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A unique radiation of marine littorinid snails in the freshwater streams of the Western Ghats of India: the genus *Cremnoconchus* W.T. Blanford, 1869 (Gastropoda: Littorinidae)

DAVID G. REID[1]*, NEELAVARA ANANTHRAM ARAVIND[2] and NEELAVARA ANANTHRAM MADHYASTHA[3]

[1]*Department of Zoology, Natural History Museum, London SW7 5BD, UK*
[2]*Biodiversity and Conservation Genetics Unit, Ashoka Trust for Research in Ecology and the Environment (ATREE), Royal Enclave, Srirampura, Jakkur PO, Bangalore, Karnataka 560064, India*
[3]*Malacology Centre, Poorna Prajna College, Udupi, Karnataka 576101, India*

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The caenogastropod family Littorinidae is almost exclusively marine, but a unique freshwater genus, *Cremnoconchus*, is known from India. Its members are restricted to montane streams on the western escarpment of the Western Ghats, at altitudes between 300 and 1400 m. Four species and several varieties were described in the 19th century, but no taxonomic study has been carried out for over 120 years and the last anatomical report was in 1935. Nevertheless, they are of unusual evolutionary interest and also of conservation concern as a genus endemic to the Western Ghats biodiversity hotspot. Based on anatomical study of newly collected material and examination of historical and type specimens, we present a systematic revision of *Cremnoconchus*, illustrating shells, radulae, and reproductive anatomy. The very large eggs, invaginated penial filament, and calcified operculum are unique among Littorinidae. Three valid, described species (*C. syhadrensis*, *C. conicus*, *C. canaliculatus*) are recognized in the northern Western Ghats in Maharashtra state, where all can occasionally be found sympatrically. We describe an additional six new species from the central Western Ghats in a small area (linear distance 80 km) of Karnataka state, over 500 km south of the previously known range of the genus. Here the species each appear to be restricted to a single drainage system. Because of their highly restricted distribution and fragile habitat, this radiation of nine species is judged to be endangered.

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ADDITIONAL KEYWORDS: conservation – Karnataka – Maharashtra – operculum – pallial oviduct – penis – radula.

INTRODUCTION

Few families of gastropod molluscs have significant representation in both marine and freshwater environments, most being restricted to one or the other. Of the 409 recognized families of Recent gastropods, 26 are almost or entirely restricted to freshwater and only four (Neritidae and three rissooidean families, Assimineidae, Hydrobiidae and Stenothyridae) span freshwater, brackish and marine environments (Strong *et al*., 2008). However, there are a few predominantly marine families that include a small number of truly freshwater species. Among these are the Buccinidae (about a dozen species of *Clea* in South-East Asia; Brandt, 1974) and Marginellidae (two species of *Rivomarginella* in Indonesia and Thailand; Coomans & Clover, 1972). To these may be

*Corresponding author. E-mail: dgr@nhm.ac.uk

added two marine families with a very few members in fresh to brackish water: Nassariidae (three species of *Pygmaeonassa* in India and two of *Nassodonta* in India and Vietnam; Cernohorsky, 1984; Kantor & Kilburn, 2001) and Lottiidae (monotypic *Potamacmaea* in India; Lindberg, 1990). Opisthobranchs are almost exclusively marine, but within the minute interstitial Acochlidia there are two freshwater lineages (Acochlidiidae in the lower reaches of streams on Pacific islands; Brenzinger *et al.*, 2011; monotypic *Tantulum* in a montane spring in the Caribbean; Neusser & Schrödl, 2007). With one exception, all these examples are found in the tropical Indo-West Pacific region, where they are often narrowly localized. Consequently, they are rarely collected and are often less well known than their marine relatives. These freshwater members of marine families raise interesting, but still largely unanswered, questions about their phylogenetic relationships, antiquity, geographical origins, physiological adaptations and the selection regimes under which they evolved (Vermeij & Wesselingh, 2002). It is intriguing that they are all ecologically or geographically restricted, suggesting that they might be ancient relicts (or possibly recent invaders) in an environment in which specialized freshwater families are competitively superior.

The Littorinidae are another family conforming to the pattern of a marine group with a localized freshwater radiation in tropical Asia. This family consists of about 205 species (Reid, 1989; Reid, Dyal & Williams, 2012) in 17 genera. Three of these (*Littoraria*, Reid, 1986a; *Mainwaringia*, Reid, 1986b; *Littorina*, Reid, 1996) include a few species that are tolerant of moderately brackish conditions, but only one, *Cremnoconchus*, is truly freshwater. This genus is restricted to the mountain escarpment on the western side of India, the Western Ghats. The first species to be discovered was named as a member of the cerithioidean genus *Anculotus* (Layard, 1855), but when W.T. Blanford introduced the genus (as *Cremnobates*) in 1863 he recognized its littorinid affinities (Blanford, 1863). Early accounts focused on aspects of its anatomy (Troschel, 1867; Stoliczka, 1871; Prashad, 1925; Linke, 1935), in order to confirm its similarity to marine littorinids. It was reported to occur on wet montane cliffs and near waterfalls, to exhibit an 'amphibious' mode of life and to aestivate during the dry seasons between the monsoons (Blanford, 1863, 1870; Annandale, 1919). This provoked interest in the reduced condition of its gill and 'pulmoniferous' character of its mantle cavity (Blanford, 1863; Stoliczka, 1871; Annandale, 1919; Prashad, 1925). There was speculation that since the Western Ghats had once been a marine cliff, *Cremnoconchus* was a descendant of similarly amphibious marine littorinids (Blanford, 1863; Prashad, 1925). Stoliczka (1871) went further, finding in *Cremnoconchus* a link between marine littorinids and terrestrial 'Cyclostomi' (Cyclophoridae).

The first formal test of the inclusion of *Cremnoconchus* in the Littorinidae was the cladistic analysis of morphological characters by Reid (1989). The results suggested a sister relationship between *Cremnoconchus* and the fully marine genera *Bembicium* and *Risellopsis*. Since the latter two are endemic to Australia and New Zealand, respectively, this raised the possibility of an ancient Gondwanaland connection (Reid, 1989). So far, molecular evidence for the phylogenetic relationships of *Cremnoconchus* has been limited. One species of *Cremnoconchus* was included among the outgroups in a phylogenetic analysis of the genera of the subfamily Littorininae based on sequences of four genes (Williams *et al.*, 2003) and again in a three-gene analysis of almost all species of Littorininae (Reid *et al.*, 2012). In neither case was the sister relationship with *Bembicium* and *Risellopsis* supported. Deeper phylogenetic relationships between outgroup and ingroup were not tested, but branch lengths did not suggest that *Cremnoconchus* is far distant from the other littorinid outgroups. There has not yet been a rigorous molecular test of the monophyly of the entire Littorinidae as defined by anatomical synapomorphies (Reid, 1989).

While the littorinid affinity of *Cremnoconchus* has not been seriously questioned, views on its rank within the family have ranged from that of subgenus (of *Littorina*; Stoliczka, 1871) to subfamily (Cremnoconchinae; Preston, 1915). In standard works on gastropod classification it has generally been treated as a genus (Tryon, 1887; Thiele, 1929; Wenz, 1938; Bouchet & Rocroi, 2005). During the 19th century a total of five specific and two varietal names were described in or assigned to *Cremnoconchus* (Layard, 1855; Blanford, 1863, 1870; Hanley & Theobald, 1876; Nevill, 1885; Bavay & Dautzenberg, 1900), although of these the latest is here shown not to belong to the genus. Since then, *Cremnoconchus* has been included in regional faunistic accounts (Hanley & Theobald, 1876; Preston, 1915; Subba Rao & Mitra, 1979; Subba Rao, 1989; Ramakrishna & Dey, 2007). Based on shell characters, a common view is that two species should be recognized: *C. syhadrensis* (W.T. Blanford, 1863) and *C. carinatus* (Layard, 1855) (synonym *C. conicus* W.T. Blanford, 1870) (Blanford, 1870; Stoliczka, 1871; Reid, 1989), although recently Subba Rao (1989) and Ramakrishna & Dey (2007) gave all three names specific status. However, no comprehensive review based on anatomical or molecular characters has been undertaken.

Despite the collecting activities of the early naturalists (Blanford, 1863, 1869, 1870, 1881; Stoliczka, 1871; Annandale, 1919; Prashad, 1925; Hora, 1926) and more recent work in India (Subba Rao & Mitra, 1979), it is remarkable that before the present study *Cremnoconchus* had been recorded at only about ten localities in the northern part of the Western Ghats in the vicinity of Pune (including literature and museum records; Supporting Table S1). These known localities lie between Nashik and Mahabaleshwar, a linear distance of about 225 km. Furthermore, the recorded habitat is highly restricted, comprising damp cliffs, streams and waterfalls at an altitude between 600 and 1400 m.

The Western Ghats region is recognized as a hotspot of terrestrial biodiversity (Myers *et al*., 2000) and a recent survey of its freshwater biota confirmed it as a 'globally significant centre of diversity and endemism for freshwater species' (Molur *et al*., 2011: vii). The northern part has been included as one of 25 worldwide hotspots of freshwater gastropod diversity and *Cremnoconchus* is one of two gastropod genera endemic to the Western Ghats (Strong *et al*., 2008; the other is *Turbinicola*, Ampullariidae). Of the global terrestrial fauna, freshwater molluscs are among the most diverse and threatened groups, so that their conservation is a matter of concern (Lydeard *et al*., 2004). Within the Western Ghats the freshwater biota is under threat from agricultural pollution, construction of roads and dams, mining and the development of tourism (Molur *et al*., 2011). Of the 52 gastropod species reported from the region the three *Cremnoconchus* species then recognized are the only ones to have been listed in the 'threatened' categories of the IUCN Red List (*C. syhadrensis* and *C. carinatus* as 'endangered' and *C. conicus* as 'vulnerable'; Aravind *et al*., 2011). The narrow ranges of these species, and the endemicity of the entire genus to the Western Ghats hotspot, should make their conservation a high priority. Their restricted distribution also suggests questions about the evolutionary mechanisms of diversification, which are poorly understood in freshwater molluscs (Glaubrecht, 2011). The first steps for both conservation of *Cremnoconchus* and evolutionary research on their radiation must be taxonomic study and recording of distribution.

The present study has been stimulated by the discovery of *Cremnoconchus* in the central Western Ghats, over 500 km south of the known localities near Pune (Williams *et al*., 2003; Madhyastha, 2008; Aravind *et al*., 2011). Our aims are: (1) to review the taxonomy of *Cremnoconchus* species based on morphological study of new material and existing museum collections; (2) to describe the habitats and geographical distributions of *Cremnoconchus* as a contribution to the assessment of their conservation status; and (3) based on our taxonomic and geographical results, to consider hypotheses of speciation and dispersal in the Western Ghats.

MATERIAL AND METHODS

Material

This study is based on examination of all material in BMNH and USNM, and on collections of new material from 14 localities (deposited in ZSI/WGRS; Supporting Table S1).

Institutional abbreviations: BMNH, Natural History Museum, London; USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC; ZSI, Zoological Survey of India, Calcutta; ZSI/WGRS, Zoological Survey of India, Western Ghats Regional Centre, Calicut.

Synonymies and types

Synonymies list all new names and new combinations, and include references to major taxonomic works and faunistic lists, standard identification guides and significant morphological descriptions. Almost all primary types have been seen, as noted, and the primary type of each valid name is figured. Lectotypes and neotypes have been designated as required. Synonymies are presented in condensed format, following each specific name through its generic combinations. For new names, no dash separates the author's name from the new epithet; a dash between the two indicates subsequent usage, which may be in a new combination. Misidentifications are indicated by a note in parentheses: 'not' followed by the name in its original form (omitted in the cases of species included in this account) with author and date; '=' is followed by the recognized valid form of the incorrectly used name. All figures quoted are of shells, unless otherwise indicated.

Descriptions

Diagnoses contain sufficient information to distinguish the species from others of similar appearance. DNA sequences of the mitochondrial COI gene (available from GenBank) are also given if available; these can be used to diagnose phylogenetic species.

The periphery of the shell is the junction between the upper part of the final whorl and the base (Fig. 1); it is usually marked by a slight angulation, or by an enlarged spiral rib. An umbilical slit may be present adjacent to the columella; as this is absent in juveniles it is termed a pseudumbilicus. If present, the sculpture of the final whorl is described in terms of the number of spiral ribs between suture and periphery, and on the shell base; the suture generally runs one or two ribs above the periphery, or is situated at the peripheral rib. Narrow ribs are referred to as threads; the spaces between the ribs are grooves. Microstriae are fine incised spiral lines that may

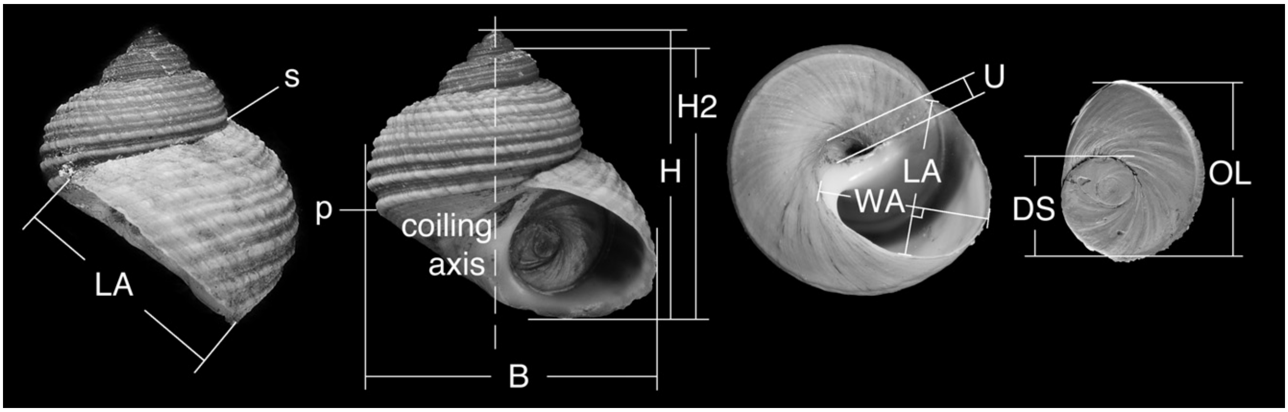

Figure 1. Measurements and terminology of shell and operculum (illustrated by *Cremnoconchus syhadrensis*). Abbreviations: B, breadth; DS, diameter of spiral part of operculum; H, height; H2, height of last two whorls; LA, length of aperture (in apertural plane); OL, opercular length (excluding flexible flange); p, periphery; U, width of pseudumbilicus; WA, width of aperture (in apertural plane). Shape indices: shell shape = H2/B; apertural shape = LA/WA; opercular ratio = OL/DS.

cover the entire surface and are visible only under low magnification (see Fig. 4). The protoconch (larval shell) is occasionally preserved at the apex and is terminated by a slight growth line. The whorls of the protoconch were counted as described by Reid (1996); for example, the protoconch in Fig. 16E has 1.5 whorls.

Shell dimensions were measured with vernier callipers to 0.1 mm (Fig. 1). Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip (measured in the plane of the aperture), and the width of the aperture (WA) the maximum dimension of the aperture perpendicular to LA. The width of the pseudumbilicus was also recorded. The shell apex was frequently eroded, so overall shell shape was quantified as the ratio of the height of the last two whorls to shell breadth (H2/B), and relative spire height as H2/LA. Apertural shape was quantified as the length to width ratio of the aperture (LA/WA). The opercular ratio describes the coiling of the operculum and is the ratio of two parallel measurements, the diameter of the spiral part divided by the maximum length (Fig. 1; Reid, 1996), excluding the thin, flexible flange projecting beyond the calcified part.

Magnesium chloride solution was ineffective for relaxing or anaesthetizing living animals. Animals were observed alive and those for dissection were fixed in 80% ethanol. Drawings of penes and pallial oviducts were made by camera lucida and drawing conventions are indicated in Figure 6. General accounts of the anatomy of littorinids and its terminology have been given by Reid (1986a, 1989, 1996, 2002). The penis of males is visible without dissection on the right side of the headfoot. The littorinid penis consists of a wrinkled, muscular base, often with glandular appendages, and a smooth, terminal, intromittent filament. In *Cremnoconchus* the filament is small and usually completely invaginated within the much larger penial base, remaining invisible unless the base is cut open. Unless otherwise noted, drawings were made as the penis appears when lying against the headfoot, i.e. in abaxial view. The shape of the penis changes somewhat with degree of contraction while alive, and with subsequent fixation (e.g. Figs 6A, B, D–G, 10A, B, 10I, J, 15A–C). In particular, the relaxed penis is narrower and more elongate, and the filament only protrudes upon fixation. Nevertheless, the shape and characteristic glandular features of the penis of each species can be seen regardless of condition or fixation. In both living animals and fixed specimens the glandular parts of the penial base usually appear more opaque than the rest. When the shell is gently cracked and removed, the pallial oviduct of females is visible, without dissection, on the right side adjacent to the columellar muscle. Although the egg groove of the pallial oviduct contains no pigment, its spiral route can usually be clearly seen by transparency (Fig. 6). Similarly, the copulatory bursa is usually visible without dissection, although its extent can readily be confirmed by sectioning of the pallial oviduct with a razor blade (Fig. 14C). Mature eggs were often found in the distal straight section of the pallial oviduct. The histological material of Reid (1989) was re-examined.

Two to four radulae were examined from each species. The relative radular length is the total radular length divided by shell height. Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 3 min, rinsed three times in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination by scanning electron microscopy (SEM). Unworn portions of the radula were viewed in two orientations: in standard flat view from vertically above the radula (to show shapes of tooth bases), and at an angle of 45° from the front end (to show shape of tooth cusps). The littorinid radula is taenioglossate, consisting of seven teeth in each transverse row: a central rachidian, flanked on each side by a lateral, an inner marginal and an outer marginal tooth. The shape of the rachidian tooth was quantified as the ratio of the total length (in flat view) to maximum width (measured at anterior end across cusp-bearing edge).

Distribution, records, maps and habitat

All distribution records have been personally verified unless otherwise noted. Literature records have only been accepted in cases where a figure or other information leaves little doubt as to the identification. The records listed in the text are not a complete record of material examined, but define the known limits of the range; a complete list of localities is given in Supporting Table S1. Modern place names are used in the text, except for type localities (see Supporting Table S1 for original spellings). All records refer to live-collected specimens. Habitat notes are those made by the authors, supplemented by information from the literature and museum labels, as indicated.

Species concept, taxonomic characters and identification

It is now customary to use an integrated approach to systematics, combining data from morphology, genetics and other sources to delimit species. Unfortunately, genetic data are not yet available to test the reciprocal monophyly and genetic distance of the species defined here. Even with genetic data the classification of freshwater gastropods can present difficulties as a result of fine-scale geographical differentiation, isolation in separate drainage systems, introgressive hybridization and ancestral polymorphism, so that morphological and genetic species definitions sometimes show a poor match (e.g. Lee *et al*., 2007; Köhler & Deein, 2010). Some freshwater caenogastropods show pronounced intraspecific local variation in shell form, which has been explained as ecophenotypic plasticity (e.g. Urabe, 2000; Dillon, 2011), but this can also result from natural selection or drift in isolated populations (Whelan, Johnson & Harris, 2012). Morphological classification of freshwater gastropods, especially if based only on the shell, have to be undertaken with caution.

In marine Littorinidae the shell (and even the radula) can also be subject to local selection or ecophenotypic effects. In this family the form of the complex penis is one of the most useful taxonomic characters, probably because it is involved in sexual recognition or sexual selection (see Reid, 1996, for a review). In *Cremnoconchus* it has been found that penial form is diagnostic for all species (although similar in the pair *C. conicus* and *C. canaliculatus*), but that neither oviduct, protoconch, nor radula are species-specific. The shells show some variability within species, but the existence of discontinuities between species supports the same groups as those defined by penial form. With experience, the known *Cremnoconchus* species can be identified from their shells alone. Useful features include overall shape, sculpture of ribs, microsculpture of fine spiral striae, presence of a pseudumbilicus, and the form and degree of calcification of the operculum.

Importantly, the discovery of four localities at which two or three distinct morphospecies are sympatric (Supporting Table S1) supports the hypothesis that these are indeed reproductively isolated, biological species.

The Western Ghats

The Western Ghats run for 1600 km along the western edge of India, between latitudes of 8 and 21°N. They consist of the western escarpment of the Deccan Plateau, and form a chain of hills or mountains separated from the Arabian Sea coast by a plain 30–60 km in width. Altitudes are modest, mostly between 600 and 1000 m, but extending to above 2000 m in parts (8–13 and 18–19°N). Rainfall averages 2500 mm and much is delivered by the south-western monsoon so is concentrated in June–October. In the central Western Ghats (i.e. the southern area of study, 12–14°N) rainfall exceeds 5000 mm and the dry season lasts for only 4–5 months, so strong perennial streams are common and moist evergreen forests extend as far north as 16°N. In the north (18–20°N) the dry season is longer, from 5 to 8 months, rainfall averages 3000 mm, streams are usually seasonal, and deforestation has left the hills with only small areas of secondary forest. (Description from Daniels, 1992; rainfall calculated by N.A.A., unpublished.)

SPECIES EXCLUDED FROM *CREMNOCONCHUS*

BYTHINIA EVEZARDI W.T. BLANFORD, 1881

This species was described by Blanford (1881) from near Khandala at the top of the Bhor Ghat Pass, from material collected by G. Evezard. In the description Blanford (1881) mentioned impressed spiral lines, conical umbilicus, and nearly vertical and angulate aperture with entire peristome. It was made the type of the monotypic bithyniid genus *Sataria* by Annandale (1920), who added that the calcified operculum had a central nucleus and concentric ridges, and described a bithyniid radula. He also commented that its range was coterminous with that of *Cremnoconchus*, having been recorded from Mahabaleshwar and Khandala. A collection of juvenile *Cremnoconchus* from Bhor Ghat in (USNM 317704, ex Evezard Colln) is labelled '*Cremnoconchus evezardi* Blanford, 1880'. This is presumably a misidentification based on the name *B. evezardi*, rather than a manuscript name for this *Cremnoconchus*. We are not aware that this taxon has ever been formally assigned to *Cremnoconchus*.

CREMNOCONCHUS MESSAGERI BAVAY & DAUTZENBERG, 1900

This species from Vietnam was initially described in the genus *Cremnoconchus* by Bavay & Dautzenberg (1900) and was figured under the same name by Dang (1980). Based on our examination of the original figure and description, it is a member of the Paludomidae, similar to *Paludomus petrosus* (Gould, 1844).

SYSTEMATIC DESCRIPTIONS

FAMILY LITTORINIDAE ANON., 1834

SUBFAMILY LACUNINAE GRAY, 1857

Risellidae Kesteven, 1903: 621–631.
Cremnoconchinae Preston, 1915: 64.
Bembiciidae Finlay, 1928: 241.

Remarks: Cremnoconchus was first placed in the subfamily Lacuninae by Stoliczka (1868, as *Cremnobates*). A new subfamily, Cremnoconchinae, was created for this genus, without discussion, by Preston (1915). If it is shown that *Cremnoconchus* deserves subfamilial or familial rank, the name Cremnoconchinae Preston, 1915 is therefore available.

CREMNOCONCHUS W.T. BLANFORD, 1869

Cremnobates W.T. Blanford, 1863: 184 (type species by monotypy *Cremnobates syhadrensis* W.T. Blanford, 1863; not *Cremnobates* Swainson, 1855; not *Cremnobates* Günther, 1861).
Cremnoconchus W.T. Blanford, 1869: 343 (new name for *Cremnobates* Blanford, 1863, not Günther, 1861).
Littorina (Cremnoconchus) – Stoliczka, 1871: 113.
Cremnoconchus (Lissoconchus) Thiele, 1929: 125 (type species by monotypy *Cremnoconchus conicus* Blanford, 1870).

Taxonomic history: Blanford's (1863) original name *Cremnobates* was preoccupied 'for a genus of fishes' (i.e. *Cremnobates* Günther, 1861; a name used even earlier by Swainson, 1855) and he therefore renamed it *Cremnoconchus* (Blanford, 1869). The genus has been treated as valid at generic rank by all subsequent authors except Stoliczka (1871), who suggested that it should be ranked as a subgenus of *Littorina*. The subgenus *Lissoconchus* was introduced by Thiele (1929) for *C. conicus* and has occasionally been employed for this and other *Cremnoconchus* species without conspicuously ribbed shells (Wenz, 1938; Subba Rao & Mitra, 1979; Subba Rao, 1989; Ramakrishna & Dey, 2007).

Diagnosis: Shell: turbinate; smooth or with spiral ribs; protoconch smooth, less than 1.5 whorls (indicating non-planktotrophic development). Operculum: paucispiral; calcified, with proteinaceous layer internally and externally. Male: prostate closed; prostate gland subepithelial; anterior vas deferens closed; penial vas deferens (sperm duct) deeply closed (i.e. no epithelial connection to surface); penial filament retracted into cavity in base; simple penial glands in base, sometimes forming a short protruberance. Female: seminal receptacle absent; oviducal glands subepithelial; egg groove coiled in one spiral. Radula: 5 cusps (plus 2 denticles) on rachidian; 3–5 cusps on outer marginal. Alimentary system: salivary glands anterior to nerve ring. Nervous system: pleurosuboesophageal connective short. (Slightly modified from Reid, 1989.)

Shell: The shell shape lies within the range of that of marine littorinids, being globular, turbinate or high-turbinate, of moderate thickness, and sometimes with strong spiral ribs (Figs 3, 9, 11). As in many freshwater molluscs, the periostracum is relatively thick. Dissolution of the shell, or radulation by other snails, occurs where the periostracum is damaged, and the apical whorls are frequently eroded away. An umbilicus is present in some species, but is usually absent in juveniles, so it is correctly termed a 'pseudumbilicus'. The surface is marked by prominent, fine or indistinct spiral microstriae that are visible under low magnification (Fig. 4) and are a useful feature for identification. As in most marine littorinids (e.g. Reid, 1986a, 1996, 2007) the shell shows striking intraspe-

Table 1. Indices of shell shape of populations of *Cremnoconchus* species; see Supporting Table S1 for full locality details

Species	Locality	*N*	H2/B (mean ± SE)	H2/LA (mean ± SE)	LA/WA (mean ± SE)	DS/OL (mean ± SE)
C. syhadrensis	Matheran	11	0.910 (± 0.013)	1.322 (± 0.018)	1.153 (± 0.020)	0.521 (± 0.010)
	Khandala	10	0.978 (± 0.012)	1.327 (± 0.011)	1.247 (± 0.012)	0.517 (± 0.007)
C. conicus	6 km W Mahabaleshwar	10	1.141 (± 0.017)	1.482 (± 0.026)	1.226 (± 0.010)	0.394 (± 0.006)
	44 km W Bhor	10	1.191 (± 0.009)	1.506 (± 0.011)	1.256 (± 0.013)	0.374 (± 0.007)
C. canaliculatus	5 km S Mahabaleshwar	10	1.167 (± 0.012)	1.528 (± 0.016)	1.279 (± 0.016)	0.426 (± 0.011)
	10 km W Mahabaleshwar	10	1.048 (± 0.024)	1.444 (± 0.025)	1.340 (± 0.013)	0.369 (± 0.007)
C. hanumani	Hanuman Gundi Falls	10	1.002 (± 0.013)	1.296 (± 0.026)	1.488 (± 0.030)	0.357 (± 0.008)
	Greater Kadambi Falls	10	1.033 (± 0.020)	1.316 (± 0.016)	1.417 (± 0.021)	0.368 (± 0.006)
C. globulus	Lesser Kadambi Falls	10	1.101 (± 0.011)	1.410 (± 0.016)	1.413 (± 0.013)	0.393 (± 0.005)
C. agumbensis	Agumbe	9	1.143 (± 0.016)	1.572 (± 0.027)	1.269 (± 0.016)	0.486 (± 0.014)
C. cingulatus	Hulikal Ghat	16	1.021 (± 0.016)	1.371 (± 0.021)	1.298 (± 0.032)	0.434 (± 0.014)
C. castanea	Belkal Thirtha Falls	10	1.111 (± 0.020)	1.390 (± 0.014)	1.369 (± 0.017)	0.381 (± 0.009)
C. dwarakii	Hulikal Ghat	11	0.970 (± 0.011)	1.376 (± 0.025)	1.296 (± 0.011)	0.466 (± 0.011)

N, sample size; H2/B, shell shape index; H2/LA, relative spire height index; LA/WA, apertural shape index; DS/OL, opercular ratio; SE, standard error of the mean. See Figure 1 for definition of dimensions B, DS, H, H2, LA,OL, and WA.

cific variability. In most species the sampling remains too limited to observe patterns in the shell variation. However, in the most well-studied species, *C. syhadrensis*, there are clear differences between the range of variation within each of four local populations (Tables 1 and 2), suggesting possible genetic differentiation. In one population (from Torna; Fig. 3F, J–M) the shells range from almost smooth to strongly ribbed, so that development of ribs is not a reliable character for identification. Similarly, in *C. canaliculatus* a sutural rib can be present or absent (Fig. 9P–EE). In both *C. conicus* and *C. canaliculatus* the overall shape of the shell (relative spire height and peripheral angulation) and development of the pseudumbilicus are variable (Fig. 9). Shell coloration ranges from pale to dark brown in these three relatively well-sampled species, sometimes with 1–3 indistinct brown bands (Figs 3, 9), but does not appear to be polymorphic (i.e. with discrete morphs) within populations. There is slight sexual dimorphism in size, males being smaller (as also noted by Stoliczka, 1871); this phenomenon is usual in littorinids (Reid, 1986a, 1996). The protoconch is similar in all species in which it has been seen (Fig. 16C–F); it is smooth, of 1.3–1.5 whorls, 0.47–0.70 mm in diameter, and therefore similar to the protoconchs of marine littorinids with non-planktotrophic development (Reid, 1989).

Headfoot and locomotion: Externally, the animal is typical of the family, with blunt snout and mobile cephalic tentacles with eyes at their bases (Fig. 2H, I). The head and sides of the foot are commonly pigmented grey to black, but the animal is paler in *C. canaliculatus*, and in *C. syhadrensis* some populations are virtually unpigmented. Where head pigmentation is pale, the reddish myoglobin of the buccal mass musculature is visible by transparency (Fig. 2I). The sole of the foot does not show an anterior transverse (propodial) groove, but a small anterior pedal gland is present (Reid, 1989). No longitudinal division of the sole is visible externally, but locomotion is nevertheless by ditaxic retrograde waves of muscular contraction; one complete wave passes back on one side of the sole of the foot, then on the other.

Operculum: The operculum of *Cremnoconchus* is paucispiral, but thickened by calcification in between internal and external proteinaceous layers. In species with the thickest calcification (e.g. *C. syhadrensis*) the calcified part is inflexible, but an uncalcified flange remains around the margin. Internally, most species show a thickened spiral boss or rib of organic material; this, however, does not show well in SEM images because it is of relatively low relief (Fig. 5). The tightness of coiling, degree of calcification and development of the internal ridge show some variation between species (Table 1; Fig. 5). The calcification of the operculum was mentioned by several early authors (Blanford, 1863; Stoliczka, 1871), but without further comment. In fact such calcification is almost unique among littorinids (Reid, 1989), the only other case being the aragonitic calcareous deposit on the outer surface of the operculum of *Tectarius niuensis*

Table 2. Comparison of populations of *Cremnoconchus syhadrensis*

Locality (sample size *N*)	Shell figures	Max. shell height (mm)	Ribs above periphery	Base	Umbilicus (mm)	Shell colour	Animal colour
Matheran (200)	Fig. 3B, C	9.4	8–10	15–24 threads, 0 developed as ribs	0.6–1.2	Pale yellow-brown; darker spire; faint brown bands; aperture white; columella stained purple-brown	Pale to dark grey or black
Khandala (200)	Fig. 3G–I	8.3	8	*c.* 20 threads, 0 developed as ribs	0.2–0.3	Mid-brown with broad bands; red-brown spire; aperture with red-brown bands; columella white	Unpigmented, but for pale grey tencles and tip of snout
Anjani, Nashik (10)	Fig. 3D, E	5.9	5–8	5–10 threads, innermost 2–3 are ribs	0.1–0.3	Pale yellow-brown, no bands; aperture and columella white	?
Torna Hill Fort (120)	Fig. 3F, J–M	9.8	2 (at shoulder and periphery); or up to 8	0 threads; 0 ribs	0.1–0.5	Pale yellow-brown; usually darker at suture and on spire; aperture and columella white	?

(Reid & Geller, 1997). The operculum can be withdrawn to a depth of about 0.1–0.2 of the final whorl, but up to 0.4 in *C. agumbensis*.

Male reproductive system: The anatomy and histology of the reproductive system have been described by Linke (1935) and Reid (1989). A closed prostate with subepithelial glands leads to a tubular anterior vas deferens and to the cephalic penis on the right side of the headfoot. The littorinid penis often bears elaborate glandular structures, but in *Cremnoconchus* the subepithelial, neutral mucous glands (staining blue in trichrome) are usually simply scattered in parts of the penial base, which appear swollen and opaque. In *C. conicus* and *C. canaliculatus* the subepithelial glands are found in a basal drum-shaped appendage, but this is unlike the penial glandular disc or complex mamilliform penial glands present in some marine littorinids (Reid, 1989). A feature of *Cremnoconchus* that is unique in the family is the invagination of the penial filament (the intromittent part) into a distal pocket of the muscular base. The filament can be extended to a considerable length and in preserved material is usually fixed in a partly extended state. In the living animal, however, the filament is generally retracted. Dissection reveals that the penial vas deferens (sperm duct) within the base is coiled and folded to allow for extension of the filament during copulation (the duct in Fig. 6F, G is 2.5 times the length of the penial base), and lies within an internal space that is presumably involved in the hydrostatic extension of the filament. Withdrawal of the filament is accomplished by a retractor muscle lying adjacent to the coiled vas deferens and inserted at the junction of the base of the filament with the bottom of the invagination (Fig. 6G). Before entering the filament, the vas deferens becomes tightly bound to the retractor muscle. As in most littorinid genera, the form of the penis is an important character for discrimination

Figure 2. Habitats and living animals of *Cremnoconchus* species. A, 10 km west of Mahabaleshwar on road to Poladpur, Raigad Dist., Maharashtra; altitude 692 m (*C. canaliculatus*). B, 6 km west of Mahabaleshwar on road to Poladpur; 1103 m (*C. conicus*). C, Hulikal Ghat, Udupi Dist., Karnataka; 475 m (*C. cingulatus*, *C. dwarakii*). D, escarpment of Western Ghats at Mahabaleshwar, Maharashtra; this stream is now polluted and contains no *Cremnoconchus*. E, *C. globulus* in flowing water at Lesser Kadambi Falls, Chikmagalur Dist., Karnataka; 967 m. F, Khandala, Pune Dist., Maharashtra; 297 m (*C. syhadrensis*). G, *C. syhadrensis* aestivating under ledges at Khandala; 297 m. H, living *C. conicus*, 6 km west of Mahabaleshwar on road to Poladpur. I, living *C. syhadrensis*, Khandala.

of species and may be a component of the specific mate-recognition system (Reid, 1996).

Spermatozoa: These have been observed only in *C. castanea*, by light microscopy. They consist only of euspermatozoa (i.e. parasperm are absent), which are filiform and up to 193 μm in length. These are among the longest recorded for Littorinidae, exceeded only by those of *Bembicium* (Reid, 1989). The sperm head is 24 μm long and a distinct helical structure is visible. This may correspond to the helical condensation of chromatin in the nucleus of developing spermatids, reported in SEM studies of sperm development in *Littorina* species (Buckland-Nicks & Chia, 1976; Paviour, Mill & Grahame, 1989); however, these reports have not mentioned a helical structure in mature eusperm.

Female reproductive system: The spiral route of the egg groove through the pallial oviduct is a well-known synapomorphy of Littorinidae (Reid, 1989). In *Cremnoconchus* the egg groove forms a single spiral loop of about 3.5 revolutions. Linke (1935) discriminated albumen, capsule and shell glands in the pallial oviduct, but did not explain the spiral structure. Histological examination suggests that the subepithelial glandular material composing the spiral portion of the pallial oviduct is mainly albumen gland, differentiated into two parts staining darker and paler blue in trichrome; these parts can sometimes be distinguished as more and less opaque cream areas in preserved specimens (Fig. 6C). The subepithelial lining of the final straight section of the pallial oviduct stains reddish in trichrome and appears to be responsible for the secretion of the outer coating of the egg capsule, which stains similarly; this gland is not, however, homologous with the capsule gland of the Littorininae (Reid, 1989). The ciliated cells lining the egg groove do not contain black pigment. There is a large copulatory bursa, opening in an anterior position (Fig. 14C). The seminal receptacle typical of most littorinids is absent; sperm are instead stored in the renal oviduct (Linke, 1935; Reid, 1989).

Eggs: Mature ova can sometimes be seen in the distal part of the ovarian oviduct. In the pallial oviduct these are coated with albumen and a firm gelatinous covering, to attain a final diameter usually in the range 0.40–0.49 mm. Between 1 and 5 such eggs can be found in the straight section of the pallial oviduct (Figs 6C, 15J); these are either uncleaved or show only the first cleavage of the embryo, suggesting that they are laid before further development proceeds.

Radula: The radula of *Cremnoconchus* has been drawn by Troschel (1867), Stoliczka (1871), Annandale & Prashad (1919) and Reid (1989), but SEM images are given here for the first time (Figs 7, 13, 16A, B). The radula is long (length relative to shell height 0.82–4.24) and the radular sac is coiled over the mid-oesophagus. As in all littorinids it is taenioglossate, with all seven teeth in each row well developed and a 'littorinid notch' in the base of the lateral tooth (Reid, 1989). The base of the rachidian tooth is relatively narrow, lacking lateral projections (Troschel, 1867), but otherwise the radula is of a generalized littorinid form (Reid, 1989).

Mantle cavity: When the anatomy was first described, *Cremnoconchus* was said to possess a vascular mantle cavity (a 'pulmoniferous sac') with no trace of gills (Blanford, 1863). Gills were subsequently described (Stoliczka, 1871; Annandale, 1919; Prashad, 1925). The leaflets are of low triangular outline, continued as ridges (not branched as stated by Stoliczka, 1871) across the roof of the mantle cavity, and number 23–50. Although it has been reported that the opening of the mantle cavity is small and can be completely closed (Annandale, 1919; Annandale & Prashad, 1919), in fact the mantle edge and wide mantle opening are the same as in marine littorinids. The observation may be a reference to the fact that, when active, the headfoot largely occludes the shell aperture. The osphradium is short (Prashad, 1925), only about one-third of the extent of the row of gill leaflets, but it is not 'papilliform' (Annandale, 1919; Annandale & Prashad, 1919). The hypobranchial gland is vestigial (Prashad, 1925).

Range: Endemic to the northern and central Western Ghats of India, in the states of Maharashtra and Karnataka (Fig. 8).

Habitat and ecology: The habitat is highly specific, restricted to streams and waterfalls on the basaltic cliffs of the western escarpment of the Western Ghats (Fig. 2D), between altitudes of 297 and 1125 m (and potentially up to 1400 m, from localities of museum specimens; Supporting Table S1; see also Blanford, 1863, 1870; Annandale, 1919; Prashad, 1925). During the heavy rain of the south-western monsoon season (June–September) these streams become torrents. However, when collections were made by the authors during October 2010 the snails were mostly to be found crawling over rocks wetted by spray, or where water was flowing in a shallow film, usually in abundance (Fig. 2E). *Cremnoconchus conicus* also occurred in shallow pools with moving water, while *C. syhadrensis* and *C. dwarakii* were sometimes found on moss and wet vegetation beside the streams. In the northern part of the range (Maharashtra state) the surrounding vegetation in the stream gullies consisted of fern and balsam (*Impatiens*), with adjacent woodland or cloud forest, depending upon altitude (Fig. 2A, B). In the southern part (Karnataka state) the streams ran through rainforest (Fig. 2C). During the dry season, small streams may disappear and *C. syhadrensis* is known to aestivate in clusters in crevices and shaded pits in the rock (Blanford, 1863; Annandale, 1919; Hora, 1926, 1928). At Khandala (October 2010) *C. syhadrensis* was observed in tight clusters of up to 1000 individuals under overhangs on shaded cliffs, where they would presumably aestivate as the rock surface dried out (Fig. 2G).

The behaviour of *C. syhadrensis* at Khandala was described by Annandale (1919: 119). At this locality it was abundant on cliffs, shaded from the midday sun, which 'supported a growth of the peculiar dull green filamentous alga on which it feeds'. The animals became inactive and closed the operculum tightly when dry. When submerged, the snails crawled out of the water but, if prevented from reaching the surface, drowned after 24 h. The mantle cavity was said to be filled with water ('never filled with air') in snails that were crawling in air, but this was not the case in animals observed during the present study, in which the mantle cavity was air-filled. Stoliczka (1871) noted that the stomach of this species contained 'minute algae'. In the present study the faecal pellets of *C. hanumani* were found to consist almost entirely of elongated diatoms.

The breeding season has not been recorded, but is presumed to be during the monsoon season. In October 2010, at the end of the monsoon, some specimens of all the species collected were mature (i.e. seminal vesicle with sperm and/or eggs in ovarian or pallial oviduct), but some were spent, suggesting that the breeding season was coming to an end. Samples of *C. castanea* collected in March and June also included some mature individuals (BMNH). Stoliczka (1871) recorded eggs in a mature female of *C. syhadrensis* in March. Since the eggs in the final section of the oviduct were always either uncleaved or at the two-celled embryonic stage, it is predicted that the large eggs are deposited and not retained until hatching. There is no evidence for ovoviviparity, as occurs in some marine littorinids (Reid, 1989). Eggs are probably laid either singly or in small numbers, and presumably on the rock surface, where development and hatching take place.

The prevalence of parasitism by trematodes was very low, being observed only in *C. canaliculatus* from a single locality.

Remarks: At present there is no strong evidence for the subgeneric division of *Cremnoconchus*. The recognition of *Lissoconchus* as a subgenus based only on the smooth shell of *C. conicus* (Thiele, 1929) is unwarranted, in view of the variability of shell ribs in *C. syhadrensis*.

CREMNOCONCHUS SYHADRENSIS (W.T. BLANFORD, 1863) (FIGS 2G, I, 3, 4B, C, 5A, B, 6, 7A, B, 8, 16C)

Cremnobates syhadrensis Blanford, 1863: 184–186, pl. 4, figs 1–7 (fig. 6, crawling animal; figs 4, 5, operculum) (Western Ghats, in the neighbourhood of Bombay, India; restricted to Khandala by Subba Rao & Mitra, 1979; here corrected to Matheran, Raigad District, Maharashtra; neotype, here designated, BMNH 1906.1.1.2247, Fig. 3A). Troschel, 1867: 90–94, pl. 2, fig. a (radula).

Cremnoconchus syhadrensis – Blanford, 1869: 343. Stoliczka, 1871: 108–115, figs 1–3 (anatomy), 4, 5 (radula). Hanley & Theobald, 1876: 58, pl. 146, fig. 6. Theobald, 1876: 12. Nevill, 1885: 173. Tryon, 1887: 256, pl. 46, fig. 47. Preston, 1915: 65 (as *syhadensis*). Annandale & Prashad, 1919: 149, pl. 4, figs 2, 3 (anatomy), 4 (radula) (in part, includes *C. canaliculatus*). Prashad, 1925: 138–139, fig. 2C (mantle cavity). Linke, 1935: 72–87, figs 1–8 (anatomy). Reid, 1989: figs 1i, 4c, d (operculum), 6i (penis), 9i (pallial oviduct). Aravind *et al.*, 2011: 58 (unnumbered fig.) (BMNH 1906.1.1.2247, same lot as neotype of *C. syhadrensis*).

Cremnoconchus (Cremnoconchus) syhadrensis – Thiele, 1929: 125, fig. 98. Wenz, 1938: 522, fig. 1376. Subba Rao & Mitra, 1979: 24–25. Subba Rao, 1989: 63, figs 88, 89, 89a, b. Ramakrishna & Dey, 2007: 111, fig. 67A, B.

Cremnoconchus 'from Mahabaleshwar' Aravind *et al.*, 2011: 58, unnumbered fig. (locality in error; BMNH 1906.1.1.2247, same lot as neotype).

Taxonomic history: No types were segregated in BMNH, but there exists a sample of four specimens from W. T. Blanford's collection labelled, in his hand, '*Cremnobates syhadrensis* picked specimens', but with no locality. One of these is here designated neotype (Fig. 3A). The type locality was restricted to Khandala by Subba Rao & Mitra (1979), but this is here corrected to Matheran (see Remarks). The specific name is derived from 'Sahyadri' (erroneously spelled 'Syhadri' by Blanford, 1863), the name for the Western Ghats in Marathi and other Indian languages.

Diagnosis: Shell turbinate with 2–8 spiral ribs above periphery; pseudumbilicus present or absent; surface dull, with fine or indistinct microstriae. Operculum thickly calcified, with internal ridge. Penis with distal glandular swelling of base, no lateral glandular

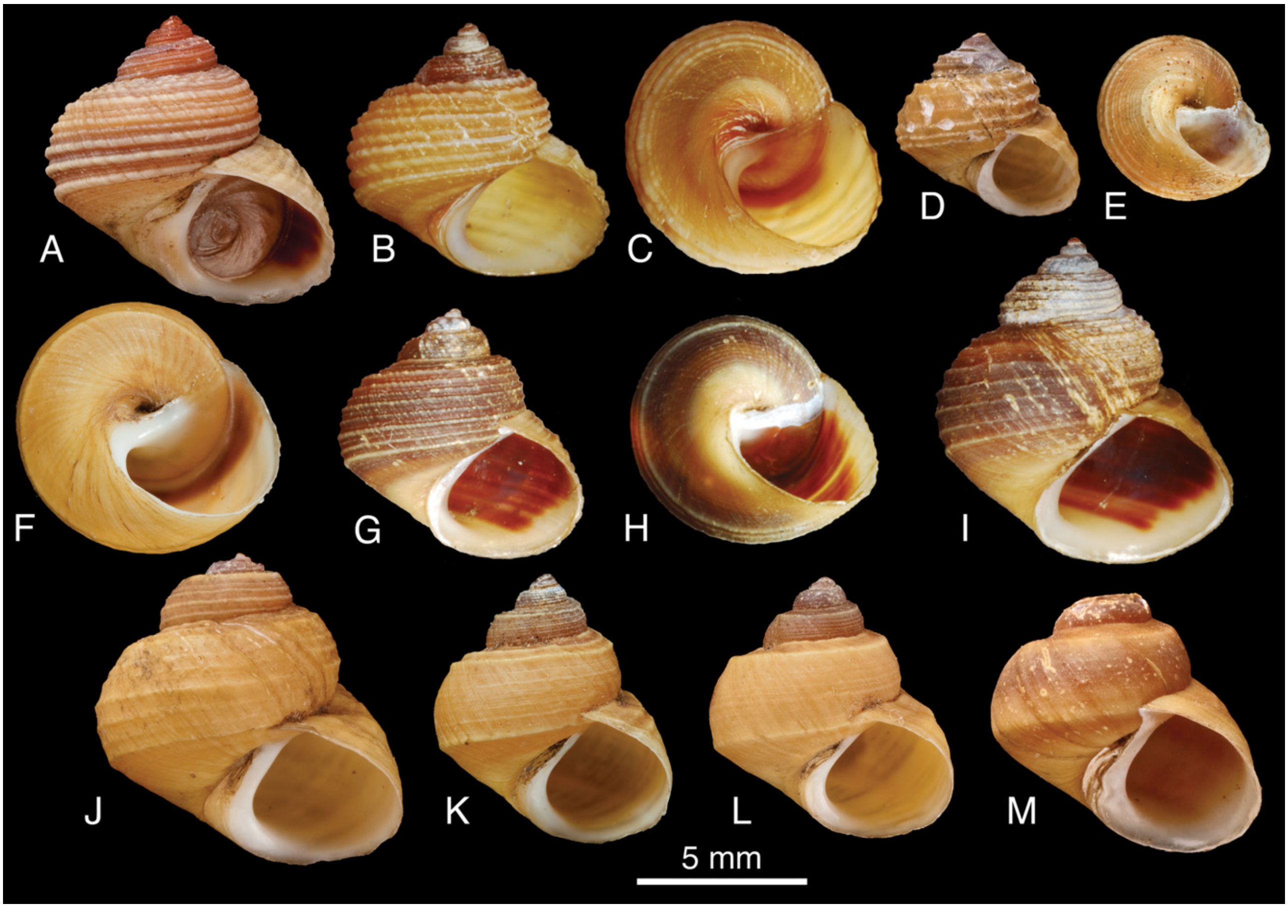

Figure 3. Shells of *Cremnoconchus syhadrensis*. A, *Cremnobates syhadrensis* W.T. Blanford, 1863, neotype, no locality (BMNH 1906.1.1.2247). B, C, Matheran, Raigad Dist., Maharashtra (two views of same specimen; ZSI/WGRS/IR.INV-2290). D, E, Anjani, Nashik Dist., Maharashtra (BMNH 1911.8.23.70–71). F, J–L, Torna Fort, Pune Dist., Maharashtra (USNM 317696). G–I, Khandala, Pune Dist., Maharashtra (G, H two views of same specimen; ZSI/WGRS/IR.INV-2293, 2292). M, Torna Fort, Pune Dist., Maharashtra (USNM 317695).

flange or drum-shaped gland, stout filament. Western Maharashtra State.

Shell (Figs 3, 4B, C): Shell H 5.0–9.9 mm. Shape (Table 1) broadly turbinate; whorls rounded, weakly angled at periphery; suture distinct; apex intact or eroded. Columella moderately broad. Pseudumbilicus usually conspicuous and perforated (Fig. 3F), 0.6–1.2 mm wide, with sharply angled margin; sometimes narrow and not perforated (Fig. 3H), 0.1–0.5 mm; may be closed in juveniles. Upper surface: usually 5–10 (mode 8) narrow ribs at and above periphery, sometimes becoming weak on last whorl (Fig. 3J); ribs (especially on spire) may be slightly granulated by intersection with growth lines; 0–3 threads in interspaces between grooves; shell sometimes smooth but for narrow rib at shoulder (giving broad sutural ramp and turreted spire profile) and at angled periphery (Fig. 3L, M). Base: usually 15–24 threads, becoming finer and ultimately indistinct towards pseudumbilicus (Fig. 3C); sometimes 5–10 ribs, of which innermost 2–3 develop as narrow ribs (Fig. 3E); base may lack sculpture (Fig. 3F). Entire surface dull, covered with fine or indistinct spiral microstriae (Fig. 4B, C). Protoconch (Fig. 16C) 1.3–1.4 whorls; diameter 0.47–0.60 mm; diameter of first whorl 0.29–0.45 mm. Colour: pale yellow-brown, often with red-brown spire (shell fading to white with purplish or pinkish spire; Fig. 3A); some have narrow brown band at suture and broader brown band between shoulder and periphery (Fig. 3G, I); base sometimes with broad brown band but paler around umbilicus (Fig. 3H); columella white, columella and umbilicus sometimes stained purple-brown (Fig. 3C); aperture yellowish with red-brown bands showing through.

Animal: Head, tentacles, and sides of foot pale to dark grey or black; sometimes unpigmented except for grey

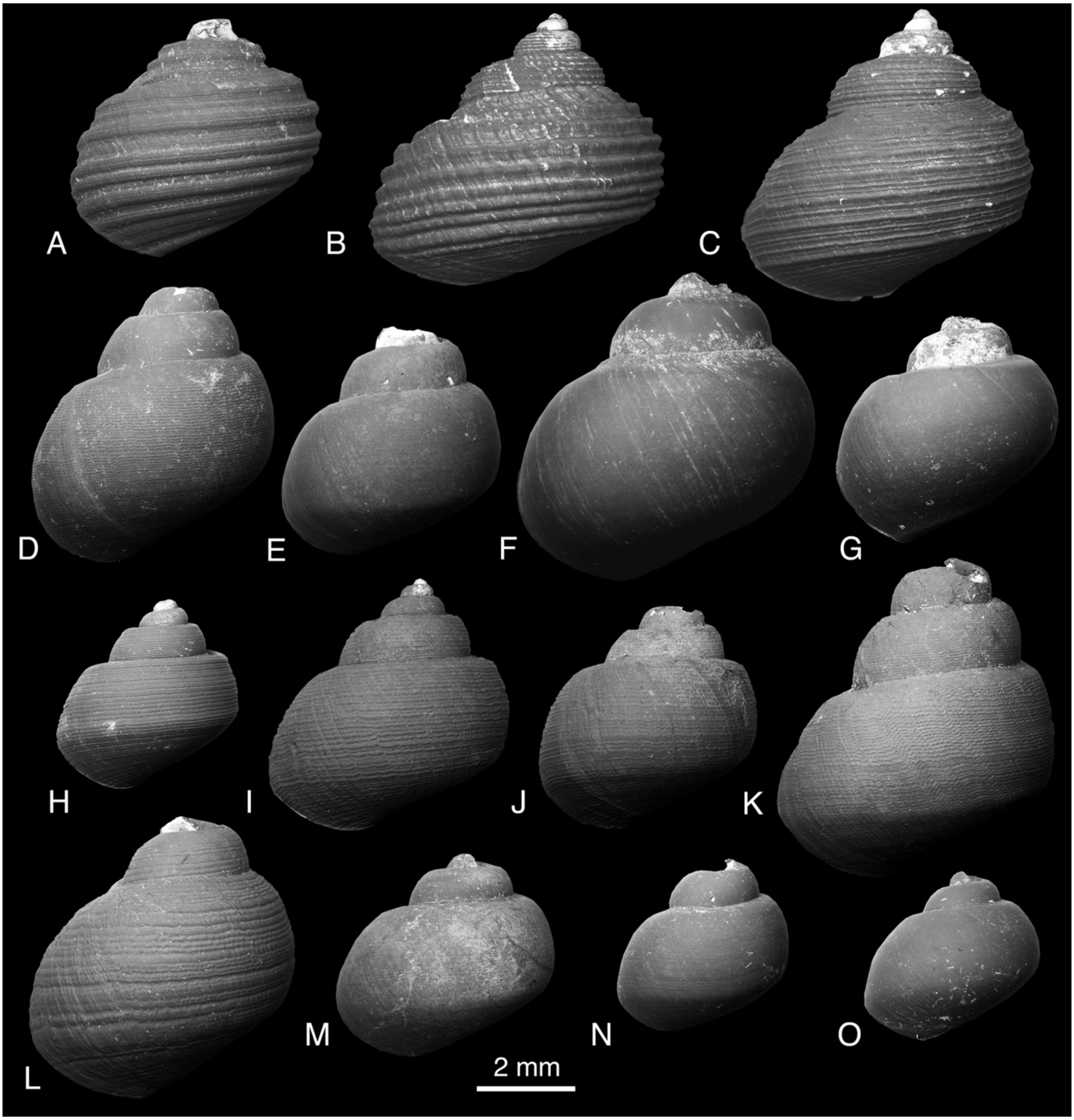

Figure 4. Microsculpture of *Cremnoconchus* species (viewed by SEM). A, *C. dwarakii*, Hulikal Ghat, Udupi Dist., Karnataka. B, *C. syhadrensis*, Matheran, Raigad Dist., Maharashtra. C, *C. syhadrensis*, Khandala, Pune Dist., Maharashtra. D, *C. conicus*, 44 km west of Bhor, Pune Dist., Maharashtra. E, *C. conicus*, 6 km west of Mahabaleshwar, Satara Dist., Maharashtra. F, *C. globulus*, Lesser Kadambi Falls, Chikmagalur Dist., Karnataka. G, *C. cingulatus*, Hulikal Ghat, Udupi Dist., Karnataka. H, *C. agumbensis*, Agumbe, Udupi Dist., Karnataka. I, *C. canaliculatus*, 10 km west of Mahabaleshwar, Raigad Dist., Maharashtra. J, *C. canaliculatus*, Dongarwadi, Tamhini, Pune Dist., Maharashtra. K, *C. canaliculatus*, 5 km south of Mahabaleshwar, Satara Dist., Maharashtra. L, *C. castanea*, Belkal Thirtha Falls, Udupi Dist., Karnataka. M, *C. castanea*, Arasinagundi Falls, Udupi Dist., Karnataka. N, *C. hanumani*, Greater Kadambi Falls, Chikmagalur Dist., Karnataka. O, *C. hanumani*, Hanuman Gundi Falls, Chikmagalur Dist., Karnataka.

tentacles and tip of snout (Fig. 2I). Gills: 30–40 leaflets; unpigmented. Operculum (Table 1; Fig. 5A, B): opercular ratio high, 0.471–0.600; strongly calcified, with thickened internal ridge. Penis (Fig. 6A, B, D–G): unpigmented; base wrinkled, distal 20–60% smooth, swollen, opaque and glandular, invagination 20–40% of length of base in ethanol-fixed specimens; filament relatively stout, usually protruding in ethanol-fixed specimens, tip can be retracted to about half length of penial base in living animals. Pallial oviduct (Fig. 6C): as for genus. Pallial oviduct containing 1–5 eggs 0.24–0.49 mm diameter, including transparent covering 0.06 mm thick (observed alive).

Radula (Fig. 7A, B): Relative radula length 1.60–4.24. Rachidian: length/width 1.51–1.57; 5 cusps (+ 1 outer denticle on either side). Lateral: 5 cusps (+ 1 inner denticle). Inner marginal: 5 cusps (+ 1 outer denticle; sometimes + 1 inner denticle). Outer marginal: 3–5 cusps (sometimes + 1 outer denticle). Major cusp of each of 5 central teeth in each row elongate leaf-shaped with rounded tip; other cusps pointed.

Range (Fig. 8): Western Maharashtra State, from about 30 km west of Nashik to 50 km south-west of Pune (185 km linear distance). Records (Supporting Table S1): Maharashtra State: Anjani, near Trimbakeshwar, Nashik District (BMNH 1907.9.25.3–4); Igatpuri (Blanford, 1870; as Egutpoora); Matheran (BMNH 20120035; ZSI/WGRS/IR.INV-2290, 2291); Bhor Ghat (BMNH 1868.12.11.38); Khandala (BMNH 1888.12.4.823–826; ZSI/WGRS/IR.INV-2292, 2293); Karlee Hill Fort, Kurkulla, near Pune (locality tentatively identified as Karli; USNM 317697); Vadgaon, near Pune (USNM 317687); Sinhgarh Fort, near Pune (USNM 317691); Torna Fort, near Pune (USNM 317695, 317696, 317683); Rajgarh Fort, near Pune (USNM 317688).

Habitat and ecology: On unshaded east-facing cliff with water seeping over rock; 442 m altitude; common, found individually, with many juveniles (Matheran population; 17 Oct. 2010). On wet basalt cliffs, clustered in tightly packed groups of up to 1000 under overhangs 30 cm in width; 297 m altitude (Khandala population; 17 Oct. 2010; Fig. 2F, G). Hora (1926: 448) recorded it as ‘quite plentiful on big rocks projecting out of the water at the edge of the pool in the neighbourhood of the fall [near Khandala, at end of December]. They were found aestivating in small pits well protected from the midday sun.’ Annandale (1919) also observed it in great abundance on cliffs at Khandala, shaded from the midday sun, where animals were active in spray from the falls, feeding on a ‘dull green filamentous alga’. Stoliczka (1871) noted that the stomach contained ‘minute algae’. Collected from 4000 ft (1219 m) at Anjani (BMNH 1907.9.25.3–4). Recorded localities range up to 1400 m (Supporting Table S1).

Remarks: This is the most well-known species in the genus and has been the subject of several anatomical studies (Stoliczka, 1871; Annandale & Prashad, 1919; Prashad, 1925; Linke, 1935; Reid, 1989) and ecological notes (Stoliczka, 1871; Annandale, 1919; Hora, 1926). It was found to be common at Matheran and extremely abundant at Khandala (October 2010). However, Matheran is a tourist destination where development is proceeding and Khandala lies in the Bhor Ghat Pass, where motorways are under construction to carry heavy traffic between Mumbai and Pune. The future of these sites cannot be regarded as secure. The Matheran site is the only known locality at which *Cremnoconchus* occurs outside the defined limits of the Western Ghats region (Fig. 8).

Populations of this species show considerable differentiation in shell form across the range. The type locality was given only as ‘in the neighbourhood of Bombay [Mumbai]’ in the original description by Blanford (1863: 184), but he subsequently recorded it from ‘Khandalla [Khandala] where the first specimens were obtained, but also on Matheran hill and at Egutpoora [Igatpuri]’ (Blanford, 1870: 11). His description was of a spirally ribbed, umbilicate, white shell with reddish apex. This, and the (unlocalized) collection from which the neotype (Fig. 3A) has been selected, correspond most closely with modern samples from Matheran (Fig. 3B, C). Differences among available local populations are summarized in Table 2. There is variation in adult size, development of ribs both above and below the periphery, size of umbilicus and colour. In USNM there are three large

Figure 5. Opercula of *Cremnoconchus* species. A, B, *C. syhadrensis*, Matheran, Raigad Dist., Maharashtra. C, D, *C. dwarakii*, Hulikal Ghat, Udupi Dist., Karnataka. E, F, *C. conicus*, 44 km west of Bhor, Pune Dist., Maharashtra. G, H, *C. canaliculatus*, 5 km south of Mahabaleshwar, Satara Dist., Maharashtra. I, J, *C. hanumani*, Hanuman Gundi Falls, Chikmagalur Dist., Karnataka. K, L, *C. globulus*, Lesser Kadambi Falls, Chikmagalur Dist., Karnataka. M, N, *C. agumbensis*, Agumbe, Udupi Dist., Karnataka. O, P, *C. cingulatus*, Hulikal Ghat, Udupi Dist., Karnataka. Q, R, *C. castanea*, Arasinagundi Falls, Udupi Dist., Karnataka. Abbreviation: b, thickened boss on inner surface of operculum of *C. syhadrensis* (indistinctly visible by SEM because of low relief and therefore indicated with dotted outline).


A
B
C
D
b
E
F
G
H
I
J
K
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M
N
O
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2 mm
Q
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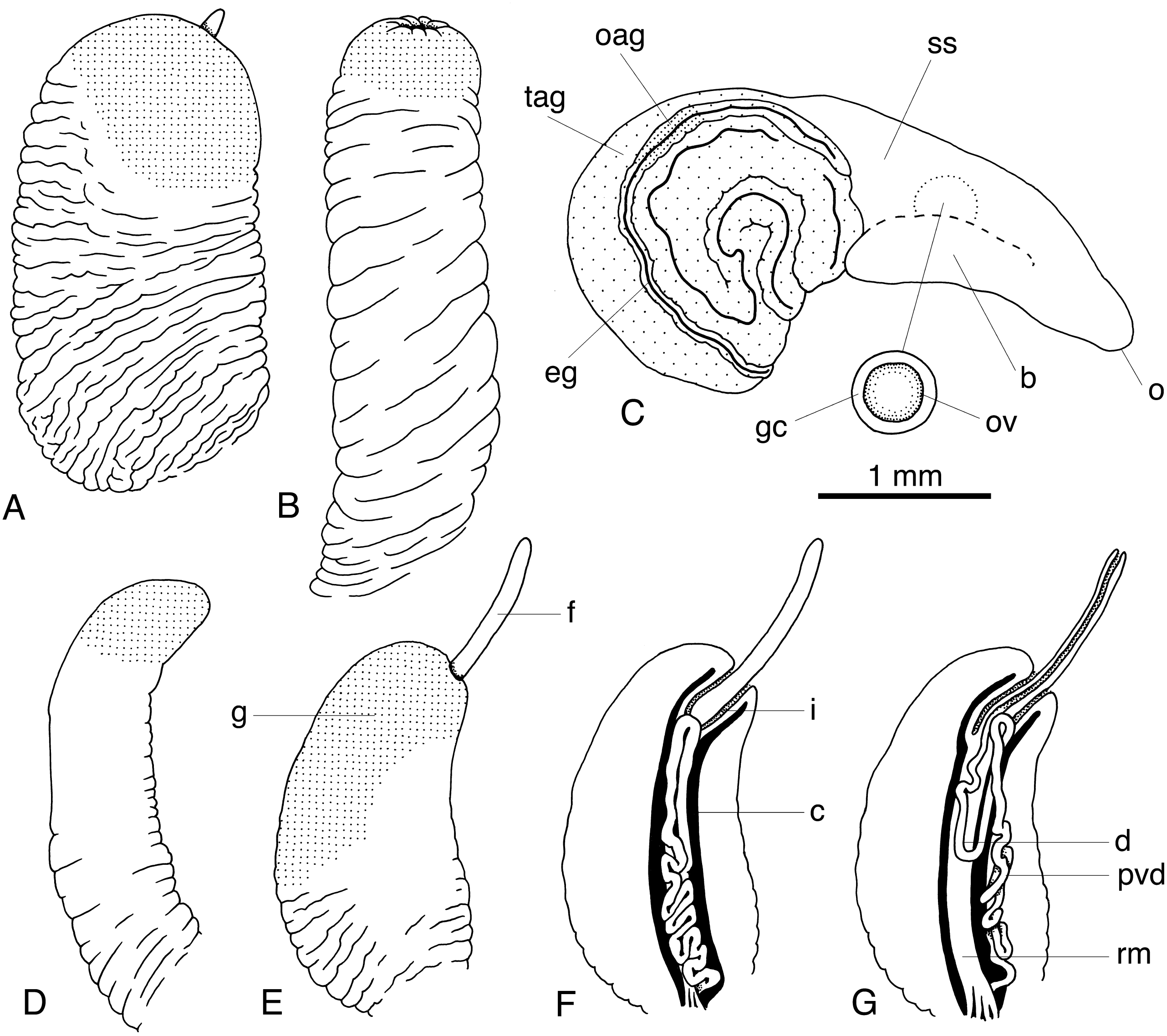

Figure 6. Anatomy of *Cremnoconchus syhadrensis*. A, B, D–G, penes (A, E–F, fixed in ethanol; B, D, live). E–G are three views of single penis, external (E), with base sectioned (F), and with coiled penial vas deferens displaced to the right to show retractor muscle and with filament sectioned to show continuation of vas deferens to its tip (G). C, pallial oviduct and egg removed from straight section. A, Matheran, Raigad Dist., Maharashtra (BMNH 20120035; shell H = 7.4 mm). B, C, E–G, Matheran, Raigad Dist., Maharashtra (ZSI/WGRS; shell H: B = 7.2 mm; C = 7.2 mm; D = 5.8 mm; E–G = 7.5 mm). D, Khandala, Pune Dist., Maharashtra (ZSI/WGRS). Abbreviations and shading conventions: b, copulatory bursa (dashed outline, visible by transparency); c, cavity surrounding penial vas deferens and retractor muscle (black); d, distal to this point the penial vas deferens is tightly bound to the sheath of the retractor muscle; e.g. egg groove visible by transparency (thick line); f, penial filament; g, opaque glandular region of penial base (medium stipple); gc, firm gelatinous coating of mature egg; i, invagination of penial base (shaded); o, position of terminal opening of pallial oviduct into mantle cavity; oag, opaque part of albumen gland (dense stipple); ov, ovum; pvd, penial vas deferens; rm, retractor muscle of penial filament; ss, straight section of pallial oviduct; tag, translucent region of albumen gland (sparse stipple).

samples from Torna Fort, near Pune, from the Evezard Collection, made in the late 19th century. These were originally sorted and labelled according to their sculpture: '*C. syhadrensis*' (normal eight-ribbed shells; USNM 317683), '*C. conicus* var. *canaliculatus*' (mostly two ribs, at shoulder and periphery only; USNM 317696); '*C. conicus* var.' (two-ribbed shells, but mixed with some *C. conicus* and *C. canaliculatus*; USNM 317695). Intermediate forms link the extremes of eight- and two-ribbed shells (Fig. 3F,

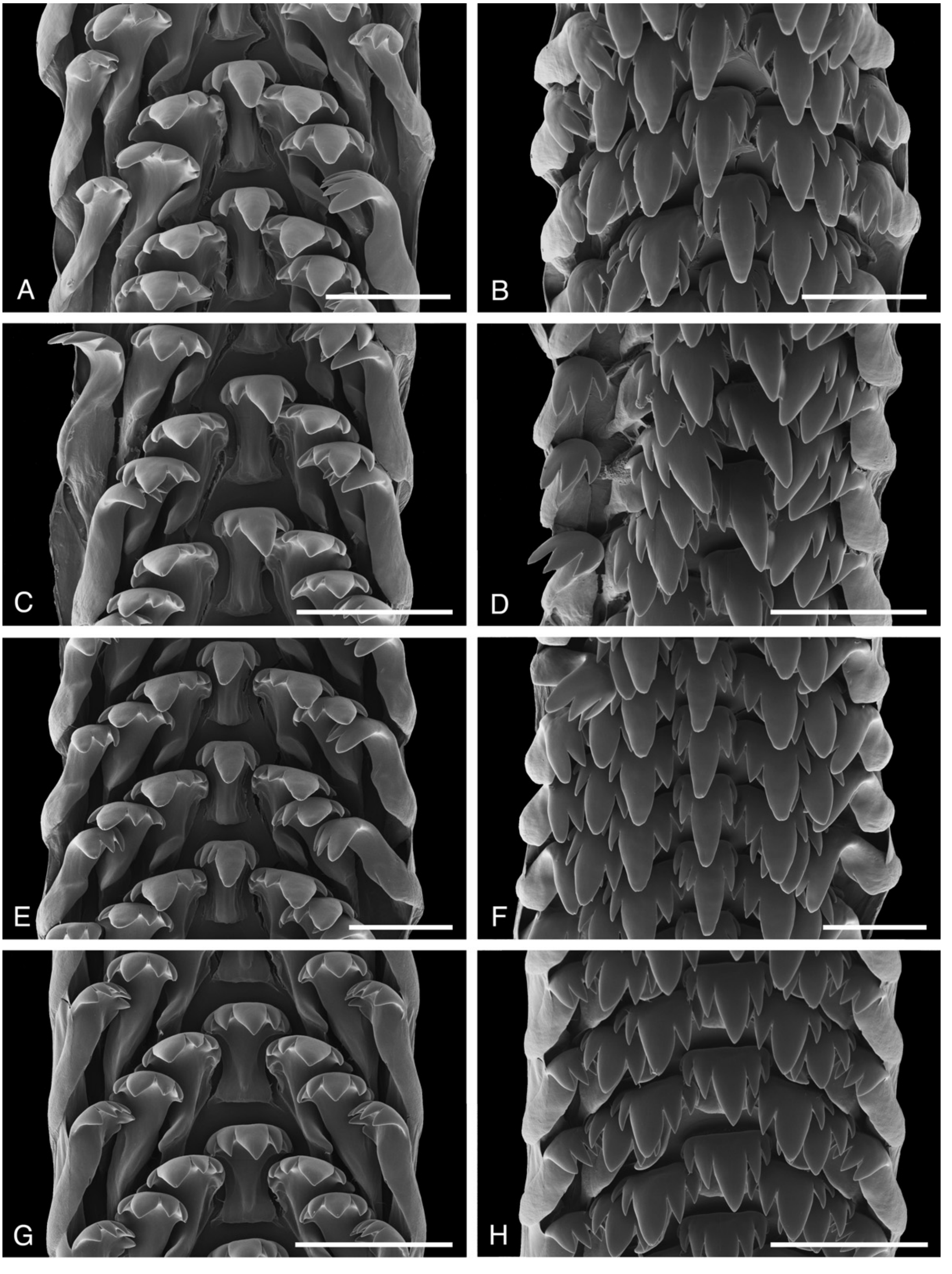

Figure 7. Radulae of *Cremnoconchus* species (two views of each radula, flat and at 45°). A, B, *C. syhadrensis*, Matheran, Raigad Dist., Maharashtra (ZSI/WGRS; shell H = 7.0 mm). C, D, *C. conicus*, 6 km west of Mahabaleshwar, Satara Dist., Maharashtra (ZSI/WGRS; shell H = 4.9 mm). E, F, *C. canaliculatus*, 10 km west of Mahabaleshwar, Raigad Dist., Maharashtra (ZSI/WGRS; shell H = 9.3 mm). G, H, *C. hanumani*, Greater Kadambi Falls, Chikmagalur Dist., Karnataka (ZSI/WGRS; shell H = 5.0 mm). Scale bars = 50 µm.

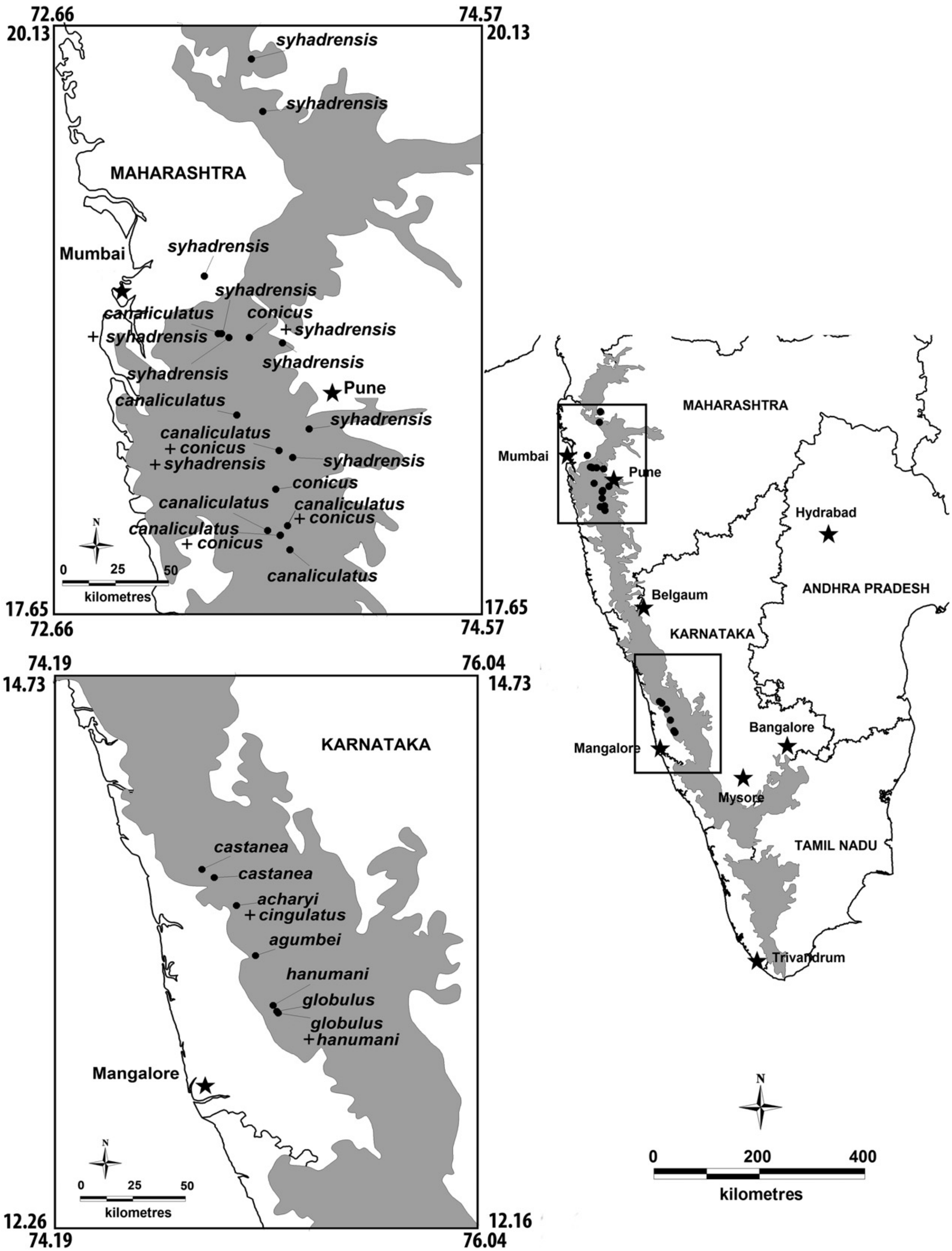

Figure 8. Distribution of *Cremnoconchus* species (solid circles). Two or more species names (e.g. *syhadrensis* + *canaliculatus*) indicate sympatric occurrence. See Supporting Table S1 for locality details. The shaded area is the Western Ghats region as defined by Irfan-Ullah & Davande (2008). Cities indicated by asterisks.

J–M) and these three samples are suggested to be from a single very variable population. The opercula of the Torna samples are the same as those of specimens from other localities, with strong calcification and a prominent inner ridge, but no anatomical material from Torna was available.

There is also variation in the size of eggs and in the diameter of the first whorl of the protoconch. In a female from Matheran the three eggs in the pallial oviduct ranged from 0.24 to 0.39 mm in diameter and the diameter of the first whorl ($N = 3$) from 0.29 to 0.39 mm in the few shells with intact apex in the sample. The overall ranges of these parameters in the species were larger still (see description above).

The shell of *C. syhadrensis* is the most robust of the *Cremnoconchus* species, being relatively thick and reinforced by spiral ribs, and the operculum is more thickly calcified than in the others. It is not known if this reflects selection by crushing predators or other mechanical forces. The frequency of repaired shell breakages (remaining as scars on the shell) has been used as an index of sublethal predation or damage (e.g. Reid, 1992). In a total of 208 adult shells (of the Matheran and Khandala types; Table 2) in BMNH, 20 (9.6%) showed a major repaired breakage. The cause is not known, but this is a low level of sublethal damage in comparison with that seen in some marine littorinids (Reid, 1992).

Only in one sample from Torna (USNM 317695) is this species mixed with others, *C. conicus* and *canaliculatus*, implying that all three are found there together. There are also separate lots of *C. syhadrensis* and *C. canaliculatus* from both Bhor Ghat and Karlee. Annandale & Prashad (1919: 149) remarked that 'two types of shells occur in a large series from the cliffs at Khandalla. The commoner of these agrees well with Blanford's figure [i.e. Blanford, 1863: figs 1–7], but in a few specimens the upper surface of the body-whorl is flattened and grooved much as in the same author's var. *canaliculatus* of *C. conicus*.' This is interpreted as a reference to *C. canaliculatus* occurring with *C. syhadrensis*, although in the present study only *C. syhadrensis* was encountered at Khandala in the Bhor Ghat Pass. At these localties of likely sympatry the shell characters of each species remain distinct, supporting their separate species status.

The low spire, 2–8 ribs, weak microstriae and strongly calcified operculum are the diagnostic traits of *C. syhadrensis* (see Table 3 for distinction of the three sympatric species). Confusion is possible with *C. canaliculatus*, but this never develops a distinct peripheral rib, is sometimes tall-spired, has stronger microstriae and a less thickly calcified operculum.

Cremnoconchus conicus W.T. Blanford, 1870 (Figs 2H, 4D, E, 5E, F, 7C, D, 8, 9A–O, 10A–H)

Anculotus carinatus Layard, 1855: 94 (Mahakeshwar Hills [Mahabaleshwar], Bombay Presidency, India; lectotype, here designated, plus 4 paralectotypes BMNH 20120031, Fig. 9D, E; not *Anculotus carinatus* Anthony 1840).

Cremnoconchus carinatus – Blanford, 1869: 343. Blanford, 1870: 11–12, pl. 3, fig. 5. Stoliczka, 1871: 109, 112 (in part, includes *C. canaliculatus*). Theobald, 1876: 13. Nevill, 1885: 172. Preston, 1915: 66. Aravind *et al.*, 2011: 58, unnumbered fig. (BMNH 20120031, lectotype of *A. carinatus*).

Cremnoconchus (Lissoconchus) carinatus – Subba Rao, 1989: 63, figs 90, 91. Ramakrishna & Dey, 2007: 112, fig. 68A, B.

Anculotus carinatus 'Anthony' – Reeve, 1860: *Anculotus* sp. 42, pl. 5, fig. 42 (not Anthony, 1840; figure is one of the types BMNH 20120031 of *A. carinatus* Layard, 1855).

Cremnoconchus conicus W.T. Blanford, 1870: 10–12, pl. 3, fig. 3 (Torna, 35 miles W of Poona, India; lectotype, here designated, BMNH 1906.1.1.2239, Fig. 9B; 17 probable paralectotypes BMNH 1906.1.1.2242). Hanley & Theobald, 1876: 58, pl. 146, figs 8, 9. Theobald, 1876: 13. Nevill, 1885: 172. Tryon, 1887: 256, pl. 46, fig. 44 (in part, includes *C. canaliculatus*). Preston, 1915: 65–66. Aravind *et al.*, 2011: 58, unnumbered fig. (BMNH 1906.1.1.2239, lectotype of *C. conicus*).

Cremnoconchus (Lissoconchus) conicus – Thiele, 1929: 125. Wenz, 1938: 522, fig. 1377. Subba Rao & Mitra, 1979: 25. Subba Rao, 1989: 64, figs 92, 93. Ramakrishna & Dey, 2007: 112–113, fig. 69A, B.

Cremnoconchus conicus var. *edecollata* Nevill, 1885: 172 (near Poona; 12 syntypes ZSI, not seen). Tryon, 1887: 256.

Cremnoconchus (Lissoconchus) conicus var. *edecollata* – Subba Rao & Mitra, 1979: 25–26.

Cremnoconchus carinatus var. *gigantea* Nevill, 1885: 173 (Bombay Presidency; 3 syntypes probably in ZSI, not seen). Tryon, 1887: 256.

Taxonomic history: This was the first of the *Cremnoconchus* species to be discovered, and was originally described as a species of *Anculotus* (an incorrect subsequent spelling of *Anculosa* and synonym of *Leptoxis*, Pleuroceridae; E. Strong, pers. comm.). This grouping among freshwater cerithioideans is explained by the resemblance of the shell to those of globose pleurocerids, including the North American *Leptoxis* species. Layard's name *Anculotus carinatus* is a junior primary homonym of that of Anthony (1840), introduced for a genuine North American pleurocerid. Owing to the confusion of these homonyms, in his monograph of *Anculotus* Reeve (1860)

Table 3. Diagnostic features of *Cremnoconchus syhadrensis*, *C. conicus* and *C. canaliculatus* in western Maharashtra

Character	*C. syhadrensis*	*C. conicus*	*C. canaliculatus*
Shell shape	Turbinate (Fig. 3)	Turbinate to tall (Fig. 9A–O)	Globular to tall (Fig. 9P–EE)
Shell ribs	2 (shoulder and periphery) to 8	0 (rarely 1 slight rib at shoulder)	0 or 1 (shoulder)
Columella	Moderate	Wide	Narrow
Pseudumbilicus	Often wide and perforated, rarely absent	Usually absent, never perforated	Absent, or wide and perforated
Shell surface	Dull; fine or indistinct microstriae (Fig. 4B, C)	Satin sheen; fine or indistinct microstriae (Fig. 4D, E)	Dull; strong microstriae (Fig. 4I–K)
Operculum	Thickly calcified, internal ridge (Fig. 5A, B)	Weakly calcified, no internal ridge, concave (Fig. 5E, F)	Moderately calcified, internal ridge (Fig. 5G, H)
Penis	Base with distal glandular swelling; no lateral gland; small invagination; stout filament (Fig. 6A, B, D–G)	Relatively large; base slightly swollen distally; large drum-shaped gland at base; deep invagination; slender filament (Fig. 10A–H)	Bluntly tapering base; small drum-shaped gland at base; deep invagination; slender filament (Fig. 10I–N)

illustrated one of the syntypes of Layard's species as an example of that of Anthony and gave a North American locality. The shells of the two are not similar.

When Blanford (1870) described the species he considered that its range of variability included shells with a strong shoulder rib, named var. *canaliculatus*, here shown to be a distinct species. There has been persistent confusion in the taxonomic literature over the names *conicus*, *carinatus*, *canaliculatus* and *fairbanki*, owing to misguided attempts to classify the two species involved, *C. conicus* and *C. canaliculatus*, using shell shape and prominence of spiral ribs. Both these characters are variable within species (see Remarks below).

The shells described by Nevill (1885) as var. *edecollata* are a sample of the nominal species with intact spires (*fide* Subba Rao & Mitra, 1979, who examined the syntypes).

Diagnosis: Shell turbinate to tall, lacking ribs; pseudumbilicus absent; surface with satin sheen, microstriae fine or indistinct. Operculum weakly calcified, without internal ridge. Penis with base

Figure 9. Shells of *Cremnoconchus* species. A–O, *C. conicus*. P–EE, *C. canaliculatus*. A, J, K, Torna Fort, Pune Dist., Maharashtra (BMNH 20120038). B, *C. conicus* W.T. Blanford, 1870, lectotype, Torna Fort, Pune Dist., Maharashtra (BMNH 1906.1.1.2239). C, Torna Fort, Pune Dist., Maharashtra (BMNH 1906.1.1.2243; from the same lot as probable paralectotypes of *C. canaliculatus*). D, E, *Anculotus carinatus* Layard, 1855, lectotype, Mahabaleshwar, Satara Dist., Maharashtra (BMNH 20120031). F–I, Torna Fort, Pune Dist., Maharashtra (USNM 317694). L, M, 6 km west of Mahabaleshwar, Satara Dist., Maharashtra (two views of same specimen; ZSI/WGRS/IR.INV-2295). N, O, 44 km west of Bhor, Pune Dist., Maharashtra (ZSI/WGRS/IR.INV-2296, 2297). P, Q, *C. conicus* var. *canaliculatus* W.T. Blanford, 1870, lectotype, Torna Fort, Pune Dist., Maharashtra (BMNH 1906.1.1.2240). R, *C. conicus* var. *canaliculatus* W.T. Blanford, 1870, probable paralectotype, Torna Fort, Pune Dist., Maharashtra (BMNH 1906.1.1.2243). S, *C. fairbanki* '[W.T.] Blanford' Hanley & Theobald, 1876, neotype, no locality (BMNH 1906.1.1.2245). T, Mahabaleshwar, Satara Dist., Maharashtra (BMNH 20120039). U, V, Torna Fort, Pune Dist., Maharashtra (USNM 317694). W–Y, Torna Fort, Pune Dist., Maharashtra (USNM 317695). Z, Mahabaleshwar, Satara Dist., Maharashtra (BMNH 20120040). AA, BB, Dongarwadi, Tamhini, Pune Dist., Maharashtra (two views of same specimen; ZSI/WGRS/IR.INV-2299). CC, DD, Dongarwadi, Tamhini, Pune Dist., Maharashtra (BMNH 20120041). EE, 10 km west of Mahabaleshwar, Raigad Dist., Maharashtra (ZSI/WGRS/IR.INV-2300).


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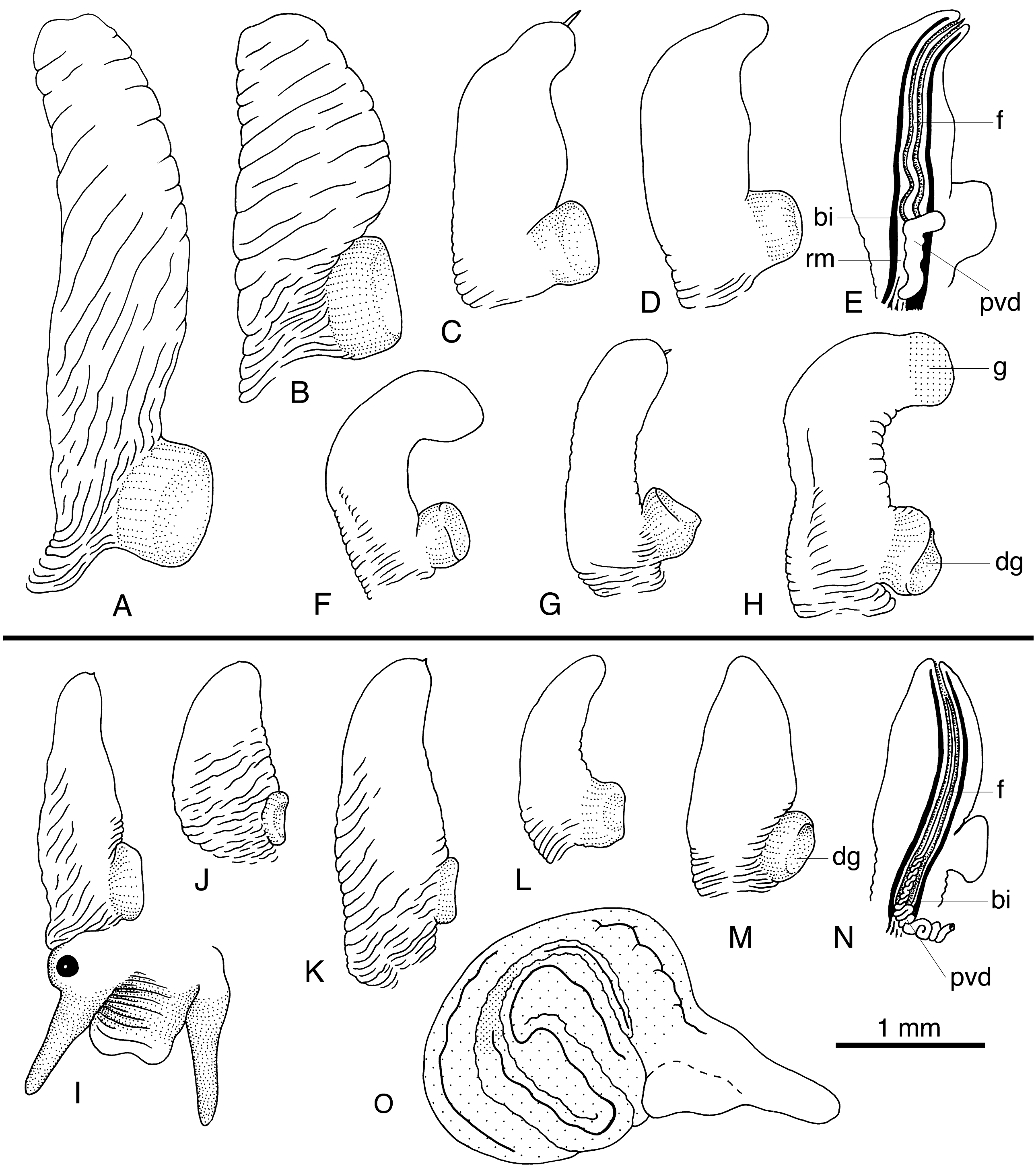


slightly swollen distally, large basal drum-shaped gland, slender filament. Western Maharashtra State.

Shell (Figs 4D–E, 9A–O): Shell H 5.0–12.1 mm. Shape (Table 1) turbinate to high-turbinate; whorls well rounded, not or only weakly angled at periphery; suture moderately or strongly impressed; apex often eroded. Columella broad. Pseudumbilicus usually absent, or a narrow chink (to 0.2 mm), or a hollowed area up to 1.2 mm wide (never perforated) with sharply angled margin continuous with apertural margin (Fig. 9E). Surface lacks distinct ribs, but a

Figure 10. Anatomy of *Cremnoconchus conicus* (A–H) and *C. canaliculatus* (I–O), all to same magnification. A–N, penes (A, live, relaxed; B, live, contracted; C–H, fixed in ethanol; I, K, live, relaxed; J, L–N, fixed in ethanol). D, E and M, N are intact and sectioned views, respectively, of same penes; I, J are the same penis viewed live and after ethanol fixation. O, pallial oviduct. A–E, 6 km west of Mahabaleshwar, Satara Dist., Maharashtra (ZSI/WGRS; shell H: A = 5.0 mm; B = 4.8 mm; C = 4.9 mm; D, E = 4.5 mm). F–H, 44 km west of Bhor, Pune Dist., Maharashtra (ZSI/WGRS; shell H: F = 5.6 mm; G = 5.8 mm; H = 6.2 mm). I–K, 10 km west of Mahabaleshwar, Raigad Dist., Maharashtra (ZSI/WGRS; shell H: I, J = 6.5 mm; K = 5.7 mm). L–N, 5 km south of Mahabaleshwar, Satara Dist., Maharashtra (ZSI/WGRS; shell H: L = 5.5 mm; M, N = 5.8 mm). O, 8 km west of Mahabaleshwar, Satara Dist., Maharashtra (ZSI/WGRS; shell H = 5.7 mm). Abbreviations: bi, bottom of invagination (shaded) for the penial filament within the penial base; dg, drum-shaped glandular appendage; f, penial filament within invagination (shaded); g, opaque glandular region of penial base (medium stipple); pvd, penial vas deferens lying coiled within cavity (black) of penial base; rm, retractor muscle of penial filament. Shading conventions as in Figure 6.

narrow flattened area may be present at suture, which is occasionally bounded by a weak rib (Fig. 9B, G, H). Surface with satin sheen; fine weak microstriae, sometimes obsolete (Fig. 4D, E). Diameter of first whorl 0.47 mm ($N = 1$). Colour: mid-brown, olive brown or golden brown, sometimes with indistinct darker bands, or up to four prominent narrow red-brown bands (at suture, mid whorl, just below periphery and around columella; Fig. 9L, N); columella white or purplish; aperture white to yellow-brown, with purple-brown bands showing through.

Animal: Head, tentacles and sides of foot grey to black, snout sometimes paler (Fig. 2H). Gills: 23–43 leaflets; black or unpigmented. Operculum (Table 1; Fig. 5E, F): opercular ratio 0.345–0.423; weakly to moderately calcified, flexible, concave, internal ridge weak or absent. Penis (Fig. 10A–H): unpigmented; relatively large, base wrinkled, strap-shaped, slightly bulbous distally (sometimes opaque) in ethanol-fixed specimens, with basal opaque cream drum-shaped gland composed of subepithelial lobules; invagination 70–90% of length of base in ethanol-fixed specimens; filament slender, rarely slightly protruding in ethanol-fixed specimens. Pallial oviduct: as for genus.

Radula (Fig. 7C, D): Relative radula length 1.13–2.45. Rachidian: length/width 1.24–1.40; 5 cusps (+1 outer denticle on either side). Lateral: 5 cusps (+ 1 inner denticle). Inner marginal: 5 cusps (+ 1 outer denticle). Outer marginal: 3–5 cusps. Major cusp of each of 5 central teeth elongate leaf-shaped with rounded tip, or elongate triangular and pointed; other cusps pointed.

Range (Fig. 8): Western Maharashtra State, between Karli and Mahabaleshwar (90 km linear distance). Records (Supporting Table S1): Maharashtra State: Karlee Hill Fort, Kurkulla, near Pune (locality tentatively identified as Karli; USNM 317693); Torna Fort, near Pune (BMNH 1906.1.1.2239, 2242, 20120038; USNM 317694, 317696); 44 km W Bhor (ZSI/WGRS/IR.INV-2296, 2297, 2298); 6 km W Mahabaleshwar (ZSI/WGRS/IR.INV-2295); Mahabaleshwar Hills (BMNH 1871.9.23.149).

Habitat and ecology: On basalt cliffs with algal mat, or bare, covered by flowing water film; on pebbles in shallow pool at foot of cliff with moving water. Collected from 645 m (44 km west of Bhor) and 1103 m (6 km west of Mahabaleshwar). Blanford (1870: 11) recorded that it was 'met with abundantly on the steep slopes of Torna one of the old Deccan hill forts . . . The specimens were taken from rocks by the sides of the small torrents running down the hill side.' His concept of the species included *C. canaliculatus*. Torna Fort is at an altitude of 1400 m (Supporting Table S1).

Remarks: Like the two other *Cremnoconchus* species with which it occurs, *C. conicus* displays shell variation, and this variability and co-occurrence have resulted in taxonomic confusion. Blanford (1870) described, in addition to the typical form, a 'var. *canaliculatus*' also from Torna, while considering *C. carinatus* from Mahabaleshwar to be distinct. He noted: 'The canaliculate variety serves to connect the typical form with *carinatus*, as many specimens have the angle at the periphery more marked than in the typical *conicus*; but specimens of *carinatus* are of a somewhat different form, with considerably less swollen whorls. Perhaps all three forms should be considered as varieties of one species, for which, however, the name *carinatus*, which is not very appropriate even for full grown specimens of the Mahableshwar shell, can scarcely be retained with propriety.' (Blanford, 1870: 11). Here it is shown that *C. canaliculatus* is a distinct species, while *C. carinatus* is a synonym of *C. conicus*. Two specimens of *C. conicus* are present among the probable syntypes of *C. canaliculatus*. To add to the confusion, *C. syhadrensis* is also found at Torna, although apparently unknown to Blanford and not present in his material from the site. For example, four large lots from Torna, each of 20–100 dry shells, are present in the Evezard Collection (USNM) made in the late 19th century. Presumably following Blanford's descriptions, these were originally sorted and labelled according to the presence of spiral ribs: '*C. syhadrensis*' (eight spiral ribs; contains *C. syhadrensis* alone; USNM 317683); '*C. conicus* vars' (variable ribs; contains *C. syhadrensis* and *C. canaliculatus*; USNM 317695); '*C. conicus* var. *canaliculatus*' (strong rib at suture; contains *C. syhadrensis* alone; USNM 317696); '*C. conicus*' (no ribs; contains mainly *C. conicus* with a few *C. canaliculatus*; USNM 317694). As discussed below, for each of the three species mixed in these lots the development of ribs and angulation of the whorls are variable. Far more significant for identification are the less readily apparent characters of surface microsculpture and form of the columella and umbilicus (Table 3).

The type series of *C. carinatus* consists of five large (H up to 9.2 mm) shells of thick texture, turbinate form, with clear but fine microstriae, weakly marked suture, slight peripheral angle (certainly not carinate; the specific epithet is indeed inappropriate, as noted by Blanford, 1870) and wide (but imperforate) pseudumbilical area (Fig. 9D, E). These shells differ from Blanford's *C. conicus* (his 'typical form'; Blanford, 1870), which has a thinner texture, taller spire, indistinct microstriae, impressed suture, rounded whorls, and minute pseudumbilical chink (Fig. 9B). The respective type localities of Mahabaleshwar and Torna are 35 km apart. No specimens exactly resembling Layard's shells were discovered during fieldwork at Mahabaleshwar in 2010. The stream flowing through the modern town of Mahabaleshwar to the 'Chinaman Falls' (Fig. 2D) is now badly polluted; if this was the type locality, *Cremnoconchus* no longer occur there. However, it may be that the type locality was another of the many small streams in the area, or in the vicinity of the small settlement of Old Mahabaleshwar. Smaller shells (H up to 6.6 mm) were collected 6 km from Mahabaleshwar. These are of thinner texture, with four dark bands and closed pseudumbilicus (Fig. 9L, M). A collection from 44 km west of Bhor, midway between Torna and Mahabaleshwar (Fig. 9N, O), includes specimens that overlap the range of variation at the other two sites, supporting the proposed synonymy.

There is also some variation in the operculum; those of the specimens from near Bhor are thin, flexible, and slightly less tightly coiled (Fig. 5E, F), but those from near Mahabaleshwar are more heavily calcified, appearing more opaque and drying flat (Table 1).

It is not known whether there is some segregation by microhabitat where *C. syhadrensis*, *C. canaliculatus* and *C. conicus* occur together, as at Torna. Only *C. conicus* has been found in shallow pools, while both it and *C. canaliculatus* occur in flowing water, and *C. syhadrensis* appears to favour damp rocks and shady overhangs. Although *C. conicus* and *C. canaliculatus* both occur in the vicinity of Mahabaleshwar, in apparently similar habitats, they were not discovered in the same streams (see Supporting Table S1 for locality details).

Table 3 summarizes the diagnostic characters of the three *Cremnoconchus* of western Maharashtra. *Cremnoconchus conicus* can be identified by its satin sheen, wide columella and thin (mainly corneous) operculum. The penial shape of *C. syhadrensis* is diagnostic, but those of the other two are more similar. Compared with that of *C. canaliculatus* the penis of *C. conicus* is relatively larger, has a more swollen apex to the base, and the drum-shaped glandular projection is larger (Fig. 10).

Cremnoconchus canaliculatus W.T. Blanford, 1870
(Figs 4I–K, 5G, H, 7E, F, 8, 9P–EE, 10I–O, 16D)

Cremnoconchus conicus var. *canaliculatus* W.T. Blanford, 1870: 11–12, pl. 3, fig. 4 (Torna, 35 miles W of Poona, India; lectotype, here designated, BMNH 1906.1.1.2240, Fig. 9Q; 7 probable paralectotypes BMNH 1906.1.1.2243, 2 of which are *C. conicus*, Fig. 9R). Theobald, 1876: 13. Nevill, 1885: 172 (as *canaliculata*). Tryon, 1887: 256, pl. 46, fig. 46. Preston, 1915: 66.

Cremnoconchus (Lissoconchus) conicus var. *canaliculatus* – Subba Rao & Mitra, 1979: 25.

Cremnoconchus carinatus – Stoliczka, 1871: 109 (in part, includes *C. conicus*; not Layard, 1855 = *C. conicus*). Hanley & Theobald, 1876: 58, pl. 146, fig. 10 (not Layard, 1855). Tryon, 1887: 256, pl. 46, fig. 43 (not Layard, 1855).

Cremnoconchus fairbanki '[W.T.] Blanford' Hanley & Theobald, 1876: 58, pl. 146, fig. 7 (no locality; neotype, here designated, BMNH 1906.1.1.2245, Fig. 9S). Blanford, 1881: 221.

Cremnoconchus conicus – Tryon, 1887: 256, pl. 46, fig. 45 (in part, includes *C. conicus*). Blanford, 1881: 221 (refers to Hanley & Theobald, 1876: pl. 146, fig. 10) (not W.T. Blanford, 1870).

Cremnoconchus syhadrensis – Annandale & Prashad, 1919: 149 (in part, includes *C. syhadrensis*). Aravind *et al.*, 2011: 58, unnumbered fig. (not W.T. Blanford, 1863; BMNH 1906.1.1.2240, lectotype of *C. conicus* var. *canaliculatus*).

Cremnoconchus 'from Pune' Aravind *et al.*, 2011: 58, unnumbered fig.

Taxonomic history: This species was first named by Blanford (1870) as a variety of the supposedly variable species *C. conicus* (see Remarks on *C. conicus* above).

The name *C. fairbanki* has a curious history. It was introduced by Hanley & Theobald (1876) with its authorship credited to Blanford, but accompanied by the remark 'An accident to our manuscript at the time of going to press prevents our saying where (if at all) this species has been published' (p. 000). It was accompanied by a figure, but without description or locality. Blanford (1881: 221) responded: 'I have [the word *never* has evidently been omitted at this point] described the species here attributed to me, and I greatly doubt my being responsible for the specific name, even in manuscript. I find amongst my collection a small box of *C. carinatus*, labelled *C. fairbanki*, but I cannot recollect whence the name was derived.' A sample of nine shells in the W.T. Blanford collection (BMNH 1906.1.1.2245) appears to be the lot mentioned by Blanford, and retains his original label '*Cremnobates fairbanki*'. These are tall, thick shells with no umbilicus, pale yellow-brown and unbanded, and one is here designated neotype.

The synonymies of *C. conicus* and *C. canaliculatus* demonstrate the persistent confusion among the available names (*conicus*, *carinatus*, *canaliculatus*, *fairbanki*) for these two taxa (see Remarks on *C. conicus*). *Cremnoconchus canaliculatus* has not previously been considered a valid species.

Diagnosis: Shell globular to tall, without ribs or with one rib at shoulder; pseudumbilicus present or absent; surface dull, with strong microstriae. Operculum moderately calcified, with internal ridge. Penis with bluntly tapering base, small basal drum-shaped gland, slender filament. Western Maharashtra State.

Shell (Figs 4I–K, 9P–EE): Shell H 4.2–9.8 mm. Shape (Table 1) globular, turbinate or high-turbinate; whorls rounded, not or only weakly angled at periphery; suture strongly impressed, with flattened ramp or angled shoulder; apex often eroded; base slightly swollen. Columella narrow. Pseudumbilicus absent in juveniles and tall-spired shells (Fig. 9Q); otherwise broadly open (to 1.2 mm), perforated, outlined by sharply angled margin continuous with apertural margin (Fig. 9AA). Surface often without distinct ribs, but a rib may develop at shoulder if this is strongly angled (Fig. 9P, R), weakening on last whorl. Surface dull, with strong regular microstriae, sometimes minutely serrated by intersection with fine growth lines (Fig. 4I–K). Protoconch (Fig. 16D) 1.5 whorls; diameter 0.66 ($N = 1$); diameter of first whorl 0.32–0.47 mm ($N = 6$). Colour: pale yellow-brown to mid-brown or pale red-brown, sometimes with indistinct darker bands, one at mid-whorl and one just below periphery (Fig. 9P, Z, DD); columella white, parietal area occasionally flushed purple; aperture white to yellow, with any bands weakly showing through.

Animal: Head, tentacles and sides of foot very pale to mid-grey, snout and tentacles darker grey or blackish. Gills: up to 38 leaflets; grey or unpigmented. Operculum (Table 1; Fig. 5G, H): opercular ratio 0.333–0.478; moderately calcified, with thickened internal ridge. Penis (Fig. 10I–N): unpigmented; base wrinkled, strap-shaped, bluntly tapering, with small basal opaque cream drum-shaped gland composed of subepithelial lobules; invagination extends full length of base in ethanol-fixed specimens; filament slender, not seen to protrude. Pallial oviduct (Fig. 10O): as for genus.

Radula (Fig. 7E, F): Relative radula length 0.94–1.98. Rachidian: length/width 1.24–1.30; 5 or 7 cusps (outermost cusp on either side often reduced to a denticle). Lateral: 5 cusps (+ 1–2 inner denticles). Inner marginal: 6 cusps (outermost sometimes reduced to denticle). Outer marginal: 3–4 cusps (sometimes + 1 inner denticle). Major cusp of each of 5 central teeth elongate leaf-shaped with rounded tip; other cusps pointed.

Range (Fig. 8): Western Maharashtra State, from 55 km north-west of Pune to Mahabaleshwar (100 km linear distance). Records (Supporting Table S1): Maharashtra State: Bhor Ghat (USNM 317704); Dongarwadi, Tamhini, 40 km west of Pune (BMNH 20120041); Torna Fort, near Pune (BMNH 1906.1.1.2240, 2243; USNM 317694, 317695); 10 km west of Mahabaleshwar (ZSI/WGRS/IR.INV-2300, 2301); 8 km west of Mahabaleshwar (ZSI/WGRS); Mahabaleshwar Hills (BMNH 1871.9.23.149); 5 km south of Mahabaleshwar (ZSI/WGRS/IR.INV-2302).

Habitat and ecology: On sides of boulders in and near fast-flowing stream; on bare rocks and mossy cliffs with flowing water film (Fig. 2A). Collected from 692 m (10 km west of Mahabaleshwar) and 1125 m (5 km south of Mahabaleshwar). Torna Fort is at an altitude of 1400 m (Supporting Table S1).

Remarks: Like the other two *Cremnoconchus* species from western Maharashtra, *C. canaliculatus* displays a wide variation in shell characters. Neither the prominent shoulder rib close to the suture (which gave rise to the specific epithet) nor the sometimes conspicuous pseudumbilicus are consistent characters. The umbilicus is absent in juveniles (hence termed a pseudumbilicus) and remains so in most tall-spired shells (Fig. 9Q). The pseudumbilicus is especially prominent in low-spired or globular shells

(Fig. 9AA). Most shells have a flattened sutural ramp (Fig. 9P, R, U–Z, CC), but this is not always strongly angled, and only infrequently marked by a definite rib (Fig. 9P, R). Individual samples are usually either low-spired and umbilicate, or tall-spired and imperforate (the type samples of both the nominal taxa are of the latter type), but in one collection (from 10 km west of Mahabaleshwar) the pseudumbilicus ranged from vestigial to wide (Fig. 9EE) among adults. In the large *Cremnoconchus* samples from Torna in the Evezard collection (USNM), 11 specimens in a lot of about 100 *C. conicus* (USNM 317694) were of the tall, imperforate type (Fig. 9U, V), whereas 22 in a mixed lot of 60 *C. syhadrensis* and 15 *C. conicus* (USNM 317695) were of the globose, umbilicate type (Fig. 9W–Y). It is unknown whether this reflects distinct populations, ecophenotypic variation across microhabitats, or sorting after collection from a single population. There were no apparent anatomical differences between a population of globose, umbilicate shells and one of tall, imperforate shells collected within 15 km of each other near Mahabaleshwar (10 km west and 5 km south of the town, respectively)

Shells of the tall, imperforate type that lack a sutural ramp (Fig. 9S, T) can closely resemble *C. conicus* (Fig. 9A–O). The consistent characters of *C. canaliculatus* are the dull surface with strongly developed microstriae and the narrow columella, which contrast with the satin surface, weak microstriae and wider columella of *C. conicus*. In addition, the sutural ramp is often more well developed in *C. canaliculatus* and the base slightly swollen. The penis of *C. canaliculatus* is relatively smaller, less bulbous distally, and the basal drum-shaped appendage is smaller than in *C. conicus* (Fig. 10). These two species were not found in the same streams in the vicinity of Mahabaleshwar, but are mixed in several dry museum lots from Torna, supporting their status as distinct species (see Remarks on *C. conicus*). The present species is also recorded together with *C. syhadrensis* at some localities (see remarks on *C. syhadrensis*; Supporting Table S1). Characters of the three *Cremnoconchus* species in western Maharashtra are summarized in Table 3.

At one locality (10 km west of Mahabaleshwar; Supporting Table S1) three of 13 (23%) specimens were parasitized, the digestive gland and gonad being packed with trematodes about 0.2 mm in length.

CREMNOCONCHUS HANUMANI SP. NOV.

(FIGS 4N, O, 5I, J, 7G, H, 8, 11A–G, 12A–G)

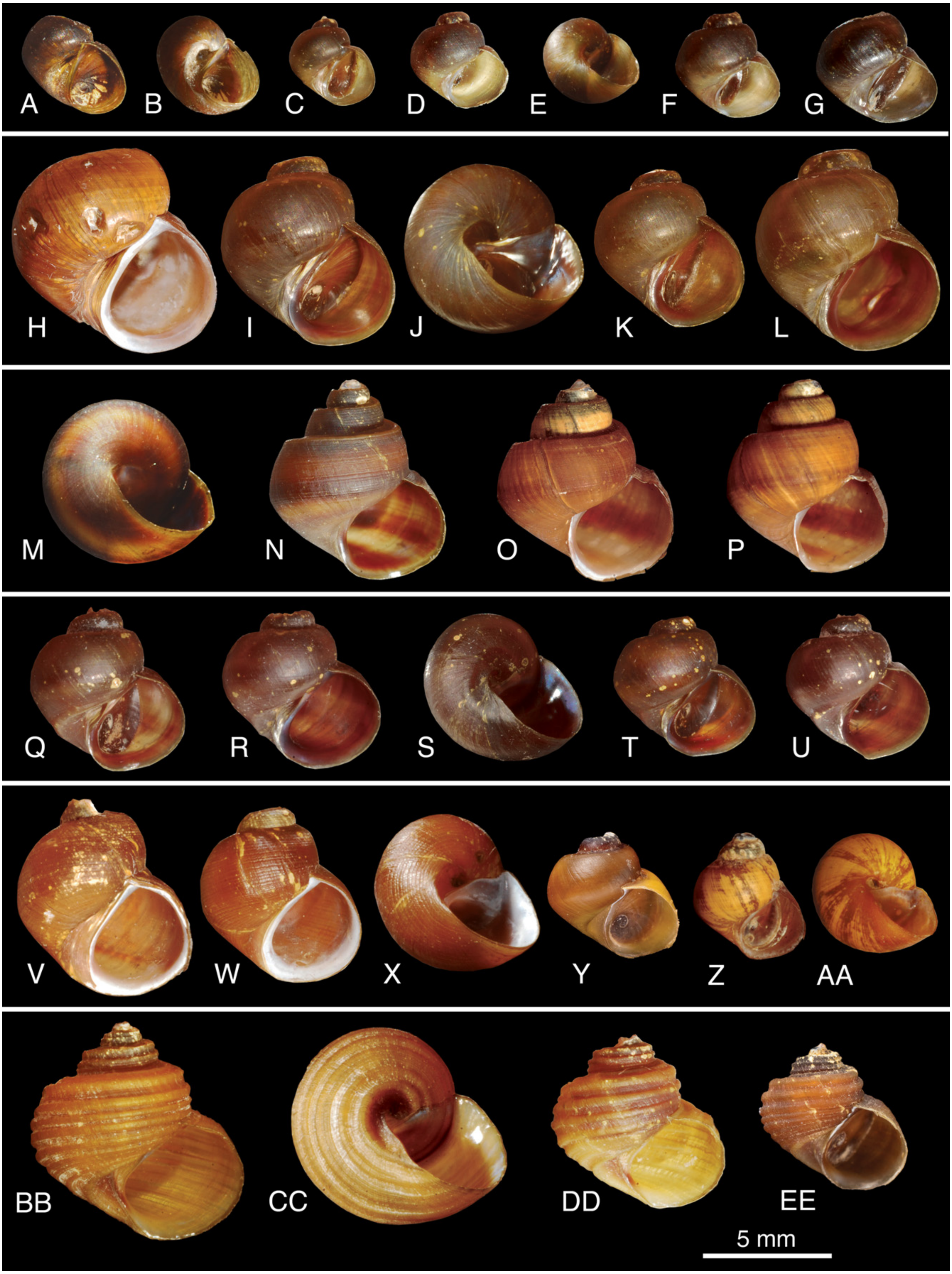
Types: Holotype ZSI/WGRS/IR.INV-2303 (Fig. 11A, B); 1 paratype ZSI/WGRS/IR.INV-2304 (Fig. 11C); Hanuman Gundi Falls, Chikmagalur Dist., Karnataka, India (13.27008°N 75.15511°E).

Etymology: After the Hindu deity Hanuman, from the type locality.

Diagnosis: Shell turbinate to globular, without ribs; pseudumbilicus broad but not perforated; surface with satin sheen, faint microstriae. Operculum weakly calcified, no internal ridge. Penis with slight distal swelling, stout filament. Western Karnataka State.

Shell (Figs 4N, O, 11A–G): Shell H 3.3–5.0 mm. Shape (Table 1) globular to turbinate; whorls rounded, not or only slightly angled at periphery; suture impressed, with slightly flattened ramp and weakly angled shoulder; apex eroded; base slightly swollen. Delicate texture. Columella narrow. Pseudumbilicus broad (to 1.0 mm; rarely 0.3–0.5 mm), hollowed but not deeply perforated, outlined by sharply angled margin continuous with apertural margin (Fig. 11B). Surface without ribs; with satin sheen; very fine or faint spiral striae (Fig. 4N, O), becoming obsolete on last whorl of largest shells. Protoconch 1.4 whorls; diameter 0.62 ($N = 1$); diameter of first whorl 0.45–0.53 mm ($N = 2$). Colour: dark brown or olive-brown,

Figure 11. Shells of *Cremnoconchus* species. A–G, *C. hanumani*. H–L, *C. globulus*. M–P, *C. agumbensis*. Q–U, *C. cingulatus*. V–AA, *C. castanea*. BB–EE, *C. dwarakii*. A–C, ***C. hanumani* sp. nov.**, holotype (A, B; ZSI/WGRS/IR.INV-2303) and paratype (C; ZSI/WGRS/IR.INV-2304), Hanuman Gundi Falls, Chikmagalur Dist., Karnataka. D–G, Greater Kadambi Falls, Chikmagalur Dist., Karnataka (D, E two views of same specimen; ZSI/WGRS/IR.INV-2305, 2306, 2307). H, L, Greater Kadambi Falls, Chikmagalur Dist., Karnataka (ZSI/WGRS/IR.INV-2308, 2309). I–K, ***C. globulus* sp. nov.**, holotype (I, J; ZSI/WGRS/IR.INV-2310) and paratype (K; ZSI/WGRS/IR.INV-2311), Lesser Kadambi Falls, Chikmagalur Dist., Karnataka. M–P, ***C. agumbensis* sp. nov.**, holotype (M, N; ZSI/WGRS/IR.INV-2313) and paratypes (O, P; ZSI/WGRS/IR.INV-2314, 2315), Someshwara to Agumbe road, Udupi Dist., Karnataka. Q–U, ***C. cingulatus* sp. nov.**, holotype (R, S; ZSI/WGRS/IR.INV-2316) and paratypes (Q, T, U; ZSI/WGRS/IR.INV-2317, 2318, 2319), Hulikal Ghat, Udupi Dist., Karnataka. V–X, ***C. castanea* sp. nov.**, holotype (W, X; ZSI/WGRS/IR.INV-2321) and paratype (V; ZSI/WGRS/IR.INV-2320), Belkal Thirtha Falls, Udupi Dist., Karnataka. Y, Arasinagundi Falls, Udupi Dist., Karnataka (BMNH 20120032). Z, AA, no locality (two views of same specimen; ZSI/WGRS/IR.INV-2322). BB–DD, ***C. dwarakii* sp. nov.**, holotype (BB, CC; ZSI/WGRS/IR.INV-2323) and paratype (DD; ZSI/WGRS/IR.INV-2324), Hulikal Ghat, Udupi Dist., Karnataka. EE, Hulikal Ghat, Udupi Dist., Karnataka (BMNH 20120036).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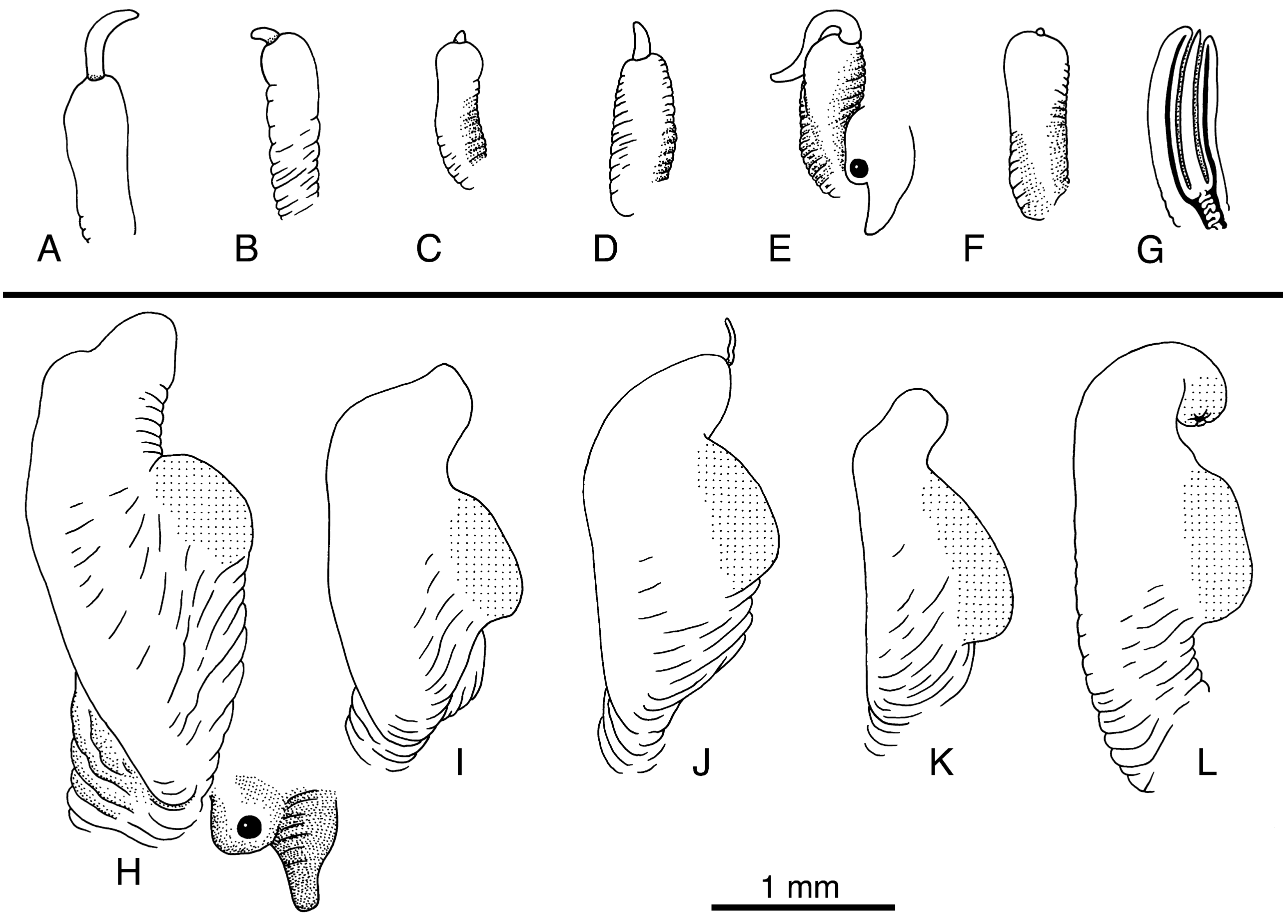


Figure 12. Anatomy of *Cremnoconchus hanumani* (A–G) and *C. globulus* (H–L), all to same magnification. A–L, penes (all fixed in ethanol); F, G are intact and sectioned views of same penis. A–C, Hanuman Gundi Falls, Chikmagalur Dist., Karnataka (ZSI/WGRS; shell H: A = 4.9 mm; B = 3.5 mm; C = 3.3 mm). D–G, Greater Kadambi Falls, Chikmagalur Dist., Karnataka (ZSI/WGRS; shell H: D = 3.9 mm; E = 4.0 mm; F, G = 5.0 mm). H–K, Lesser Kadambi Falls, Chikmagalur Dist., Karnataka (ZSI/WGRS; shell H: H = 7.0 mm; I = 6.0 mm; J = 7.0 mm; K = 6.3 mm). L, Greater Kadambi Falls, Chikmagalur Dist., Karnataka (ZSI/WGRS; shell H = 7.9 mm). Shading conventions as in Figure 6.

sometimes a narrow purple-brown band at suture; columella whitish or slightly tinged purple-brown; aperture pale with sutural band showing through.

Animal: Head, tentacles, and sides of foot dark grey to black. Gills: 24–30 leaflets; grey or unpigmented. Operculum (Table 1; Fig. 5I, J): opercular ratio 0.318–0.400; weakly calcified, translucent mid-brown, no internal ridge. Penis (Fig. 12A–G): unpigmented or slightly pigmented; base wrinkled, slightly swollen (possibly glandular) distally; invagination 70–90% of length of base in ethanol-fixed specimens; filament relatively stout, usually protruding in ethanol-fixed specimens. Pallial oviduct: as for genus. One pallial oviduct contained single egg with firm covering 0.47 mm diameter (ethanol fixed).

Radula (Fig. 7G, H): Relative radula length 2.50–3.06. Rachidian: length/width 1.09–1.21; 5 cusps (+ 1 outer denticle on either side). Lateral: 5 cusps (+ 1–2 inner denticles). Inner marginal: 6 cusps. Outer marginal: 6–7 cusps (+ 1 inner or outer denticle). Major cusp of each of 5 central teeth leaf-shaped with pointed tip; other cusps pointed.

Range (Fig. 8): Western Karnataka State, Kudremukh (55 km north-east of Mangalore). Records (Supporting Table S1): Karnataka State: Hanuman Gundi Falls (ZSI/WGRS/IR.INV-2303, 2304); Greater Kadambi Falls (ZSI/WGRS/IR.INV-2305, 2306, 2307).

Habitat and ecology: On rocks and cliff wetted by spray from strong waterfall; in crevices; in partial shade of riparian vegetation in wet evergreen forest. Altitude 830 m and 941 m.

Remarks: The small, globose shell with delicate texture and wide (but not perforated) pseudumbilicus are distinctive of this species. *Cremnoconchus castanea* has a taller, thicker shell and well-calcified operculum (Table 4). *Cremnoconchus globulus* can be found together with *C. hanumani* (Supporting Table S1); the former is larger, more solid, with a moderate umbilicus; the operculum is weakly calcified in both, but dark red-brown in *C. globulus* and translucent mid-brown in *C. hanumani*. The penis of *C. hanumani* is diagnostic.

Where this species occurs in the same stream as the larger *C. globulus* there is no obvious difference in microhabitat.

CREMNOCONCHUS GLOBULUS SP. NOV.
(FIGS 2E, 4F, 5K, L, 8, 11H–L, 12H–L, 13A, B)

Types: Holotype ZSI/WGRS/IR.INV-2310 (Fig. 11I, J); 2 paratypes ZSI/WGRS/IR.INV-2311, 2312 (Fig. 11K); Lesser Kadambi Falls, Chikmagalur Dist., Karnataka, India (13.24384°N, 75.17056°E).

Etymology: Latin *globulus*, globular, in reference to shell shape.

Diagnosis: Shell globular, without ribs; pseudumbilicus moderate, sometimes perforated; surface with satin sheen, no microstriae. Operculum weakly calcified, no internal ridge. Penis with lateral glandular flange, slender filament. Western Karnataka State.

Shell (Figs 4F, 11H–L): Shell H 6.0–8.8 mm. Shape (Table 1) globular; whorls rounded, without angulation; suture impressed; apex eroded; base slightly swollen. Columella moderately narrow, wider at base. Pseudumbilicus moderate (to 0.8 mm), sometimes perforated, outlined by angled margin, sometimes forming a slight rounded rib. Surface almost always without ribs above periphery; rarely a slight thickening or indistinct rib near suture. Surface with satin sheen; spiral striae almost or entirely absent (Fig. 4F). Diameter of first whorl 0.50–0.66 mm ($N = 3$). Colour: dark brown or olive-brown, sometimes darker on spire and in band at suture; columella and umbilicus purple-brown; aperture pale brown to whitish, with sutural band showing through.

Animal: Head, tentacles, and sides of foot pale grey to black, tentacles darker, paler at tip of snout. Gills: up to 40 leaflets; black. Operculum (Table 1; Fig. 5K, L): opercular ratio 0.364–0.421; weakly calcified, dark red-brown, no internal ridge. Penis (Fig. 12H–L): unpigmented or slightly pigmented; base wrinkled, with long thickened flange running across left side towards eye, glandular knob on right side, and slight glandular swelling distally (sometimes opaque); invagination about half length of base in ethanol-fixed specimens; filament slender, rarely protruding in ethanol-fixed specimens. Pallial oviduct: as for genus.

Radula (Fig. 13A, B): Relative radula length 2.66–3.43. Rachidian: length/width 1.10–1.22; 5 cusps (+ 1 outer denticle on either side). Lateral: 5 cusps (+ 1 inner denticle). Inner marginal: 5 cusps. Outer marginal: 4–5 cusps. Major cusp of each of 5 central teeth triangular leaf-shaped with pointed to slightly rounded tip; other cusps pointed.

Range (Fig. 8): Western Karnataka State, Kudremukh (55 km north-east of Mangalore). Records (see Supporting Table S1): Karnataka State: Lesser Kadambi Falls (ZSI/WGRS/IR.INV-2310, 2311, 2312); Greater Kadambi Falls (ZSI/WGRS/IR.INV-2308, 2309).

Habitat and ecology: Common in film of water flowing over rock face beside waterfall (Fig. 2E); on stones in shallow streams (to 30 cm deep) with fast-flowing water; in partial shade of riparian vegetation in wet evergreen forest. Altitude 941 and 967 m.

Remarks: Four *Cremnoconchus* species have similar umbilicate, globular to turbinate, smooth shells (Table 4). *Cremnoconchus globulus* is distinguished by its lack of a basal rib (present in *C. cingulatus*), moderate pseudumbilicus and weakly calcified operculum (well calcified in *C. castanea*). Distinction from *C. hanumani*, with which it occurs in the same microhabitat, is discussed in the Remarks on that species. The penes of all four are diagnostic (Figs 12, 14, 15).

CREMNOCONCHUS AGUMBENSIS SP. NOV.
(FIGS 4H, 5M, N, 8, 11M–P, 13C, D, 14A–C, 16E)

Types: Holotype ZSI/WGRS/IR.INV-2313 (Fig. 11M, N); 2 paratypes ZSI/WGRS/IR.INV-2314, 2315 (Fig. 11O, P); Someshwara to Agumbe road, Udupi Dist., Karnataka, India (13.49342°N, 75.07783°E).

Etymology: From the type locality.

Diagnosis: Shell high turbinate, shoulder angled or with rib; pseudumbilicus absent; surface dull, with strong microstriae. Operculum calcified, no internal ridge. Penis large, with distal glandular thickening, stout filament. Western Karnataka State.

Table 4. Diagnostic features of *Cremnoconchus dwarakii*, *C. agumbensis*, *C. castanea*, *C. cingulatus*, *C. globulus*, and *C. hanumani* in western Karnataka

Character	*C. dwarakii*	*C. agumbensis*	*C. castanea*	*C. cingulatus*	*C. globulus*	*C. hanumani*
Shell shape	Turbinate (Fig. 11BB–EE)	High turbinate (Fig. 11M–P)	Turbinate (Fig. 11V–AA)	Globular (Fig. 11Q–U)	Globular (Fig. 11H–L)	Turbinate to globular (Fig. 11A–G)
Shell ribs	8–11 (including base)	0 or 1 (strong shoulder angle)	0	1 on base	0	0
Columella	Narrow	Narrow	Narrow	Narrow	Moderate	Narrow
Pseudumbilicus	Narrow, perforated	Absent	Wide, perforated	Narrow, perforated	Moderate, sometimes perforated	Broad, not perforated
Shell surface	Dull; fine strong microstriae (Fig. 4A)	Dull; strong microstriae (Fig. 4H)	Indistinct or strong microstriae (Fig. 4M)	Satin sheen; indistinct or absent microstriae (Fig. 4G)	Satin sheen; microstriae absent (Fig. 4F)	Satin sheen; faint microstriae (Fig. 4N)
Operculum	Weakly calcified, no internal ridge (Fig. 5C, D)	Calcified, no internal ridge (Fig. 5M, N)	Calcified, internal ridge (Fig. 5Q, R)	Weakly calcified, no internal ridge, concave (Fig. 5O, P)	Weakly calcified, no internal ridge (Fig. 5K, L)	Weakly calcified, no internal ridge (Fig. 5I, J)
Penis	No drum-shaped gland; slight glandular flange; small invagination; slender filament (Fig. 15E–I)	Relatively large; no drum-shaped gland; distal glandular thickening; stout filament (Fig. 14A, B)	Relatively large; no drum-shaped gland; distal glandular pad; small invagination; slender filament (Fig. 15A–D)	No drum-shaped gland; distal glandular pad; small invagination; slender filament (Fig. 14D–I)	No drum-shaped gland; lateral glandular flange; small invagination; slender filament (Fig. 12H–L)	No drum-shaped gland; slight distal swelling; deep invagination; stout filament (Fig. 12A–G)

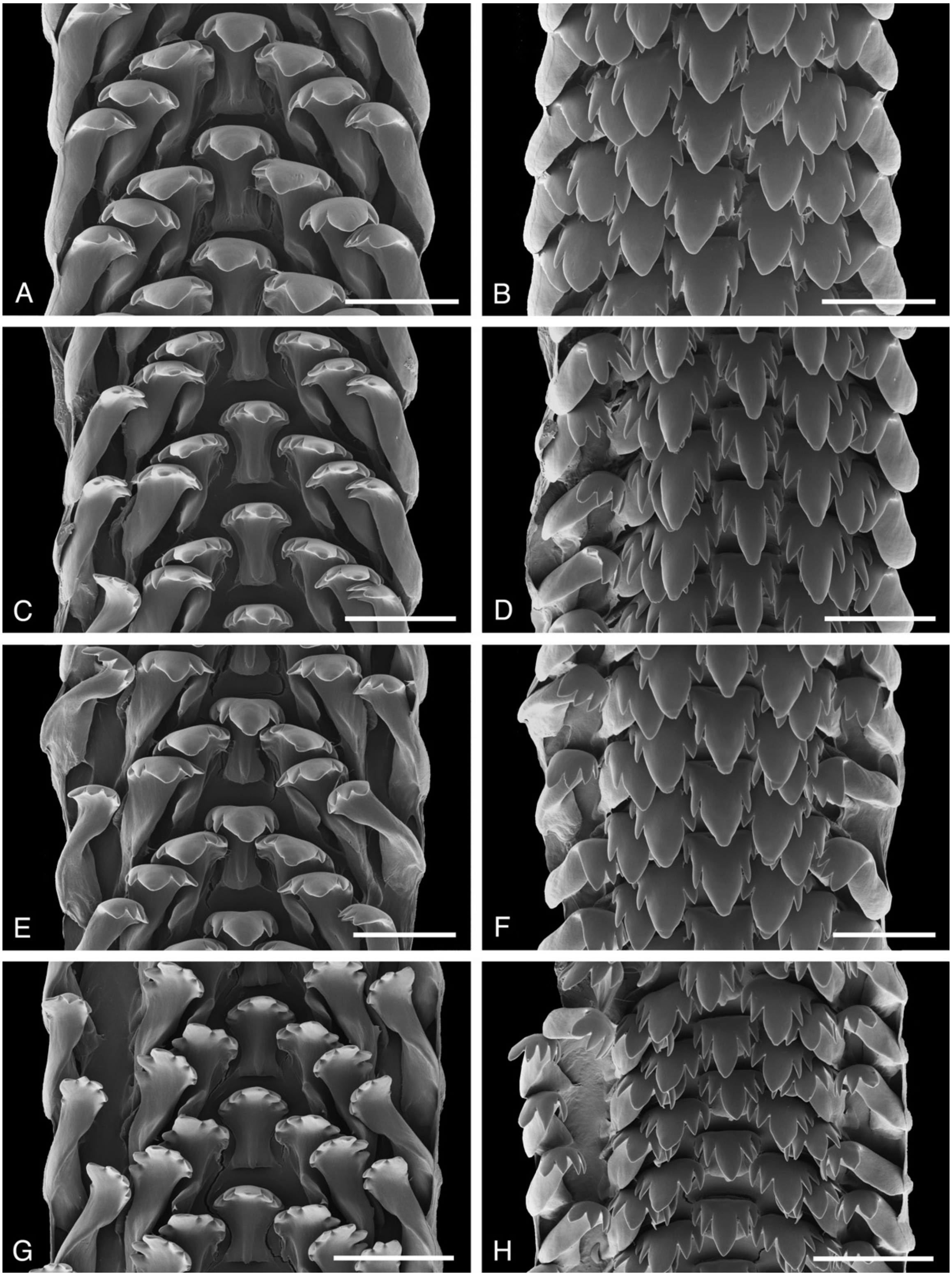


Figure 13. Radulae of *Cremnoconchus* species (two views of each radula, flat and at 45°). A, B, *C. globulus*, Lesser Kadambi Falls, Chikmagalur Dist., Karnataka (ZSI/WGRS; shell H = 7.4 mm). C, D, *C. agumbensis*, Agumbe, Udupi Dist., Karnataka (ZSI/WGRS; shell H = 9.5 mm). E, F, *C. cingulatus*, Hulikal Ghat, Udupi Dist., Karnataka (ZSI/WGRS; shell H = 5.7 mm). G, H, *C. castanea*, Arasinagundi Falls, Udupi Dist., Karnataka (ZSI/WGRS; shell H = 8.5 mm). Scale bars = 50 μm.

Shell (Figs 4H, 11M–P): Shell H 5.5–10.4 mm. Shape (Table 1) high turbinate; whorls strongly angled at shoulder (sometimes raised as a rib; Fig. 11N), giving pronounced sutural ramp or channel, but becoming weak at end of last whorl; slight angle at periphery; suture impressed; apex slightly eroded; base slightly swollen. Columella narrow. Pseudumbilicus absent. Surface with single narrow rib at shoulder; dull, with irregular but distinct microstriae, fainter on last whorl and on base (Fig. 4H). Protoconch (Fig. 16E) 1.5 whorls; diameter 0.68 mm; diameter of first whorl 0.53 mm ($n = 1$). Colour: dark brown, darker on spire, three more or less distinct broad black-brown bands at shoulder, above periphery and on inner part of base; aperture pale brown, columella and interior bands purple-brown.

Animal: Head, tentacles and sides of foot black, paler at tip of snout. Gills: up to 50 leaflets; unpigmented. Operculum (Table 1; Fig. 5M, N): opercular ratio 0.439–0.565; calcified, no internal ridge. Penis (Fig. 14A, B): relatively large; unpigmented; base wrinkled, strap-shaped, with slightly thickened distal glandular region; filament relatively stout, protruding in ethanol-fixed specimens. Pallial oviduct (Fig. 14C): as for genus. One pallial oviduct contained two eggs 0.40 mm diameter (ethanol fixed).

Radula (Fig. 13C, D): Relative radula length 1.09–1.79. Rachidian: length/width 1.19–1.42; 5 cusps (+ 1 outer denticle on either side). Lateral: 6 cusps (sometimes + 1 inner denticle). Inner marginal: 5 cusps (sometimes + 1 inner denticle). Outer marginal: 4 cusps (sometimes + 1 inner denticle). Major cusp of each of 5 central teeth elongate-triangular with rounded and slightly papillose tip; other cusps pointed.

Range (Fig. 8): Western Karnataka State, Agumbe (75 km north-northeast of Mangalore). Records (Supporting Table S1): Karnataka State: Someshwara to Agumbe road (ZSI/WGRS/IR.INV-2313, 2314, 2315).

Habitat and ecology: Damp rock face shaded by evergreen forest. Altitude 379 m.

Remarks: Among the known *Cremnoconchus* species of Karnataka, *C. agumbensis* is the only one with turreted whorls produced by a sharp angulation (or rib) at the shoulder, and without a pseudumbilicus (Table 4). In these characters it resembles the canaliculate form of *C. canaliculatus* from Maharashtra (Table 3; Fig. 9P, R, U–Z, CC), but that has a more solid shell and the penis bears a drum-shaped gland (Fig. 10I–N).

CREMNOCONCHUS CINGULATUS SP. NOV.
(FIGS 4G, 5O, P, 11Q–U, 13E, F, 14D–I)

Types: Holotype ZSI/WGRS/IR.INV-2316 (Fig. 11R, S); 3 paratypes ZSI/WGRS/IR.INV-2317, 2318, 2319 (Fig. 11Q, T, U); Hulikal Ghat, Udupi Dist., Karnataka, India (13.71742°N 74.99445°E).

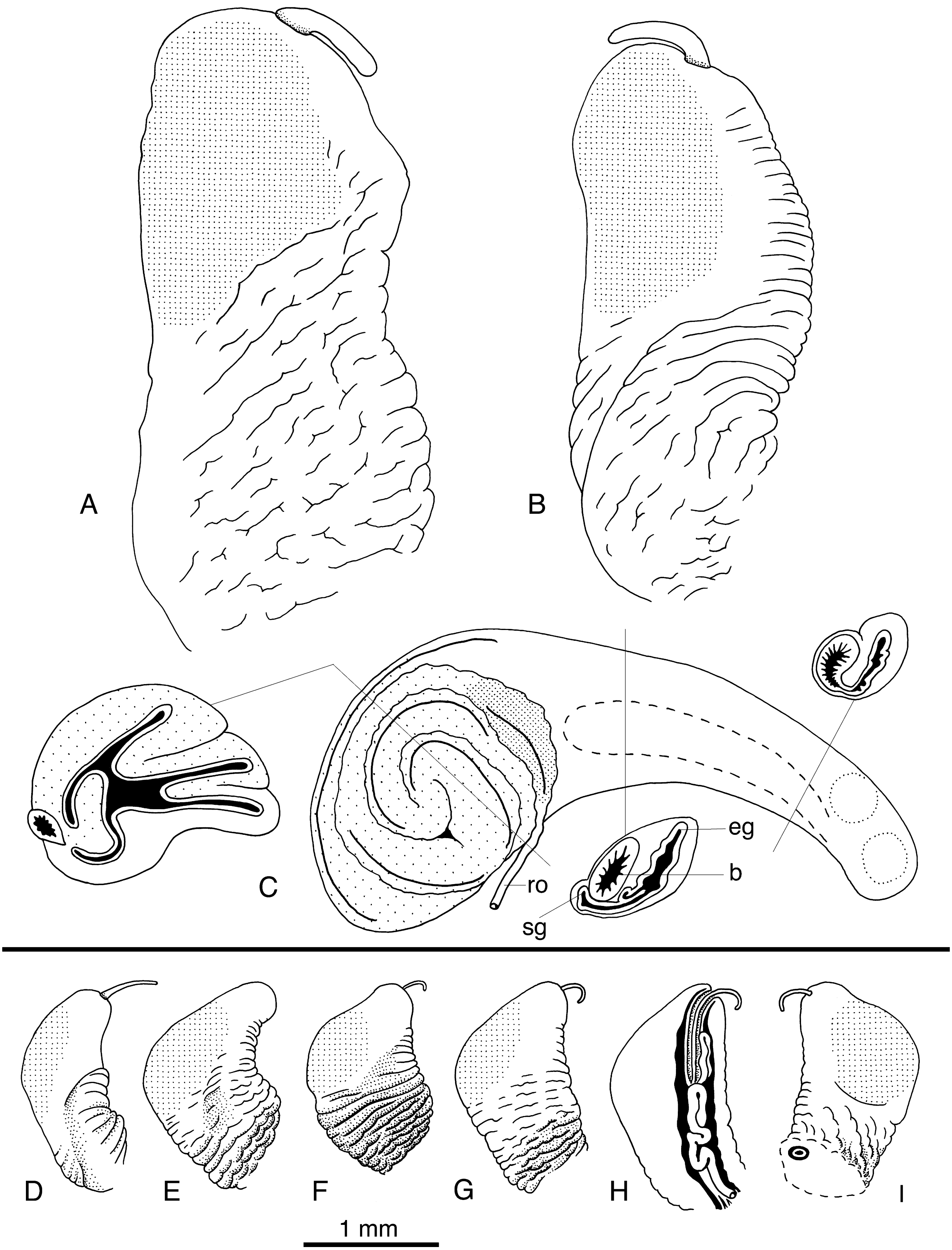
Etymology: Latin *cingulatus*, girdled, in reference to sculpture of base.

Diagnosis: Shell globular; one rib on base; pseudumbilicus narrow, perforated; surface with satin sheen, microstriae weak or absent. Operculum weakly calcified, no internal ridge. Penis with distal glandular pad, slender filament. Western Karnataka State.

Shell (Figs 4G, 11Q–U): Shell H 3.5–6.7 mm. Shape (Table 1) globular; whorls rounded; a weak rib close to suture outlines the flattened sutural area, but rib becomes obsolete on largest shells; suture impressed; peripheral angle absent; apex eroded; base slightly swollen, with thick rib at one-third radius. Columella narrow, wider at base. Pseudumbilicus narrow, 0.2–0.6 mm, perforated. Surface with satin sheen; spiral striae indistinct or absent, weakly present on base (Fig. 4G). Colour: reddish brown, three indistinct darker brown bands at suture, above periphery and at middle of base; aperture and columella purple-brown, with bands showing through.

Animal: Head and tentacles dark grey to black, tip of snout paler; body and sides of foot black. Gills: up to 35 leaflets; black. Operculum (Table 1; Fig. 5O, P): opercular ratio 0.334–0.472; weakly calcified, concave, no internal ridge. Penis (Fig. 14D–I): base lightly pigmented, wrinkled, solid, with large glandular pad on left of reverse side; invagination about half length of base in ethanol-fixed specimens; filament slender, protruding in ethanol-fixed specimens. Pallial oviduct: as for genus.

Figure 14. Anatomy of *Cremnoconchus agumbensis* (A–C) and *C. cingulatus* (D–I), all to same magnification. A, B, D–I, penes (all fixed in ethanol); G–I are abaxial, sectioned and adaxial views of same penis. C, pallial oviduct, with transverse sections in three positions. A–C, Agumbe, Udupi Dist., Karnataka (ZSI/WGRS; shell H: A = 9.5 mm; B = 8.8 mm; C = 9.1 mm). D–I, Hulikal Ghat, Udupi Dist., Karnataka (ZSI/WGRS; shell H: D = 3.5 mm; E = 4.6 mm; F = 3.7 mm; G–I = 4.4 mm). Shading conventions as in Figure 6.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Radula (Fig. 13E, F): Relative radula length 1.93–2.09. Rachidian: length/width 1.10–1.13; 5 cusps (+ 1 outer denticle on either side). Lateral: 5 cusps (sometimes + 1 inner denticle). Inner marginal: 5 cusps. Outer marginal: 4–5 cusps. Major cusp of each of 5 central teeth triangular with rounded and slightly papillose tip; other cusps pointed.

Range (Fig. 8): Western Karnataka State, Hulikal Ghat (95 km north-northeast of Mangalore). Records (Supporting Table S1): Karnataka State: Hulikal Ghat, Udupi District (ZSI/WGRS/IR.INV-2316, 2317, 2318, 2319).

Habitat and ecology: In rushing stream on rock face and sides of boulders, in fast-flowing water and spray, partly shaded by trees (Fig. 2C). Altitude 475 m.

Remarks: The conspicuous rib on the base, narrow but deep pseudumbilicus, and concave, weakly calcified operculum are the distinguishing features of the shell of this species. Except for the basal rib, these characters resemble *C. globulus*, but their respective penes are diagnostic (Figs 12H–L, 14D–I). Characters of the *Cremnoconchus* species of Karnataka are summarized in Table 4.

There appears to be sexual dimorphism: shells of males are smaller (males: mean ± sample SD = 3.840 ± 0.619 mm, $N = 4$; females: 5.575 ± 0.697 mm, $N = 12$) and the aperture is slightly enlarged.

At Hulikal Ghat it was found together with *C. dwarakii* and the two occupied different microhabitats. *Cremnoconchus cingulatus* occurred on rocks in rushing water, while *C. dwarakii* was found on mossy rocks dampened only by spray.

CREMNOCONCHUS CASTANEA SP. NOV.
(FIGS 4M, 5Q, R, 11V–AA, 13G, H, 15A–D)

Types: Holotype ZSI/WGRS/IR.INV-2321 (Fig. 11W, X); 1 paratype ZSI/WGRS/IR.INV-2320 (Fig. 11V); Belkal Thirtha Falls, near Kollur, Udupi Dist., Karnataka, India (13.842°N 74.897°E).

Etymology: Latin *castanea*, a chestnut, in reference to shell colour, used as a noun in apposition.

Diagnosis: Shell turbinate; ribs absent; pseudumbilicus wide, perforated; surface with indistinct or strong microstriae. Operculum calcified, with internal ridge. Penis large, with distal glandular pad, slender filament. Western Karnataka State.

Shell (Figs 4M; 11V–AA): Shell H 4.7–9.4 mm. Shape turbinate; whorls slightly angled at shoulder and periphery; ribs absent; suture impressed; apex eroded; base slightly swollen. Columella narrow. Pseudumbilicus broad, 0.5–1.0 mm, with sharply angled margin, perforated. Surface dull or with satin sheen; indistinct or strong, coarse microstriae cover surface (Fig. 4M). Diameter of first whorl 0.32–0.53 mm ($N = 2$). Colour: orange-brown to chestnut brown, darker on spire and with indistinct darker band at suture; aperture pale brown, columella pinkish-brown to white.

Animal: Head, tentacles, sides of foot, and body pale grey to black. Gills: unpigmented. Operculum (Table 1; Fig. 5Q–R): opercular ratio 0.341–0.450; well calcified, flat, with internal ridge. Penis (Fig. 15A–D): relatively large, unpigmented; base wrinkled, elongate, solid, with large triangular glandular pad on reverse side; invagination about half length of base in ethanol-fixed specimens; filament slender, protruding in ethanol-fixed specimens. Pallial oviduct: as for genus.

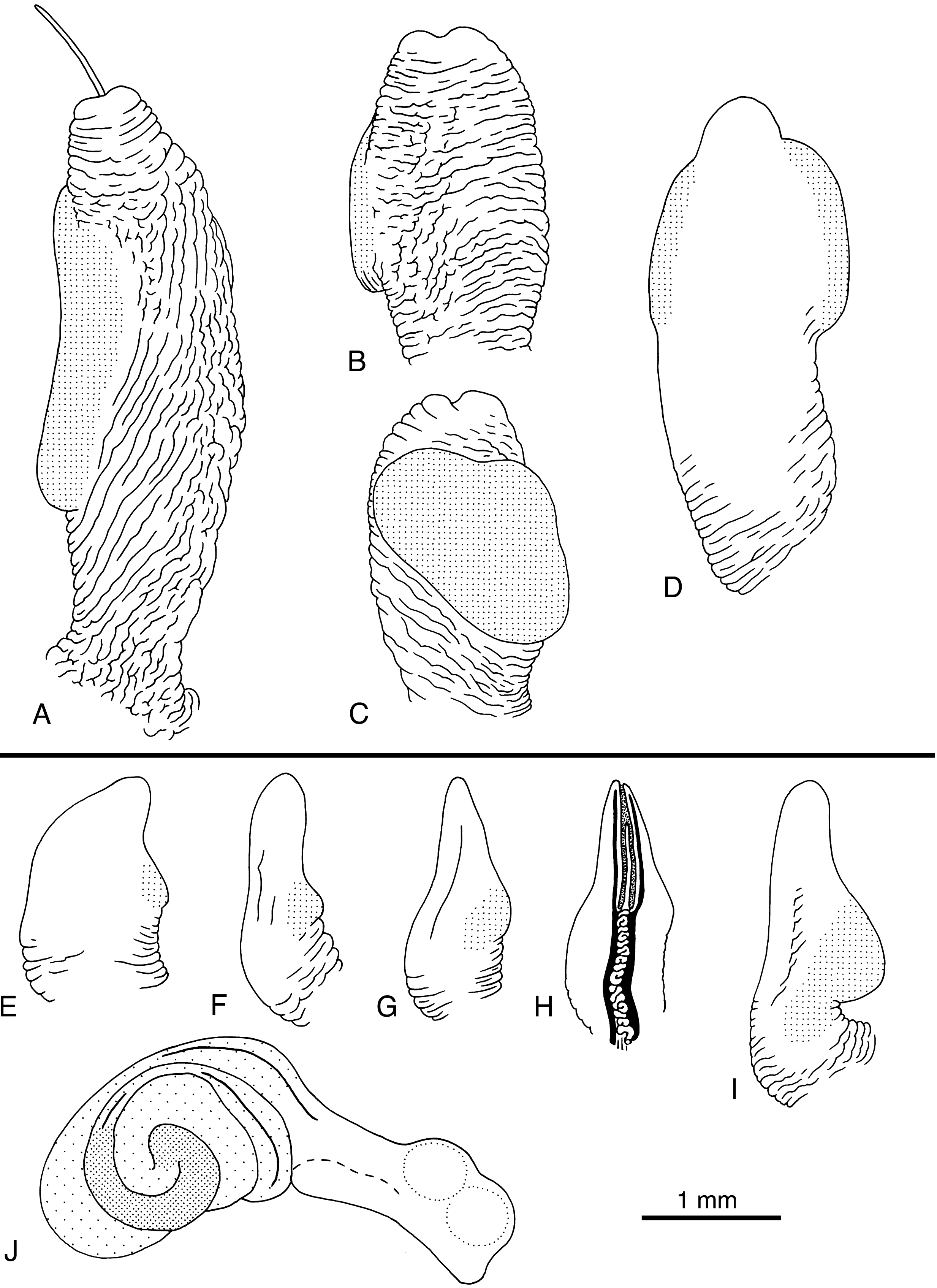
Radula (Fig. 13G, H): Relative radula length 2.37–2.59. Rachidian: length/width 1.08–1.26 (–1.64); 5 cusps (+ 1 outer denticle on either side). Lateral: 5 cusps (+ 1 inner denticle). Inner marginal: 5 cusps (+ 1 inner denticle). Outer marginal: 4–5 cusps. Major cusp of each of 5 central teeth leaf-shaped with pointed or slightly papillose tip; other cusps pointed.

Range (Fig. 8): Western Karnataka State, near Kollur (110 km north of Mangalore). Records (Supporting Table S1): Karnataka State: Belkal Thirtha Falls (ZSI/WGRS/IR.INV-2320, 2321); Arasinagundi Falls (BMNH 20120032).

Habitat and ecology: Spray zone of strong waterfalls. Large groups found aestivating in crevices during summer at Arasinagundi Falls. Altitude 373–384 m.

Remarks: Four species (*C. castanea*, *C. cingulatus*, *C. globulus*, *C. hanumani*) from Karnataka show similarities in their turbinate to globular shells

Figure 15. Anatomy of *Cremnoconchus castanea* (A–D) and *C. dwarakii* (E–J), all to same magnification. A–D, E–I, penes (A, live, relaxed; B, C, live, contracted; D–I, fixed in ethanol); B, C, are abaxial and adaxial views of same penis; G, H, are abaxial and sectioned views of same penis. J, pallial oviduct. A–C, Arasinagundi Falls, Udupi Dist., Karnataka (BMNH 20120034; shell H: A = 7.6 mm; B, C = 4.7 mm). D, Belkal Thirtha Falls, Udupi Dist., Karnataka (ZSI/WGRS; shell H = 7.0 mm). E–J, Hulikal Ghat, Udupi Dist., Karnataka (ZSI/WGRS; shell H: E = 6.4 mm; F = 6.2 mm; G, H = 6.1 mm; I = 6.9 mm; J = 6.9 mm). Shading conventions as in Figure 6.


A
B
C
D
E
F
G
H
I
J
1 mm

without ribs on their upper surface. Details of the relative size of the pseudumbilicus and degree of calcification of the operculum can aid discrimination, but penial shape is most useful (Table 4). Of these four, only *C. castanea* is known to develop strong, coarse microstriae, but these can sometimes be indistinct. The combination of large umbilicus and strong microstriae is similar to some examples of *C. canaliculatus* from Maharashtra (Fig. 9AA–EE), but that species has a basal drum-shaped gland on the penis (Fig. 10I–N).

An additional unlocalized sample (ZSI/WGRS/IR.INV-2322) could belong to this species. The shells (Fig. 11Z, AA) differ in that the pseudumbilicus, while perforated, is narrower than in the shells described above (0.3–0.5 mm in shells with H = 4.3–5.6 mm; Fig. 11V–Y) and has a rounded (not sharp) edge. Shell and operculum are otherwise similar. Only a single penis was seen and this was similar to those described.

CREMNOCONCHUS DWARAKII SP. NOV.

(FIGS 4A, 5C, D, 11BB–EE, 15E–J, 16A, B, F)

Cremnoconchus syhadrensis – Williams *et al*., 2003: 63 (not Blanford, 1863).

Cremnoconchus dwaraki Madhyastha, 2008: *The Hindu* 29 June 2008 (as *Cremenoconchus*; *nomen nudum*).

Taxonomic history: This species was misidentified by Williams *et al*. (2003) as *C. syhadrensis*, because the two share strong spiral ribs on the shell.

Types: Holotype ZSI/WGRS/IR.INV-2323 (Fig. 11BB, CC); four paratypes ZSI/WGRS/IR.INV-2324, 2325 (Fig. 11DD); Hulikal Ghat, Udupi District, Karnataka, India (13.71742°N, 74.99445°E).

Etymology: Named after Acharya Dwarakanth, of the Indian Naturalist Club. He was known for his knowledge of animals and plants of Karnataka and, as secretary of the club, supported many research activities and encouraged the younger generation in birding and nature conservation. The name *dwarakii* is derived from that of the legendary city of Dwaraka in Western Gujarat, the dwelling place of Lord Krishna and the capital of the Yadus who ruled the Anarta Kingdom during the Mahabaratha period.

Diagnosis: Shell turbinate; 8–11 ribs (including base); pseudumbilicus narrow, perforated; surface dull, with fine strong microstriae. Operculum weakly calcified, no internal ridge. Penis with slight glandular flange, slender filament. Western Karnataka State. COI: GenBank AJ488605.

Shell (Figs 4A, 11BB–EE): Shell H 6.0–9.2 mm. Shape (Table 1) turbinate; whorls slightly angled at shoulder; suture impressed; apex slightly eroded; base slightly swollen. Columella narrow. Pseudumbilicus narrow, 0.2–0.7 mm, with sharply angled margin, perforated. Spire whorls with three strong ribs. Last whorl with 8–11 strong ribs, of which largest are sutural rib (outlining flattened sutural ramp, which may also bear an additional riblet) and rib close to pseudumbilicus. Surface dull, covered by fine, strong microstriae, intersecting with fine growth lines to give minutely lamellose effect (Fig. 4A). Protoconch (Fig. 16F) 1.4 whorls; diameter 0.70 mm; diameter of first whorl 0.45 mm ($N = 1$). Colour: usually orange-brown, darker brown on spire and with indistinct darker band at suture and outlining pseudumbilicus; occasionally all rib interspaces are dark brown, but fading on last whorl; aperture yellow-brown, columella and pseudumbilicus purple-brown, exterior bands showing through.

Animal: Head, tentacles, sides of foot, and body dark grey to black; tip of snout pale. Gills: up to 36 leaflets; grey to black. Operculum (Table 1; Fig. 5C, D): opercular ratio 0.385–0.511; weakly calcified, no internal ridge, slightly concave. Penis (Fig. 15E–I): unpigmented; base wrinkled, tapering to rounded tip; with triangular glandular pad on reverse side, slightly projecting anterolaterally; invagination about half length of base in ethanol-fixed specimens; filament slender, not protruding in ethanol-fixed specimens. Pallial oviduct (Fig. 15J): as for genus. One pallial oviduct contained two eggs 0.40 mm in diameter (ethanol fixed), one at two-cell embryo stage.

Radula (Fig. 16A, B): Relative radula length 0.82–1.25. Rachidian: length/width 1.23; 5 cusps (+ 1 outer denticle on either side). Lateral: 5 cusps (+ 1 inner denticle). Inner marginal: 6 cusps. Outer marginal: 3–5 cusps. Major cusp of each of 5 central teeth leaf-shaped with narrowly rounded or slightly papillose tip; other cusps pointed.

Range (Fig. 8): Western Karnataka State, Hulikal Ghat (95 km north-northeast of Mangalore). Records (Supporting Table S1): Karnataka State: Hulikal Ghat, Udupi District (ZSI/WGRS/IR.INV-2323, 2324, 2325; BMNH 20120036).

Habitat and ecology: On mossy rocks dampened by spray from rushing stream; shaded by trees (Fig. 2B). Altitude 475 m.

Remarks: This species is distinguished from all others in Karnataka by the strong ribs of the shell (Table 4).

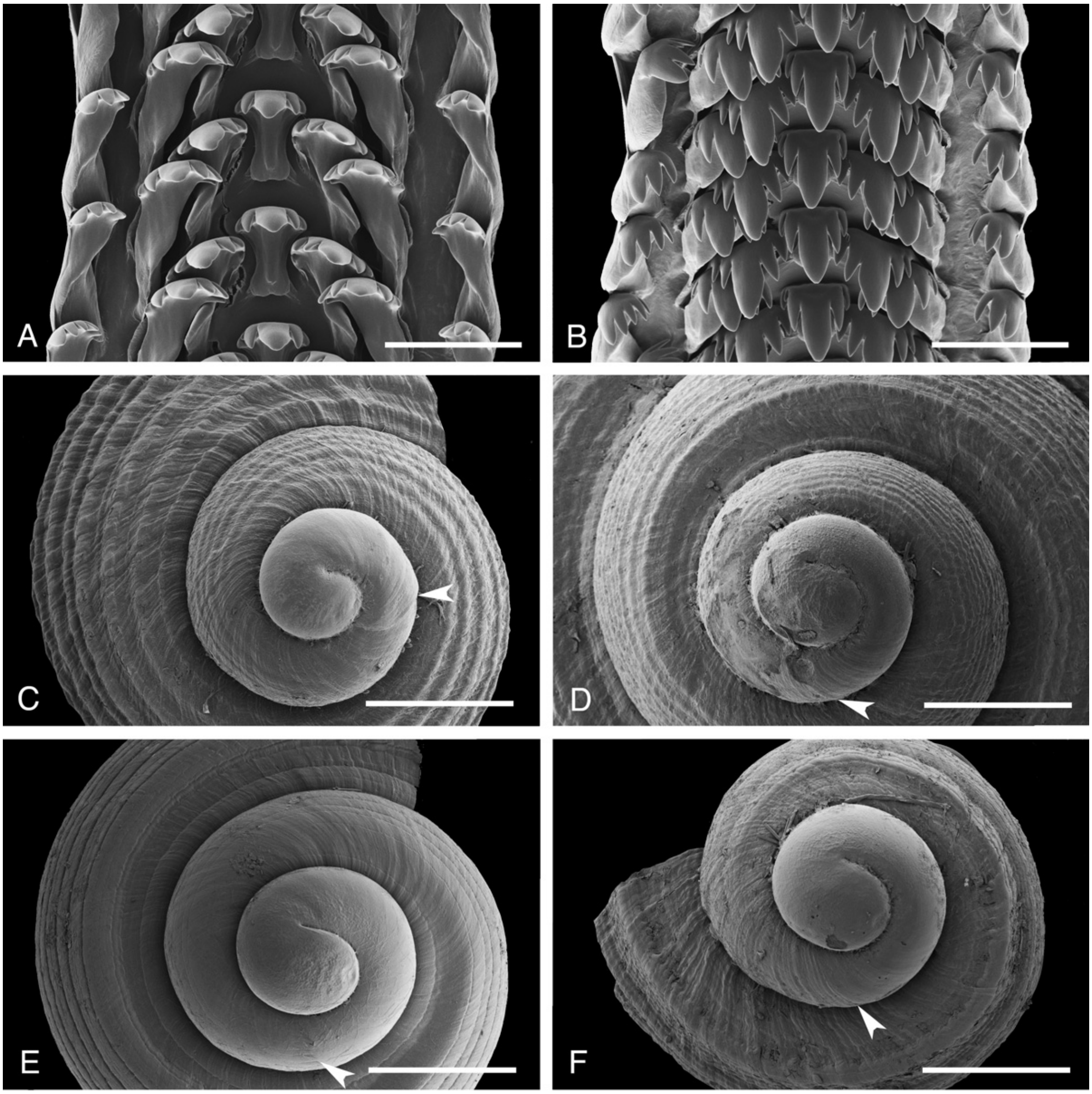


Figure 16. Radula (A, B) and protoconchs (C–F) of *Cremnoconchus* species. A, B, *C. dwarakii* (two views of radula, flat and at 45°), Hulikal Ghat, Udupi Dist., Karnataka (shell H = 6.4 mm). C, *C. syhadrensis*, Matheran, Raigad Dist., Maharashtra. D, *C. canaliculatus*, 10 km west of Mahabaleshwar, Raigad Dist., Maharashtra. E, *C. agumbensis*, Agumbe, Udupi Dist., Karnataka. F, *C. dwarakii*, Hulikal Ghat, Udupi Dist., Karnataka. Scale bars A, B = 50 μm; C–F = 0.5 mm. White arrowhead marks junction of protoconch and teleoconch.

These create a superficial resemblance to ribbed forms of *C. syhadrensis* from Maharashtra (Fig. 3), but in those the ribs are restricted to the upper surface (i.e. above the periphery), the pseudumbilicus is usually wide and the columella is broad; there are also differences in the penes of these two species (Table 3, Fig. 6A, B, D–G, 15E–I).

At Hulikal Ghat this species was found with *C. cingulatus* (see Remarks on that species).

DISCUSSION

TAXONOMY

Previous systematic accounts of *Cremnoconchus* have recognized two (Blanford, 1870; Stoliczka, 1871; Reid, 1989) or three species (Subba Rao, 1989; Ramakrishna & Dey, 2007). Here we have presented the first taxonomic study of the genus since the 19th century, revealing a radiation of nine species, six of them undescribed. Only the most well-studied species, *C. syhadrensis* (Blanford, 1863; Troschel, 1867; Stoliczka, 1871; Annandale & Prashad, 1919; Prashad, 1925; Linke, 1935; Reid, 1989), is retained in its traditional usage and even here the range of morphological variation is greater than previously recognized.

Discrimination of these species is based on clear morphological discontinuities. The most useful taxonomic character is the form of the penis, which is diagnostic for each species; this has long been used successfully in the systematic study of marine Littorinidae, because it is apparently involved in sexual selection or recognition (e.g. Reid, 1986a, 1996). Correlated with penial differences are characters of the shell, by which all species can be recognized. Overall shell shape and development of spiral ribs are shown to be more variable than previously understood, again as in other littorinids (e.g. Reid, 1986a, 1996, 2007). Important features of the shell for identification are the development of spiral microstriae and size of the pseudumbilicus, and also the coiling and degree of calcification of the operculum.

The identity of these taxa as phylogenetic species (i.e. reciprocally monophyletic units) has yet to be tested with molecular data. Nevertheless, the finding of up to three species sympatrically (in the same stream; Supporting Table S1) supports the status of at least some of them as biological (i.e. non-interbreeding) species.

Evolutionary origin

Remarkably, in view of its freshwater habitat, *Cremnoconchus* has been classified in the largely marine family Littorinidae since the first brief anatomical account of one of its species (Blanford, 1863). In fact Blanford's concept of the family was broader than that now current, presumably following that of Gray (1847, 1857) and of Adams & Adams (1854), because it included some genera now classified in Cerithioidea and Rissooidea. Blanford (1863: 184–186) assigned *Cremnoconchus* to Littorinidae largely on the basis of its shell and operculum, and observed that the 'amphibious habits' of the animal, short foot and thick periostracum 'induce me to place it in the vicinity of *Lithoglyphus*' (now Rissooidea: Lithoglyphidae). A closer connection to Littorinidae was proposed by Stoliczka (1871), who classified *Cremnoconchus* as a subgenus of *Littorina*. In a formal phylogenetic analysis of the genera of Littorinidae, Reid (1989) identified the spiral form of the pallial oviduct as the unique and unreversed synapomorphy of the family, which is considered a strong character supporting its monophyly. However, this has yet to be tested with molecular data.

The phylogenetic analysis of morphological characters indicated placement in the subfamily Lacuninae and supported the sister relationship of *Cremnoconchus* with the two marine genera *Risellopsis* and *Bembicium* (based on their shared simple crossed-lamellar shell microstructure, salivary glands anterior to nerve ring, and short pleuro-suboesophageal connective; Reid, 1989). Since these marine genera are restricted to New Zealand and Australia, respectively, this relationship suggested the possibility of an ancestral distribution of all three in Gondwana. Under this scenario *Cremnoconchus* was carried to its present position on the Indian plate, following the breakup of the southern continent during the Cretaceous and subsequent northward drift of India to reach Asia in the Eocene. However, the morphological evidence did not include any unique, unreversed synapomorphies, and limited molecular evidence has not supported (or comprehensively rejected) the phylogenetic relationship between *Cremnoconchus* and *Bembicium* (Williams *et al*., 2003; Reid *et al*., 2012). A hypothesis of Gondwanan origin has been proposed for the pachychilid snail genus *Paracrostoma*, endemic to southern India, but was rejected by molecular data (Köhler & Glaubrecht, 2007); a similar test is required for *Cremnoconchus*. So far, the weak evidence for the phylogenetic relationships of *Cremnoconchus* is consistent merely with an ancient divergence from (or within) the Littorinidae. The available molecular evidence unequivocally excludes *Cremnoconchus* from the subfamily Littorininae, so that there is no possibility of a recent derivation from marine littorinines such as those that inhabit the present coastline of India, as proposed by early authors (Blanford, 1863; Stoliczka, 1871; Prashad, 1925). The age and relationships of this genus require study with suitable molecular markers. Among the few other marine gastropod groups with a small number of freshwater members (e.g. Buccinidae, Nassariidae, Marginellidae, Lottiidae; see Introduction) the phylogeny and age of the freshwater members is generally unknown, but the fact that the freshwater species are considered distinct at generic level suggests that their origin has not been recent. For the Acochlidia the age of the limnic radiation has been estimated as Palaeogene (Jörger *et al*., 2010).

Some of the 'freshwater' members of largely marine gastropod groups could more accurately be described as tolerant of very low, or seasonally fluctuating, salinities. These include members of the Nassariidae (Cernohorsky, 1984; Kantor & Kilburn, 2001) and Lottiidae (Lindberg, 1990). Others, such as members of the Buccinidae (Brandt, 1974), Marginellidae (Coomans & Clover, 1972), and Acochlidiidae (Brenzinger *et al*., 2011) are found in rivers and streams, but in their lower reaches. Only the acochlidiid *Tantulum*

(Neusser & Schrödl, 2007) and *Cremnoconchus* are restricted to montane habitats. Another common feature of these freshwater members is that almost all (the exception is the Caribbean *Tantulum*) are found in the tropical Indo-Pacific region. In part this could simply reflect the fact that this area includes the highest diversity of marine species. Commenting on the relatively frequent invasion of freshwater by marine groups in South and South-East Asia, Vermeij & Wesselingh (2002) noted that not only is the mangrove habitat (the likely source of freshwater invaders) most diverse in this region, but that in addition the freshwater environments are seasonally stable, and that predation pressure is intense in the Indo-Pacific region. All these factors may have made the difficult transition from marine to freshwater realms easier to accomplish (or more strongly driven by selection) here than elsewhere.

At all the localities where *Cremnoconchus* was collected during the present study, these were the only aquatic snails to be found, and were usually present in abundance (Fig. 2). Annandale (1919) mentioned that the succineid *Lithotis* also occurred in damp habitats adjacent to waterfalls at Khandala, but this is of more terrestrial than aquatic habit. At altitudes below those occupied by *Cremnoconchus* species (300–1400 m) they were replaced by species of Paludomidae and Ampullariidae. Whether this reflects competitive exclusion or a specialized habitat requirement is unknown.

Adaptation to freshwater habitat

Since the freshwater habitat of *Cremnoconchus* is unique among Littorinidae, it is reasonable (assuming a marine ancestry of littorinids) to interpret its unique morphological, behavioural, or other attributes as possible adaptations to the freshwater environment.

The shells of *Cremnoconchus* species are remarkably similar to those of marine littorinids (e.g. *Lacuna*, *Littorina*, *Risellopsis*, *Tectarius*; Reid, 1989: pl. 1). The relatively thicker periostracum of *Cremnoconchus* is a likely adaptation in relation to shell dissolution and/or radulation by other snails in freshwater of low calcium content, and is seen in most freshwater snails. The shells of some of the *Cremnoconchus* species are relatively thick in comparison with those of freshwater pulmonates, although this is not unusual among freshwater caenogastropods. In *C. syhadrensis* and *C. dwarakii* the shell appears to be strengthened by the spiral ribs; at least in the former, the rate of sublethal damage (measured by scarring frequency) is low (9.6%), so it is unclear whether crushing predation could have been a selective force.

The calcified operculum is almost unique among littorinids (Reid, 1989), the only other case being the aragonitic calcareous deposit on the outer surface of the operculum of *Tectarius niuensis* (Reid & Geller, 1997). Elsewhere in gastropods, where calcification is present it is likewise on the outer surface (e.g. Turbinidae and Naticidae; Checa & Jiménez-Jiménez, 1998) or on outer and inner sides of an organic layer (e.g. Neritidae; Sasaki, 2001). Calcification in between inner and outer organic layers, as found in *Cremnoconchus*, is highly unusual. The possible significance in relation to the freshwater habitat is unclear. While a thick operculum with a flexible edge may provide an effective seal during aestivation, marine littorinids from high shore levels survive long periods out of water with a purely proteinaceous operculum (Boss, 1974; Reid, 1989).

Despite the interest of the early naturalists in the 'pulmoniferous' character of *Cremnoconchus* and speculation about modification of the gills for air-breathing (Blanford, 1863; Stoliczka, 1871; Annandale, 1919; Prashad, 1925), the gill leaflets are no more reduced than in the marine littorinids from high-shore habitats (e.g. *Echinolittorina*, *Littoraria*, *Tectarius*; Reid, 1989). Evidently the moist, vascular mantle chamber with only small gill leaflets serves for respiration in air (Prashad, 1925). The hypobranchial gland is vestigial and therefore smaller than in marine littorinids from the upper shore (Reid, 1989). The radula is typical for the family (Reid, 1989).

The spawn of *Cremnoconchus* has not been seen but, judging from the few large eggs (0.40–0.49 mm diameter) found within the pallial oviduct, it is predicted that these are deposited singly or in small groups on the rock surface. Essentially similar spawn occurs in the marine members of the basal littorinid subfamilies Laevilitorininae and Lacuninae, and the eggs of the non-planktotrophic species are of similarly large size (Picken, 1979; Reid, 1989). Suppression of an ancestral planktonic larval stage is a universal feature of freshwater gastropods, but should not therefore be interpreted as an adaptation to this particular environment. A wide range of selective regimes can lead to loss of planktonic stages in purely marine lineages. For example, if loss of planktotrophy occurred in the marine ancestors of *Cremnoconchus* as an adaptive response to cold water, the lineage may have been preadapted to freshwater existence (Reid, 1989), but this suggestion requires testing in a phylogenetic context. Viviparity has evolved in several lineages of freshwater cerithioideans (Köhler *et al*., 2004) and is recorded in a few marine littorinid species, but there is no evidence of this in *Cremnoconchus*.

The streams occupied by *Cremnoconchus* are often seasonal, fed by monsoonal rainfall. At least one species, *C. syhadrensis*, has the ability to aestivate during dry periods, as observed by early authors (Blanford, 1863; Annandale, 1919; Hora, 1926, 1928). Clusters of snails about to enter aestivation were found on shaded cliffs at Khandala (Fig. 2G). The behavioural (and presumably physiological) traits associated with aestivation are clearly functional in ephemeral freshwater environments, and this ability is found in many freshwater molluscs (Boss, 1974). If *Cremnoconchus* is correctly classified in the subfamily Lacuninae, and because no other lacunines are known to aestivate, then this trait is arguably an adaptation to the freshwater environment. Nevertheless, in the Littorininae, which all occupy the upper intertidal zone, most species can aestivate to some degree, sometimes surviving without moisture for over a year (Boss, 1974).

Diversification

A resolved phylogeny and knowledge of geographical range are prerequisites for hypotheses about speciation and evolutionary radiation. Unfortunately a molecular phylogeny of *Cremnoconchus* is not yet available, so that suggestions about speciation patterns remain highly speculative. The apparent restriction of the group to two disjunct areas (in Karnataka and Maharashtra states, separated by over 500 km; Fig. 8) suggests a possible division into two clades. However, there is no morphological support for this suggestion. Indeed, the only reasonable inference about relationships from the morphological data presented here is that *C. conicus* and *C. canaliculatus* (both in the northern group) are sister species. This is based on the interpretation of the drum-shaped glandular structure at the base of the penis as a synapomorphy of these two taxa; their shells can also be closely similar. The range of intraspecific variation in shell characters is such that no likely synapomorphies can be suggested. Since penial form is diagnostic, it could be significant that a robust filament is shared by *C. syhadrensis*, *C. hanumani* and *C. agumbensis*, while in the remaining six species the filament is slender; this division does not correspond with the geographical one.

Whether the disjunct distribution of *Cremnoconchus* in the northern and central Western Ghats is a true representation of its distribution, or an artefact of collecting effort or accessibility, is not yet clear. In Karnataka, in the southern area of occurrence (Fig. 8), the six endemic species are each recorded from only a single locality or from two localities from 1 km (*C. globulus*) to 5 km (*C. hanumani*) or 8 km (*C. castanea*) apart. In this area there are two examples of sympatry (involving two different species pairs) and the maximum linear distance between the localities of different species is only 80 km (Fig. 8). The seven localities in this area are arranged in linear fashion along the escarpment of the Western Ghats. This pattern may well change as more waterfalls are investigated in this poorly accessible region. It does, nevertheless, suggest a highly localized radiation in which speciation has followed geographical isolation in separate drainage systems, a not uncommon pattern for riverine species (Glaubrecht, 2011). If this is so, some limited dispersal must have occurred to account for the two sympatric occurrences. A possible ecological dimension to speciation has been suggested by other studies of radiations of freshwater gastropods (review by Glaubrecht, 2011); either this, or competition following range expansion, could explain the microhabitat difference between the two species at one locality (*C. cingulatus* and *C. dwarakii* at Hulikal Ghat).

In the northern area, in Maharashtra, the pattern is somewhat different. About 17 localities have been recorded, covering a linear distance of about 220 km. There are five cases of sympatry (one involving three species). The species are far more widespread, extending over 95 km (*C. conicus*), 100 km (*C. canaliculatus*), and 185 km (*C. syhadrensis*). This may reflect enhanced dispersal or dispersal over a longer period, or perhaps merely the longer history of collecting in this area.

Conservation

The genus *Cremnoconchus* should be recognized as an iconic component of the fauna of the Western Ghats hotspot. It is not only endemic to India, but entirely restricted to the Western Ghats. On a global scale it is a unique freshwater radiation of the otherwise marine family Littorinidae, and one of only five localized radiations of predominantly marine caenogastropod families. It is found only in seasonal streams at altitudes between 300 and 1400 m along the escarpment of the Western Ghats. This highly restricted habitat makes the nine known species vulnerable to the threats of pollution, construction, mining and tourism (Aravind *et al*., 2011). These pressures are most severe in Maharashtra, close to the cities of Mumbai and Pune. Development is still limited in western Karnataka, but in this area the known species appear to be far more localized, increasing their vulnerability. As an example of this vulnerability, a stream flowing through the tourist town of Mahabaleshwar appears from a distance to provide suitable habitat for *Cremnoconchus* (Fig. 2D), and was possibly the type locality of *Anculotus carinatus* (= *C. conicus*), yet is now polluted by sewage and effluent, and contains no *Cremnoconchus*. It is desirable that the distributions of the known *Cremnocon-*

chus species be investigated in more detail and further study may well reveal additional members of this radiation. Meanwhile, it is suggested that all the nine known species are threatened and therefore deserving of protection.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Localities from which *Cremnoconchus* species have been recorded (in literature, as represented by museum collections, and personal collection by authors). Where historic collections are from sites revisited by the authors, the former are not listed (e.g. Matheran, Khandala, Mahabaleshwar). Interpretation of historic records and labels is not always straightforward and is justified here. Dates of collection of historic material are not known, but the material in the Blanford Collection must predate his publications (Blanford 1863, 1870, 1881) and the Evezard Collection was made in the late nineteenth century. Localities arranged by latitude from north to south.