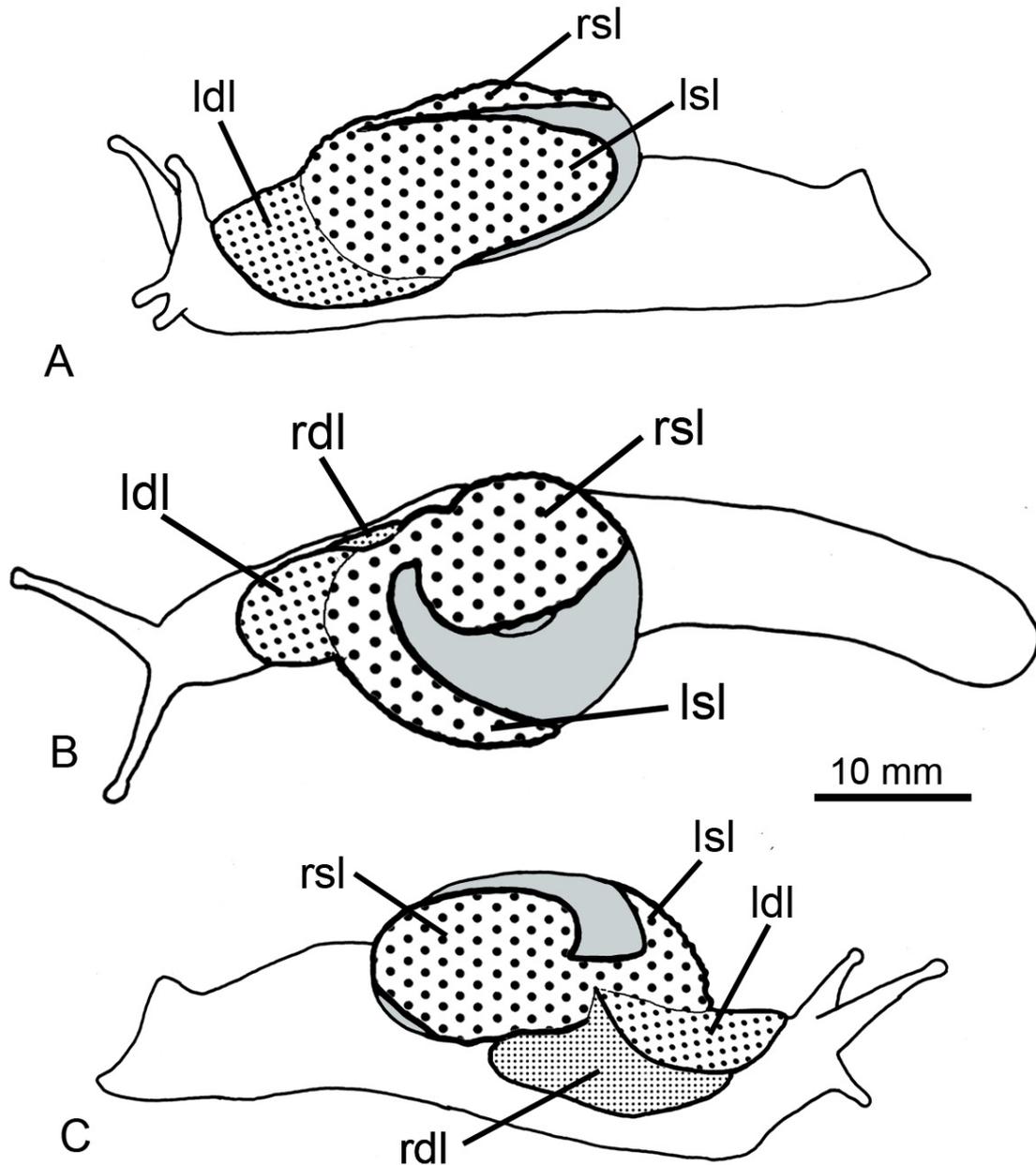


Fig. 7. Arrangement of the mantle in *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A.** Left lateral view. **B.** Dorsal view. **C.** Right lateral view. The shell is shaded in grey. Abbreviations: ldl = left dorsal lobe; rdl = right dorsal lobe; lsl = left shell lobe; rsl = right shell lobe.

extend outwards on either side of each pilaster. Opening of epiphallus into most proximal part of epiphallic caecum clearly visible (Fig. 10). Inner wall of epiphallic caecum (Fig. 10) has one major longitudinal pilaster (surface marked by irregular, fine longitudinal and/or transverse ridges; not shown in Fig. 10) running along its length; a large, reticulate mass of ridges proximally; and several short longitudinal pilasters distally. The short pilasters tend to be crenulated proximally and are smoother distally. Lumen of vas deferens widens with increasing distance from epiphallus, with part of vas deferens nearest to epiphallus being noticeably narrower-lumened than remaining two thirds (Fig. 8A). Right eye retractor

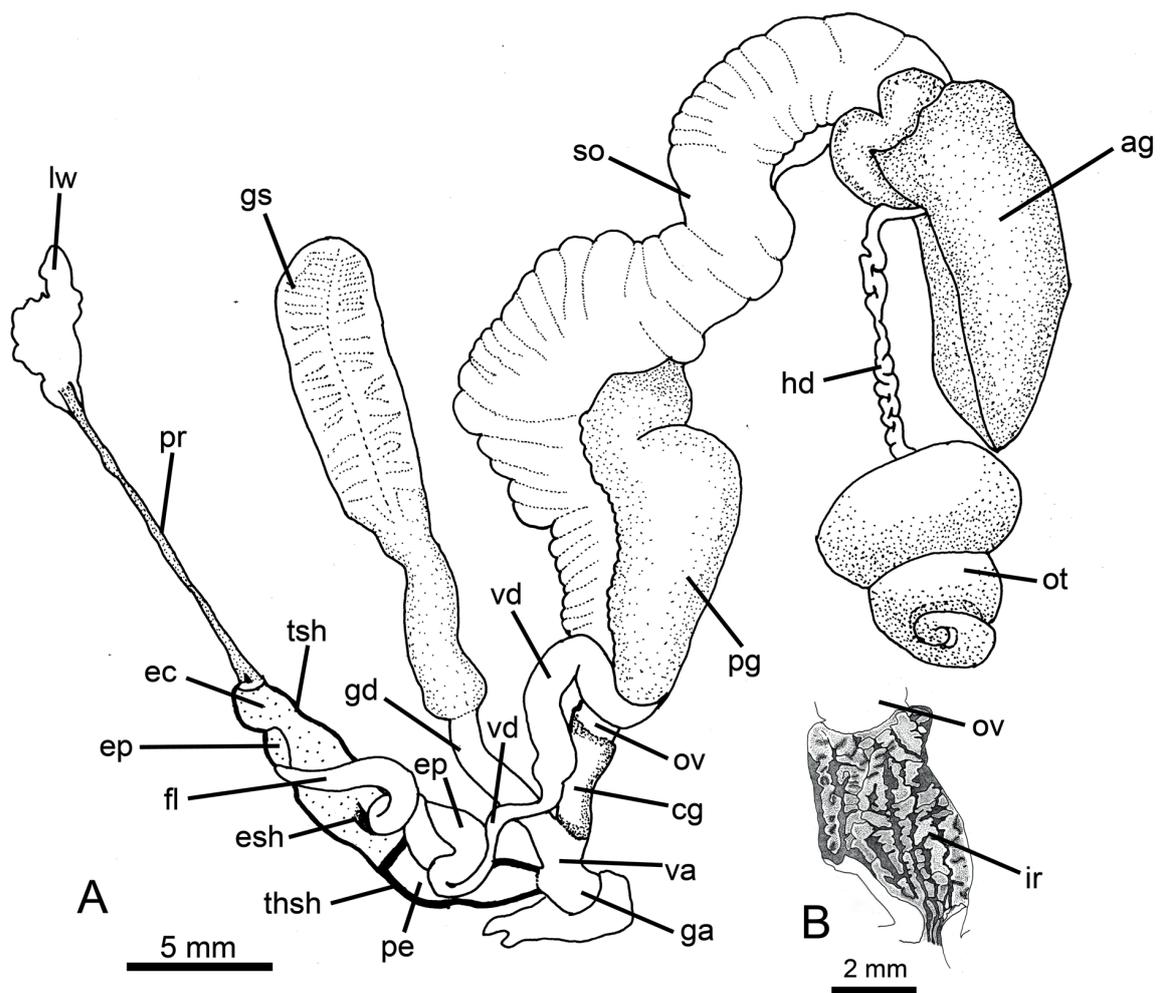


Fig. 8. Reproductive system of the holotype (BNHS GAS 113) of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A.** Gross morphology. **B.** Dissection of capsular gland, showing morphology of inner wall. Abbreviations: ag = albumen gland; cg = capsular gland; ec = epiphallic caecum; ep = epiphallus; esh = extension of penial sheath around epiphallus; fl = flagellum; ga = genital atrium; gd = gametolytic duct; gs = gametolytic sac; hd = hermaphrodite duct; ir = irregularly-marked papillate ridges; lw = lung wall; ot = ovatestes; ov = oviduct; pe = penis; pg = prostate gland; pr = penial retractor muscle; thsh = thick penial sheath; tsh = thin penial sheath; so = spermoviduct; va = vagina; vd = vas deferens.

muscle passes between male and female genitalia. Amatorial organ absent. Genital atrium cylindrical, well defined but short, with junction between male genitalia and vagina located at a short distance from genital orifice. Vagina cylindrical and shorter in length than genital atrium (Fig. 8A). Proximal part of oviduct, near junction with gametolytic gland, consists of pale yellowish, indistinctly-defined region, which is most likely the capsular gland (see Dasen 1933); inner wall of this gland irregularly marked by papillate ridges and papillae (Fig. 8). Gametolytic gland (Fig. 8A) comprises narrow gametolytic duct and long, voluminous sac that is ca 3–3.5 times length of duct; duct noticeably constricted at its junction with sac and has 1–3 longitudinal ridges on its inner wall.

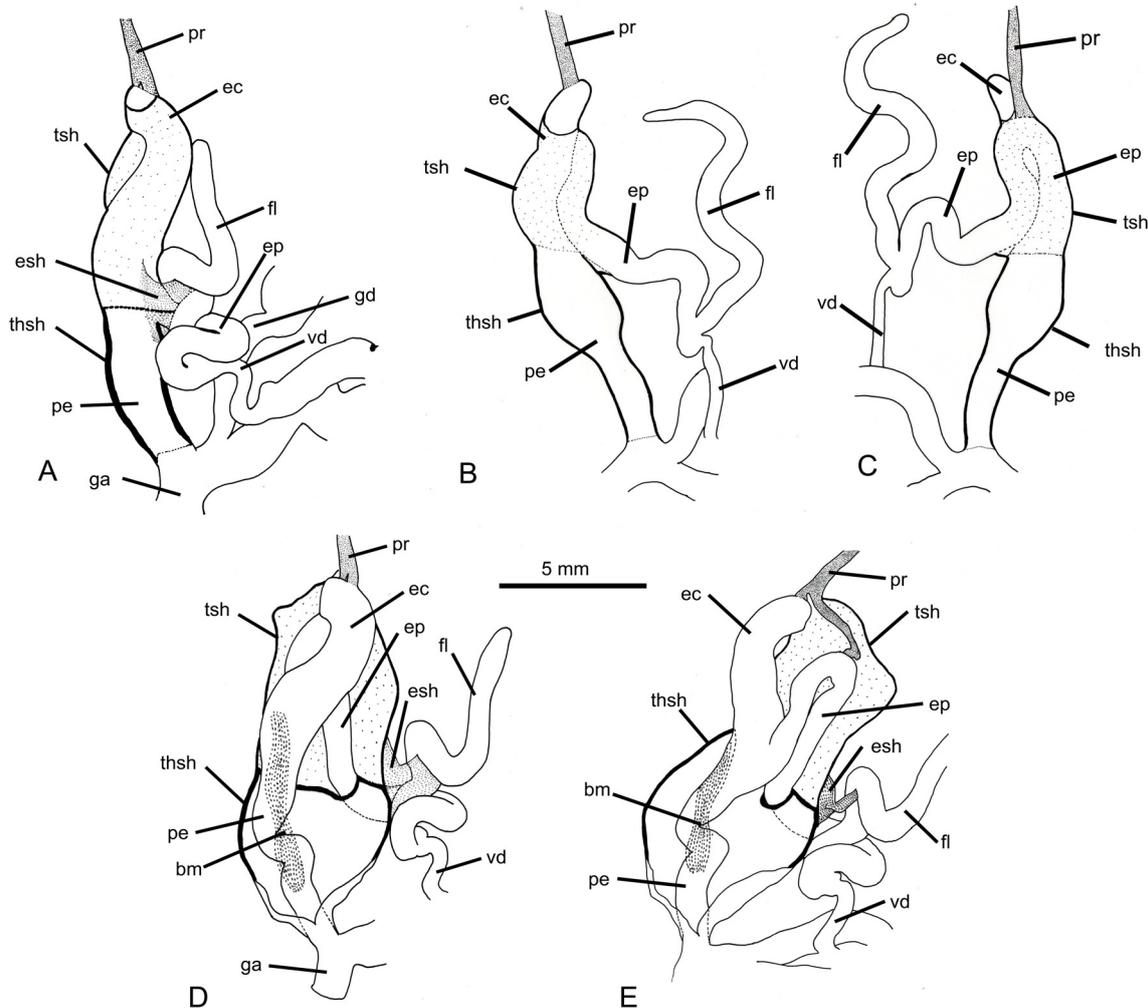


Fig. 9. Male genitalia of the holotype (A, D–E; BNHS GAS 113) and one of the paratypes (B–C; BNHS GAS 116) of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A.** After dissecting out from the body and with penial sheath in situ. **B–C.** With extension of penial sheath around epiphallus dissected open; dorsal (B) and lateral (C) views are shown. **D–E.** With penial sheath cut open; dorsal (D) and lateral (E) views are shown. Thick part of penial sheath shown by bold outline and thin part by dotted outline. Abbreviations: bm = band of muscle; ec = epiphallic caecum; ep = epiphallus; esh = extension of penial sheath around epiphallus; fl = flagellum; ga = genital atrium; gd = gametolytic duct; pe = penis; pr = penial retractor muscle; thsh = thick penial sheath; tsh = thin penial sheath; vd = vas deferens.

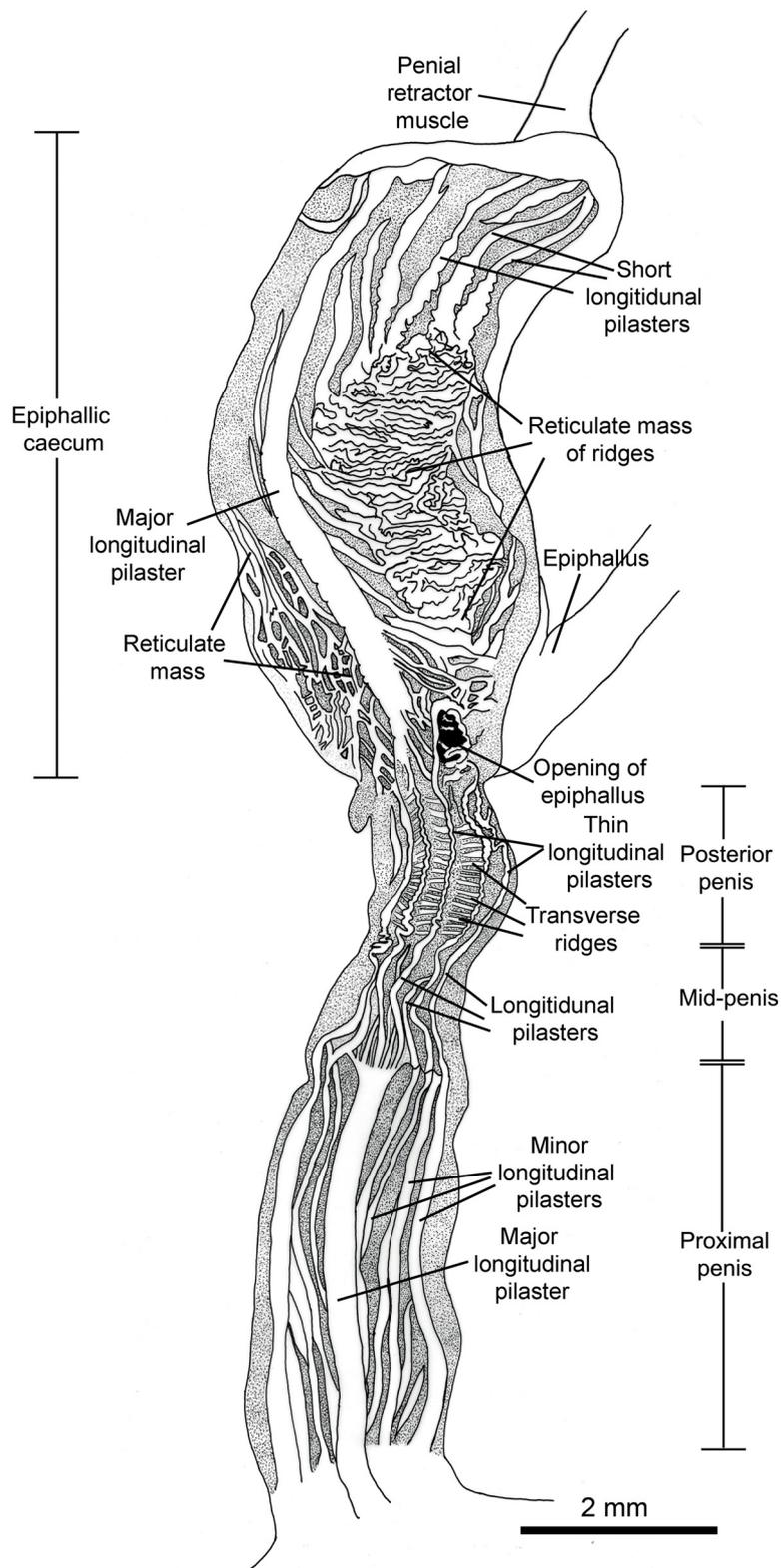


Fig. 10. Inner surface of penis in the holotype (BNHS GAS 113) of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. Note that the short longitudinal pilasters of the epiphallus caecum are crenulated proximally. The close, fine longitudinal ridges between the longitudinal pilasters of the proximal penis are not illustrated.

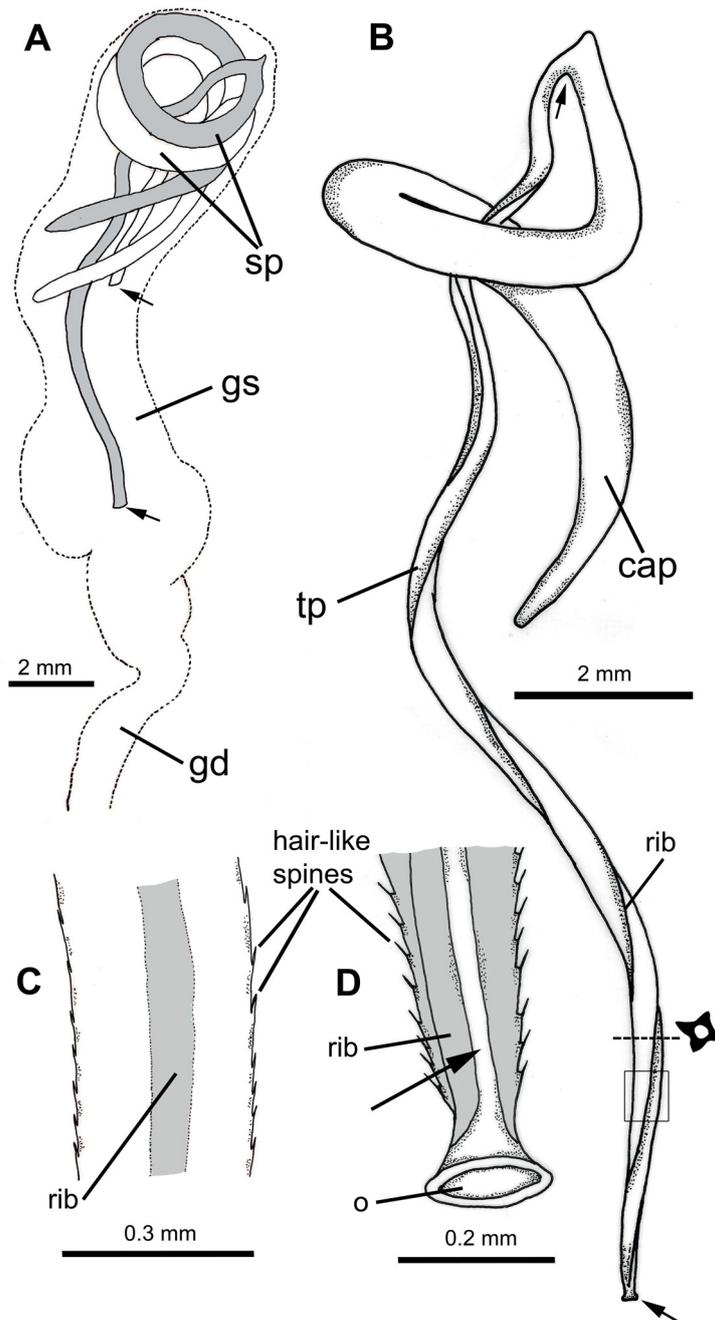


Fig. 11. Spermatophore of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A.** Fragments of two spermatophores (part of the tail-pipe is missing in both), as found in situ in the gametolytic sac of the paratype BNHS GAS 125. **B–D.** Morphology of the fully-intact spermatophore found in the gametolytic sac of the paratype ZSI Moll/1820. **B.** The upper arrow indicates the U-shaped bend at the junction of the capsule and tail-pipe, and the lower arrow shows the funnel-like opening at the tip of the tail-pipe. Also shown is the cross section of the spermatophore (indicated by the dotted line) close to the tip of the tail-pipe; note the hollow central area. **C.** Detail of a small section of the tail-pipe (indicated by rectangle in B), showing one of the four longitudinal ribs and the hair-like spines on the spermatophore surface. **D.** Detail of tip of tail-pipe, showing the funnel-like opening that leads into the hollow central area (shown by arrow). Note the hair-like spines. Abbreviations: cap = capsule; gd = gametolytic duct; gs = gametolytic sac; o = opening at tip of tail-pipe; sp = spermatophore; tp = tail-pipe.

One or two spermatophores (i.e., only one wholly intact; the rest damaged/partially digested) present in gametolytic gland of each of six specimens (Fig. 11A). Intact spermatophore consists of elongated, soft capsule with long tail-pipe. Sharply-angled, U-shaped bend at junction of capsule and tail-pipe; apex of bend noticeably hooked towards tail-pipe. Capsule wider-lumened than tail-pipe and twisted spirally (Fig. 11B). Tail-pipe flexible, internally hollow and externally sculptured obliquely along its length with four fine ribs. Tail-pipe in vicinity of tip hollow centrally and this passes into funnel-like opening (perforation) (Fig. 11D); surface of spermatophore near tip of tail-pipe has short, hair-like spines that point towards capsule (Fig. 11C).

RADULA AND JAW. Central tooth tricuspid, with large mesocone, which is shorter than tooth base, and smaller, more basal ectocones (Fig. 12A–B). Inner laterals 17–21, uniformly tricuspid (Fig. 12A–B); mesocone large, equal in size to those of central tooth and shorter than tooth base, endocone barely defined and ectocone prominent but more basal than other cusps. Outer 2 lateral teeth grade into marginal teeth. Marginal teeth 45–53, uniformly bicuspid (endocone absent), with shorter, narrower and more basal ectocone (Fig. 12C–D). Formulae for the 8 specimens examined are as follows (the plus sign indicates that the outermost marginal teeth could not be counted):

Holotype BNHS GAS 113	(+50.20.1.18.2.50+)
Paratype BNHS GAS 114	(+49.21.1.19.2.49+)
Paratype BNHS GAS 115	(53.19.1.17.2.53)
Paratype BNHS GAS 116	(+45.21.1.19.2.45+)
Paratype BNHS GAS 117	(+50.19.1.17.2.50+)
Paratype BNHS GAS 118	(+48.23.1.21.2.48+)
Paratype BNHS GAS 119	(+48.19.1.17.2.48+)
Paratype BNHS GAS 120	(52.22.1.20.2.52)

Jaw oxygnath (smooth), having a concave cutting edge with well-defined or barely evident median projection (Fig. 12E).

Distribution and ecology

Varadia amboliensis gen. et sp. nov. is endemic to the northern and central Western Ghats of India and is currently known from only 5 localities. These are: Hiranyakeshi temple, Amboli, Sindhudurg District, Maharashtra State (15°57'17.8" N, 74°01'39.1" E; 839 m a.s.l.); Amboli Forest Park, Sindhudurg District, Maharashtra State (15°57'37.4" N, 73°59'58.1" E; 724 m a.s.l.); near Amboli waterfall, Sindhudurg District, Maharashtra State (15°56'26.9" N, 73°59'41.2" E; 645 m a.s.l.); Kodali, Kolhapur District, Maharashtra State (15°46'42.4"N, 74°10'40.0"E; 620 m a.s.l.); Yana Forest, Uttara Kannada District, Karnataka State (14°35'16.4"N 74°34'00.3"E; 272 m a.s.l.) (A. Bhosale, 2018, personal observation). The species occurs at elevations ranging from 272 to 839 m. Although it has been observed among human habitation on forest edges (Fig. 13), *V. amboliensis* gen. et sp. nov. appears to be primarily a species of tropical semi-evergreen and evergreen forest (sensu vegetation classification of Pascal 1991). The range of this species, as currently known, is restricted and disjunct. While 4 of the 5 known localities are in the extreme south of Maharashtra State (northern Western Ghats), the only other known locality, Yana Forest in northern Karnataka (central Western Ghats), is ca 160 km to the south. Further surveys are required to establish if this species occurs in the intervening area.

Varadia amboliensis gen. et sp. nov. is primarily a ground-living snail. It can be encountered at night in leaf litter or on rocks and the bases of trees; in rainy weather it can be seen on the exterior walls of buildings close to the forest edge (e.g., it was observed at the entrance of Amboli Forest Park in September 2017). The species can be seen throughout the monsoon (June to October) and as late as the end of November.

A few individuals have been seen in late February (late winter) on the banks of fast-flowing streams at Amboli.

This species appears to be omnivorous. It has been observed feeding on decaying plant matter (leaf litter, discarded banana peel) and on the remains of at least two different invertebrate taxa (a cricket and an earthworm) (A. Bhosale, personal observation) (Supp. file 1). Data on its predators are scarce,

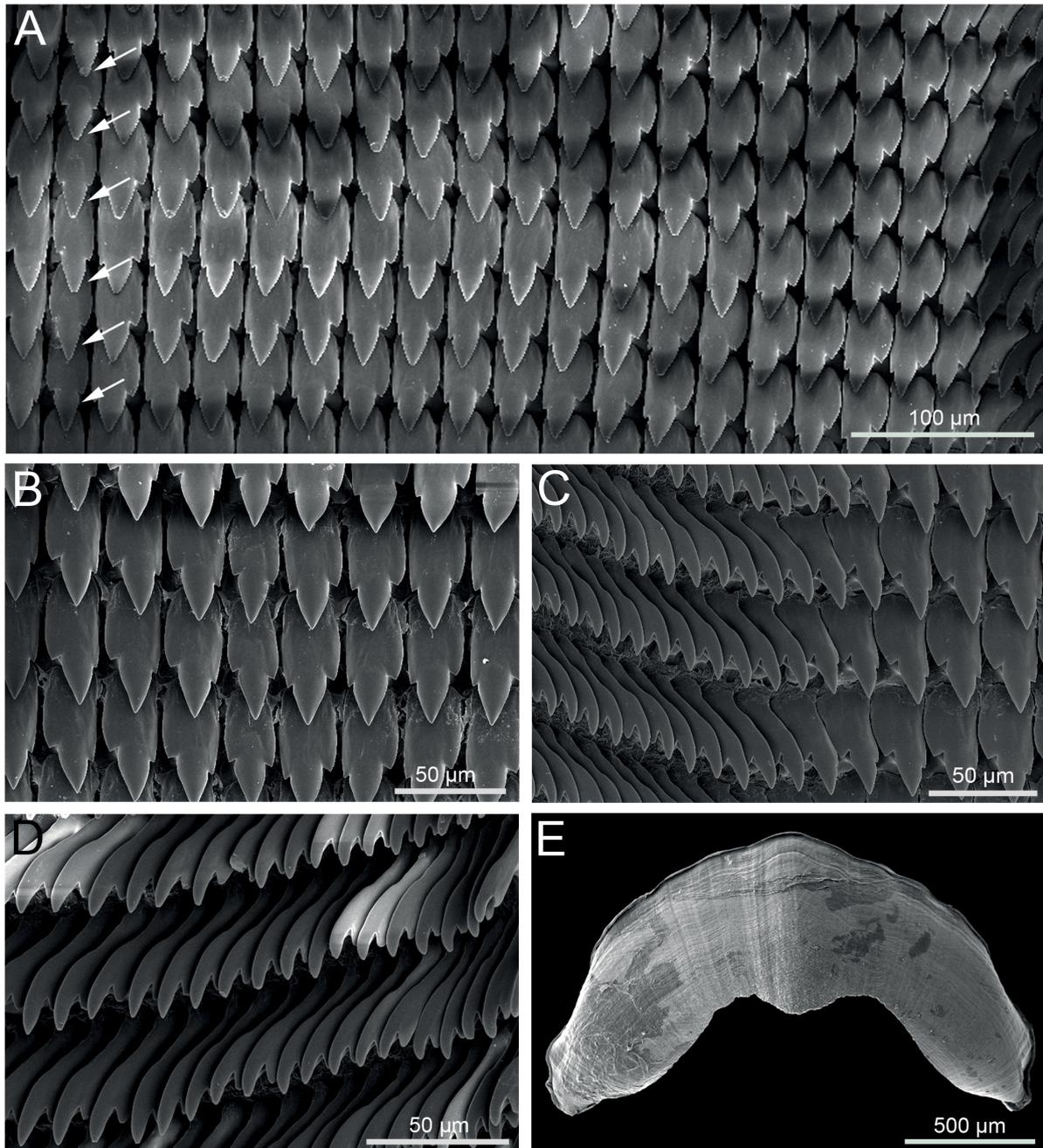


Fig. 12. Radula and jaw of a paratype (BNHS GAS 127) of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A.** Central (indicated by arrows), inner lateral and outer lateral teeth. **B.** Central and inner lateral teeth. **C–D.** Marginal teeth. **E.** Jaw. Note median projection.

but a scorpion of the genus *Heterometrus* Ehrenberg, 1828 (Scorpionidae) was observed feeding on an individual of this species (Supp. file 1).

DNA analysis

The three phylogenetic analyses (NJ, ML and Bayesian) yielded broadly similar results (Fig. 14), with disagreements occurring only for internal branches lacking strong support in any of the analyses. Most deeper relationships within the Limacoidea were not strongly supported, with the optimal ML and NJ trees having fewer strongly supported branches than the Bayesian tree. All three trees included a sister-



Fig. 13. Habitat of *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. **A.** Hiranayakeshi temple. **B–C.** Amboli Forest Park; snails were observed on the walls of the temple and other structures and in the surrounding forest. **D–E.** Amboli waterfall; snails were observed on the wall near the sunshade (D) and on the roadside safety barrier (E). **F.** Yana Forest, where snails were found on the forest floor, close to the footpath.

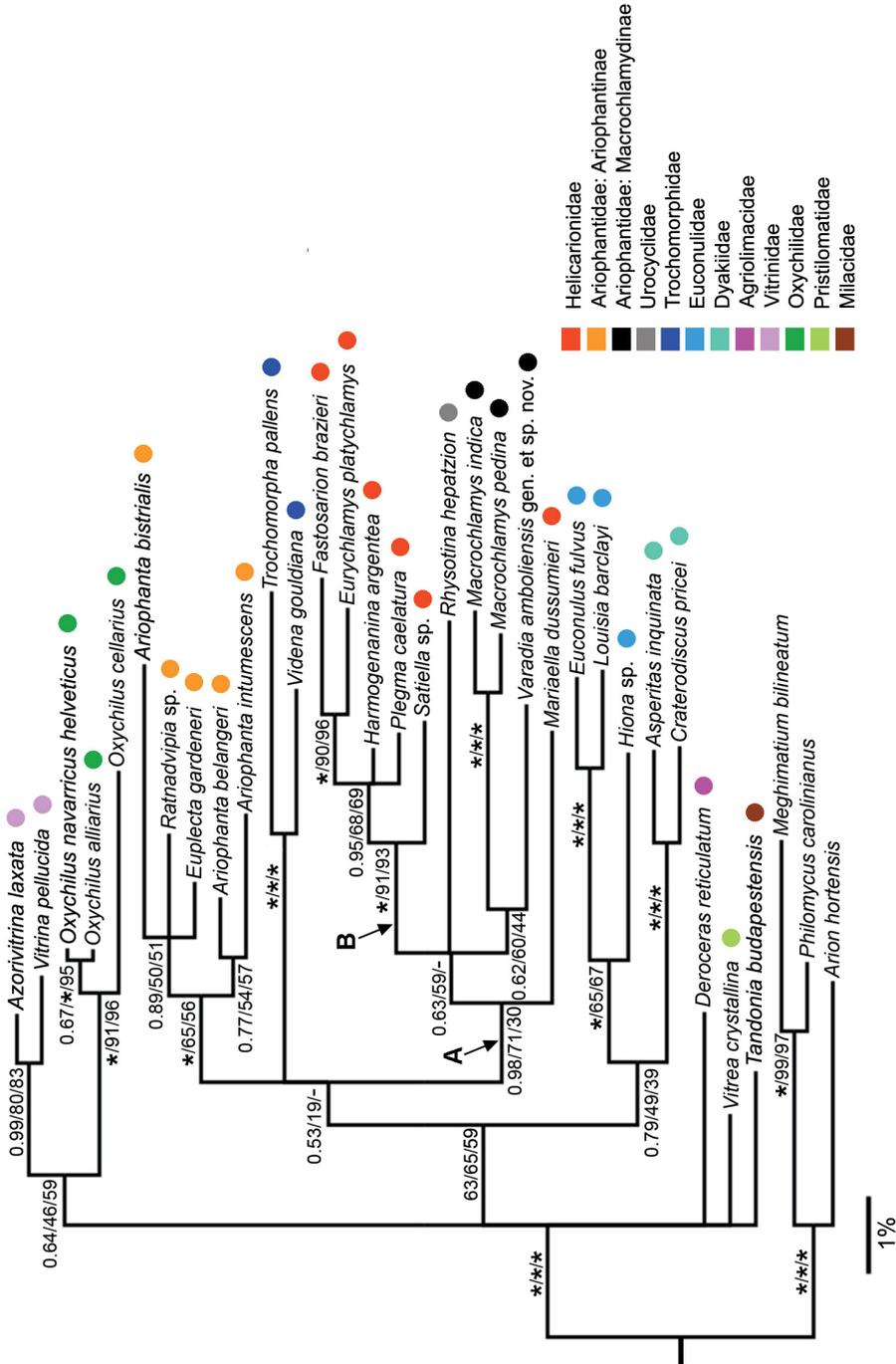


Fig. 14. Bayesian majority rule consensus tree of the rRNA gene cluster dataset (874 bp) for the Limacoidea. Ingroup taxa are colour-coded by their family-level placements, with subfamily-level placements being shown only for Ariophantidae (see Table 1). The tree is rooted with an outgroup consisting of three members of the Arionoidea (*Arion hortensis* Férussac, 1819, *Meghimatium bilineatum* (Benson, 1842) and *Philomycus carolinianus* (Bosc, 1802)). Clades A and B are indicated by arrows. Branch support values are shown in the following sequence: Bayesian posterior probabilities, ML bootstraps and NJ bootstraps. Symbols: '*' = maximal support (Bayesian = 1; NJ, ML = 100%); '-' = differences in branching pattern between Bayesian and NJ trees. Scale bar indicates substitutions per site.

group relationship between *Varadia* gen. nov. and the always maximally supported *Macrochlamys* clade (*Macrochlamys indica* Benson, 1883 + *M. pedina* (Benson, 1865)), but this was not strongly supported in any of the analyses (Bayesian: PP = 0.62; ML: BS = 60%; NJ: BS = 44%). All analyses also provided maximal support for the clade composed of five of the six helicarionid taxa, *Fastosarion brazieri* (Cox, 1873), *Eurychlamys platyichlamys* (Blanford, 1880), *Harmogenanina argentea* (Reeve, 1852), *Plegma caelatura* (Férussac, 1821) and *Satiella* sp. (clade B in Fig. 14). Within clade B, support for the sister-group relationship between *Fastosarion* Iredale, 1933 and *Eurychlamys* was consistently strong (ML: BS = 90%; NJ: BS = 96%) or maximal (Bayesian). Two of the three analyses (ML: BS = 71%; Bayesian: PP = 0.98) provided strong support for clade A, comprising clade B, *Rhysotina hepatzion* (Gould, 1848), the *Macrochlamys* clade, *Varadia* gen. nov. and *Mariaella dussumieri* Gray, 1855. All analyses provided maximal support for the monophyly of the Trochomorphae Möllendorff, 1890, of the Dyakiidae Gude & B.B. Woodward, 1921 and of the Euconulidae H.B. Baker, 1928 (i.e., clade comprising *Euconulus fulvus* (Müller, 1774) and *Lousia barclayi* (Benson, 1850)). The monophyly of the Vitrinidae Fitzinger, 1833 and of the Oxychilidae Hesse, 1927 (1879) was also consistently strongly supported. Within the ingroup, nearly all the other branches were either strongly supported only in the Bayesian tree (e.g., clade comprising the five species of Ariophantinae sensu stricto) or were not strongly supported in any of the analyses.

Examination of all bipartition frequencies for the ML bootstrap trees (n = 1008) showed that the best supported bipartition that is not compatible with *Varadia* gen. nov. forming a clade with the two species of *Macrochlamys* is one in which *Macrochlamys* forms a clade with the five helicarionids, *Fastosarion brazieri*, *Eurychlamys platyichlamys*, *Harmogenanina argentea*, *Plegma caelatura* and *Satiella* sp. (BS = 12%). Similarly, for the NJ bootstrap trees (n = 1000), the best supported bipartition that is incompatible with the clade of *Varadia* gen. nov. + *Macrochlamys* is the clade uniting all the helicarionids and *Rhysotina hepatzion* with *Macrochlamys* (BS = 14%).

Discussion

Two of the three phylogenetic analyses (ML and Bayesian) showed strong support for clade A (consisting of clade B, *Rhysotina hepatzion*, the *Macrochlamys* clade, *Varadia* gen. nov. and *Mariaella dussumieri*). We note, however, that while this clade is strongly supported (BS = 71%) in the ML tree it is only very weakly supported in the NJ tree (BS = 30%), so its robustness requires substantial further investigation (e.g., by expanded sampling of taxa and/or gene regions). The five members of the Ariophantinae sensu stricto (Blanford & Godwin-Austen 1908; an almost exclusively Peninsular Indian–Sri Lankan group) lie outside clade A. Although this suggests that *Varadia* gen. nov. is not a member of the Ariophantinae sensu stricto, the position of *Varadia* gen. nov. within clade A was not compellingly resolved, and that includes uncertainty about the sister group of *Varadia* gen. nov.

On the basis of characters of the reproductive system, particularly the male genitalia and the gametolytic sac, we provisionally place *Varadia* gen. nov. in the Macrochlamydiae. This is consistent with the results of our DNA analyses and there are two key points here. First, although the sister-group relationship of *Varadia* gen. nov. to *Macrochlamys* was not strongly supported (Bayesian: PP = 0.62; ML: BS = 60%; NJ: BS = 44%), it was consistently recovered by all analyses, and is much better supported than the best supported incompatible bipartition in both the ML (BS = 12%) and NJ (BS = 14%) analyses, though, taxon sampling could be an issue here, and further investigations are required to address this. Second, in two of the three analyses, *Varadia* gen. nov. was strongly supported (ML: BS = 71; Bayesian: PP = 0.98) as a member of a clade uniting the helicarionids with the *Macrochlamys* clade and the urocyclid *Rhysotina hepatzion*. In *V. amboliensis* gen. et sp. nov., as in many Macrochlamydiae, the penial retractor muscle inserts not on the tip or distal-most end of the epiphallic caecum but on the side. Hausdorf (1998) considered the lateral insertion of the penial retractor muscle on the epiphallic caecum to be the only known autapomorphy of the Macrochlamydiae; we note, however, that in the Indian species

Macrochlamys pedina and in several Thai members of the Macrochlamyidae (e.g., *Sarika* Godwin-Austen, 1907 and some *Taphrenalla* Pholyotha & Panha, 2020), the penial retractor muscle inserts on the tip of the epiphallic caecum (Blanford & Godwin-Austen 1908; Pholyotha *et al.* 2020a, 2020b).

While the form of the epiphallic caecum in South Asian Macrochlamyidae is varied, the most widespread form is a distinctly coiled mass that is enclosed in a thin and translucent outer covering (e.g., *Macrochlamys*, *Euaustenia* Cockerell, 1891 and *Bensonies* H.B. Baker, 1938; Blanford & Godwin-Austen 1908: 77–141, 148–152, 172–177). The epiphallic caecum may also be a loose, open coil (*M. richilaensis* Godwin-Austen, 1907, *M. zemoensis* Godwin-Austen, 1907; Blanford & Godwin-Austen 1908: 90–93), an irregular mass (*M. castaneolabiata* Godwin-Austen, 1883; Blanford & Godwin-Austen 1908: 101–102, 105) or straight and cylindrical (e.g., *M. pedina*; Blanford & Godwin-Austen 1908: 132–133). It is this last form of epiphallic caecum that occurs in *V. amboliensis* gen. et sp. nov. The new genus shares three other characters with some genera in the Macrochlamyidae (e.g., *Macrochlamys* and *Bensonies*): a well-developed epiphallus, a well-developed flagellum and a long, elongated gametolytic gland with a long stalk (cf. Blanford & Godwin-Austen 1908: 77–179).

In external morphology and in the form of the radula tooth *V. amboliensis* gen. et sp. nov. is similar to other Macrochlamyidae, as well as to some helicarionids. The broad shell lobes found in *V. amboliensis* gen. et sp. nov. also occur in other Indian Macrochlamyidae, such as *Parvatella* Blanford & Godwin-Austen, 1908 and *Euaustenia* from northern India, as well as in Indian helicarionids, such as *Satiella* (Blanford & Godwin-Austen 1908; Bhosale *et al.* 2019). We suggest that the expansion/retraction of the shell lobes in *V. amboliensis* gen. et sp. nov. and in other taxa (e.g., *Eurychlamys platychlamys*) may be related to air humidity, with the shell being largely covered by the mantle during rainy weather and the mantle lobes being largely retracted during drier conditions. In the new species the tripartite structure of the sole is clearly evident, the furrows demarcating the three sole fields being well defined. This condition is characteristic of both the Macrochlamyidae and the Helicarionidae; in the Ariophantinae sensu stricto, the tripartite structure is not obvious because the sole furrows are indistinct (Hausdorf 1998; Hyman & Ponder 2010; see also Blanford & Godwin-Austen 1908).

In the radula of *V. amboliensis* gen. et sp. nov., the central tooth has a large mesocone and two small ectocones; the lateral teeth have a large mesocone, a small/minute endocone and a larger, more basal ectocone; and the marginal teeth are bicuspid (endocone absent with no subdivision of the ectocone). Some Macrochlamyidae (e.g., Godwin-Austen 1908: *M. indica*; Hyman & Ponder 2010: *M. petrosa* (T. Hutton, 1834); Pholyotha *et al.* 2020a: *Taphrenalla*) and helicarionids, such as *Eurychlamys platychlamys* (Bhosale *et al.* 2019) and the Australian genera *Helicarion* Férussac, 1821 and *Stanisicarion* Hyman & Ponder, 2010 (Hyman & Ponder 2010) exhibit similar radular tooth form.

There are several clear differences between *V. amboliensis* gen. et sp. nov. and *Macrochlamys*. The amatorial organ (= stimulator of Hausdorf 1998), which is usually but not always present in the Macrochlamyidae (Blanford & Godwin-Austen 1908), is absent in the new genus. In comparison, the amatorial organ is nearly always present in the Ariophantinae sensu stricto, is usually absent in the Helicarioninae (Blanford & Godwin-Austen 1908)—all the Australian taxa lack it (Hyman & Ponder 2010)—and is sometimes absent in the Durgellinae (Blanford & Godwin-Austen 1908; e.g., present in *Durgella* W.T. Blanford, 1863 but absent in *Satiella*). We also note that *V. amboliensis* gen. et sp. nov. and *Macrochlamys* differ in the morphology of the capsular gland. In *Macrochlamys* and in the Ariophantinae (Dasen 1933) the capsular gland is a wide-lumened structure that is constricted at both ends and distinctly yellow in colour; in *V. amboliensis* gen. et sp. nov. it is slightly swollen but is otherwise not well defined. Another difference between the two genera is in the diameter of the vas deferens. This is more-or-less uniform in *Macrochlamys*; in *V. amboliensis* gen. et sp. nov., the section of the vas deferens (ca 60–70% of length) nearest to the spermoviduct/prostate gland is markedly wider (i.e., as wide as the epiphallus).

Also, on the basis of available data, the insertion of the penial retractor muscle at two separate points (near the tip of epiphalliac caecum and on the epiphallus) and the presence of a thin but noticeable band of muscle on the outer wall of the penis are unique to *Varadia* gen. nov.

Published data on the morphology of the penial sheath and inner wall of the penis are scarce for South Asian helicarionoideans (but see Hyman & Ponder: *M. petrosa*; Raheem & Naggs 2006: *Ratnadvipia* Godwin-Austen, 1899; Bhosale *et al.* 2019: *Eurychlamys*). While detailed anatomical studies of Thai and Myanma Macrochlamyinae have been published recently (e.g., Pholyotha *et al.* 2018, 2020a, 2020b), these do not include details on the structure of the penial sheath. We compared *M. cf. indica* from Kolkata (formerly Calcutta), West Bengal, India (4 specimens dissected; reg no. BNHS GAS 142 to 145) with *V. amboliensis* gen. et sp. nov., and this revealed some clear differences between the two. In the Kolkata examples of *M. cf. indica*, the penial sheath extends from the most proximal part of the penis to the area where the penis gives way to the coiled epiphalliac caecum; it is attached to the penial wall at these two ends but is otherwise free. In *V. amboliensis* gen. et sp. nov., in contrast, the penial sheath extends over the whole of the epiphalliac caecum, part of the epiphallus and a small part of the flagellum. Interestingly, our dissections of *M. cf. indica* indicate that like in *V. amboliensis* gen. et sp. nov., the penial sheath is divisible into a proximal section that is thick and opaque, and a distal section that is thin and transparent (to our knowledge, this has not been reported before). These dissections also suggest that the section of the epiphallus nearest to the epiphalliac caecum and penis is firmly attached to the penial sheath; again, this is similar to *V. amboliensis* gen. et sp. nov. Further studies of other species of *Macrochlamys* as well of other taxa in the subfamily Macrochlamyinae are required to investigate the generality of these observations. Internally, the penis of *M. cf. indica* is divisible into proximal and distal parts, with a well-developed penial verge (= penial papilla) demarcating the two; a similar arrangement has also been reported for Thai and Myanma *Macrochlamys* (Pholyotha *et al.* 2018, 2020b). In contrast, in *V. amboliensis* gen. et sp. nov., a penial verge is absent and the penis is divisible into three parts on the basis of the morphology of the inner surface.

The whole spermatophore and spermatophore fragments recovered from *V. amboliensis* gen. et sp. nov. were found in a loosely coiled state in the gametolytic sac. These spermatophores are broadly similar with those described and figured for *M. pedina* and *M. flemingi* (L. Pfeiffer, 1856) by Godwin-Austen (1899: 133, pl. 83: figs 5, 5a–c; pl. 87: figs 2, 2a–d), the capsule being relatively long and elongated in all three species. In *M. pedina* and *M. flemingi*, however, the entire length of the tail-pipe is covered with relatively large, branching spines that point towards the capsule; in *V. amboliensis* gen. et sp. nov., the spines are minute and confined to the free, terminal part of the tail-pipe (cf. the Australian helicarionid genus *Fastosarion*; Hyman & Köhler 2019). Godwin-Austen (1899: 133, 134; pl. 94: 1, 2, 2a, 4) also described and figured the spermatophores of *M. udus* Godwin-Austen, 1899 and *M. lecythis* (Benson, 1852). In these species, the capsule is short relative to the tail-pipe and spines (of varied complexity) are present only at the two ends of the tail-pipe. Spermatophores of broadly similar morphology have also been reported for some Thai *Macrochlamys* species (e.g., *M. aurantia* Pholyotha & Panha, 2018 and *M. coleus* Pholyotha & Panha, 2018; Pholyotha *et al.* 2018). The spermatophore of *V. amboliensis* gen. et sp. nov., unlike those described to date for *Macrochlamys*, has a pronounced U-shaped bend at the junction of the capsule and tail-pipe. We note that similarly bent spermatophores are characteristic of some urocyclid taxa (Van Goethem 1977: 34–35); these urocyclids, like *V. amboliensis* gen. et sp. nov., also have a perforated tip to the tail-pipe.

In external morphology (the combination of large size, broad, densely tuberculated shell lobes and a shell with ca 4 whorls and a disproportionately large body whorl), *V. amboliensis* gen. et sp. nov. is unique among the helicarionoidean taxa of the Western Ghats. *Eurychlamys platychlamys*, *M. indica* and *M. pedina* are superficially similar, but the first two are smaller (particularly *E. platychlamys*) and all have tightly-wound shells composed of ca 5 whorls (cf. Raheem *et al.* 2014: fig. 67a–b; Bhosale *et al.*

2019: fig. 2). In addition, the shell lobes in the two species of *Macrochlamys* are narrow, ribbon-like and highly mobile (Bhosale *et al.* 2019: fig. 8a; A. Bhosale, unpublished data).

Acknowledgements

We are grateful to the Maharashtra Forest Department, Government of India (GoI) for providing the relevant collecting and fieldwork permits. Financial support was provided to AB by the IPLS programme, Department of Biotechnology, GoI (grant no. BT/PR4572/INF/22/147/2012); DST PURSE Phase I and Phase II of the Department of Science and Technology, GoI; and the Systematics Research Fund of the Systematics Association and the Linnean Society of London, UK. Lab facilities were provided by the Department of Zoology, Shivaji University, Kolhapur, India. We would like to thank the following people at Shivaji University: Shantakumar Manne (Head of Department of Zoology), for his help during the study; J.P. Jadhav (Head of Department of Biotechnology), for facilitating this work under a DBT-IPLS project; S.P. Govindwar (former Head of Department of Biochemistry), for giving AB permission to work in the molecular biology lab in his department; and Manoj Jadhav and Mansingh Nimbalkar (Department of Botany), for assisting AB with SEM work. Omkar Yadav, Tejas Patil, Rupesh Yadav, Gopal Raut, Pramod Lawand, Rupali Khandekar, Mayur Jadhav and Shirraj Patil assisted with fieldwork. Santosh Saste (DFO), Akshay Khandekar, Swapnil Pawar, Priyanka Patil, Yogesh Mane and Suraj Patil helped us at various stages. We would also like to acknowledge Fred Naggs for helping us in our initial efforts to identify the new genus, Rahul Khot for assisting us with the deposition of specimens at BNHS, P.S. Bhatnagar and S. Talmale for helping us with the deposition of specimens at WRC ZSI, David Gower for feedback on phylogenetic analysis, David Reid for advice on the formation of taxon names, Bernhard Hausdorf and Isabel Hyman for reviewing the manuscript; Thierry Backeljau for valuable editorial feedback; and František Kovařík for identifying the scorpion photographed preying on *Varadia* gen. nov.

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Manuscript received: 4 December 2020

Manuscript accepted: 4 March 2021

Published on: 29 June 2021

Topic editor: Rudy C.A.M. Jocqué

Section editor: Thierry Backeljau

Desk editor: Radka Rosenbaumová

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Supplementary file

Supp. file 1: A–B. *Varadia amboliensis* Bhosale, Thackeray, Muley & Raheem gen. et sp. nov. feeding on a banana skin (A; photographed at Amboli) and on a dead cricket (B). **C.** A scorpion of the genus *Heterometrus* Ehrenberg, 1828 feeding on *V. amboliensis* gen. et sp. nov. (image: V. Giri).
<https://doi.org/10.5852/ejt.2021.757.1413.4535>