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Research article

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Review of *Coelostoma* of the Indian subcontinent (Coleoptera: Hydrophilidae) Part 1: *Coelostoma* s. str. and *Holocoelostoma*

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Abstract. Species of the genus *Coelostoma* Brullé, 1935 belonging to the subgenera *Coelostoma* s. str. and *Holocoelostoma* Mouchamps, 1958 from the Indian subcontinent are revised. Six species of *Coelostoma* s. str. and two species of *Holocoelostoma* are recognized, of which two are described as new: *C. (Coelostoma) lyratum* sp. nov. (India: Maharashtra) and *C. (Coelostoma) nostocinum* sp. nov. (India: Maharashtra, Goa, Karnataka, Kerala). *Coelostoma (Coelostoma) fallaciosum* Orchymont, 1936 and *C. (Coelostoma) vividum* Orchymont, 1936 were recorded for the first time from India and Bangladesh, respectively. Lectotypes are designated for *C. aeneolum* Régimbart, 1903 and *Hydrobius stultus* Walker, 1858. The previously confusing situation with *Coelostoma (Holocoelostoma) stultum* (Walker, 1858) and *C. (Holocoelostoma) bhutanicum* Jayaswal, 1972 is clarified based on new material of both species from India. *Coelostoma sulcatum* Pu, 1963 from China is removed from the synonymy of *C. stultum* and considered as a likely synonym of *C. bhutanicum*, a status which needs to be confirmed by a detailed study of type specimens. All species are (re)described and illustrated. Diagnosis of the subgenera of *Coelostoma* are modified in order to accommodate the species of the Indian subcontinent, resulting in narrowing down the concept of *Coelostoma* s. str. and widening the concept of *Lachnocoelostoma* Mouchamps, 1958.

Keywords. Hydrophiloidea, Oriental Region, new species, lectotype designation, biodiversity shortfalls.

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Introduction

Hydrophilidae Latreille, 1802 is a major group of water beetles with about 3000 described species classified in 6 subfamilies and 12 tribes (Short & Fikáček 2013). This group is ancestrally aquatic, but one of its lineages colonized terrestrial habitats ca 175 million years ago (Bloom *et al.* 2014). This lineage gave rise to a diverse fauna currently classified in the subfamilies Sphaeridiinae Latreille, 1802 and Cylominae Zaitzev, 1908 (Toussaint & Short 2018). A few lineages of these secondarily terrestrial groups returned to water. This is the case with *Cylomissus* Broun, 1903 and *Anticura* Spangler, 1979 (Minoshima *et al.* 2015) and larvae of the otherwise flower inhabiting *Rygmodes* White, 1846 (Minoshima *et al.* 2018) in Cylominae, a few lineages of the genus *Cercyon* Leach, 1817 (Arriaga-Varela, unpubl. data) and the whole genus *Coelostoma* Brullé, 1835 in Sphaeridiinae.

The coelostomatine genus *Coelostoma* is mainly distributed in the Afrotropical and Oriental regions, with a few species also present in the Palearctic and Australian regions (Hansen 1999). About 120 species have been described in this genus, with the highest known diversity occurring in China (Jia *et al.* 2014, 2017, 2019). All known species with available biological data are aquatic, occurring in habitats ranging from shallow ponds to horizontal and vertical wet cliffs (Jia *et al.* 2019).

The genus is characterised by broadly oval and dorsally convex body, dark brown to black colour, loosely arranged antennal club, prosternum bulging medially and dentiform anteriorly, mesoventrite with an elevated arrowhead-shaped structure in the middle, metaventrite with strongly elevated median portion, anteriorly projecting between mesocoxae and abutting mesoventral elevation, the first metatarsomere longer than second tarsomere, elytra with sutural stria and usually without serial punctures (with few exceptions), and the first abdominal ventrite not carinate medially (with a few exceptions; Hansen 1991; Jia *et al.* 2014).

The Asian fauna of *Coelostoma* is rather species-rich, but the lack of modern revisions prevents reliable identification. However, the fauna was recently revised in China (Jia *et al.* 2014, 2017, 2019), Taiwan (Liu *et al.* 2020) and Japan (Hayashi 2008). These studies provided good quality illustrations of genital characters crucial for the species identification and recognized many previously undescribed species. Other parts of tropical and subtropical Asia remain unrevised, including the Indian subcontinent, a region characterized by high species diversity and endemism (Myers *et al.* 2000; Mittermeier *et al.* 2005). So far, sixteen species of *Coelostoma* have been recorded from the Indian subcontinent (Walker 1858; Orchymont 1923a, 1923b, 1928, 1936; Mouchamps 1958; Jayaswal 1972; Hebauer 2000, 2002), but a detailed taxonomic revision is wanting, and the status of many of these species remains unclear (Linnean shortfall; Hortal *et al.* 2015). Thus, the aim of this revision is to overcome Linnean and Wallacean shortfalls (as defined by Hortal *et al.* 2015) by providing basic information about the diversity and distribution of species and to provide taxonomic keys, descriptions and illustrations allowing an easy identification of *Coelostoma* species.

For practical purposes, we divided the revision into two parts. Here we present the revision of two subgenera: *Coelostoma* s. str. Brullé, 1835 and *Holocoelostoma* Mouchamps, 1958. The revision of the more diverse subgenus *Lachnocoelostoma* Mouchamps, 1958 from India will be presented later. Here, we describe two new species from India, provide new distribution records of all known species from the Indian subcontinent and illustrate the characters of all of them.

Material and methods

Study area

The Indian Peninsula is located north of the Equator including India, Pakistan, Sri Lanka, Nepal, Bhutan and Bangladesh (Fig. 1). This subcontinent is bounded by the geologically unstable Himalayan

Mountains in the north, because of which the region experiences tropical monsoon. Additionally, the subcontinent is lined by shoreline on western, eastern and southern sides. Diverse ecological conditions ranging from dry deserts, evergreen forests to temperate and alpine environments exist in the region. Furthermore, the Western and Eastern Ghats form the edges of the geologically stable Peninsular Plateau of the subcontinent, which was one of the parts of the ancient Gondwana. All these physical features contribute to gradients of interacting climatic conditions of precipitation, altitude and temperature on the subcontinent (Mani 1974).

Specimen examination

The genitalia were dissected from water-relaxed specimens and examined on temporary glycerine slides or in permanent mounts in Euparal, in both cases without a cover glass. Photographs of glycerine mounted genitalia were taken with a Canon D1100 digital camera attached to an Olympus BX41 compound microscope. Photographs of external morphology were taken using a Canon EOS 550D digital camera with an attached Canon MP-E65 mm f/2.8 1–5 × macro lens. We standardized

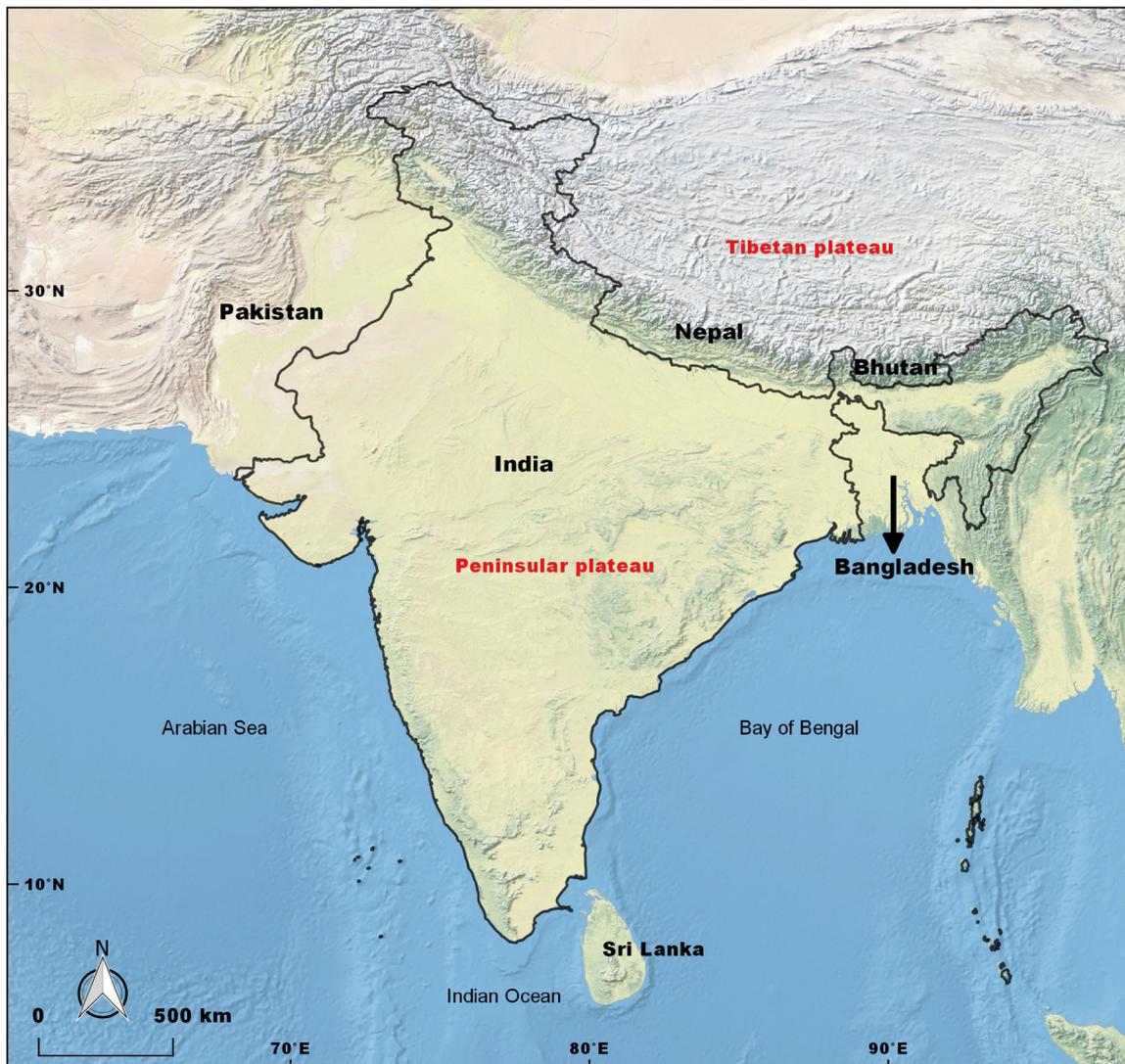


Fig. 1. Overview of the Indian subcontinent and its main geographic features.

the photographic documentation provided for each species to include principal characters important for the reliable identification of all Indian *Coelostoma* (including the subgenus *Lachnocoelostoma* not treated here). For this reason, the plates even include characters which seem invariable (e.g., dorsal punctation) but are crucial for diagnosing the species treated here from some Indian species of *Lachnocoelostoma*. Original unedited photographs are available in the Zenodo archive under <https://doi.org/10.5281/zenodo.3949349>. For details of the methods used, see Sheth *et al.* (2018) and Fikáček & Liu (2019). Geographical coordinates were obtained from GoogleMaps and GoogleEarth® in case they are not listed on the labels. Incorrect coordinates provided on labels were rectified, based on locality data interpreted from the label and additional data (e.g., altitude) was added in some cases; all these data that we added are placed in brackets. Maps were constructed in QGIS (ver. 2.18.5, <https://qgis.org/downloads/>).

Review of published data

We have reviewed the literature referring to the occurrence of *Coelostoma* species on the Indian subcontinent. These publications are listed in the synonymy section, and faunistic data from corresponding publications are summarized under Published records. Publications with records outside of the Indian subcontinent are not listed in these sections.

Depositories

Examined specimens ([Supplementary file SM.01](#)) are deposited in the following collections:

- BMNH = The Natural History Museum, London, UK
- IRSNB = Institute royal des Sciences naturelles, Brussels, Belgium
- IZCAS = Chinese Academy of Sciences, Institute of Zoology, Beijing, China
- MNHN = Muséum national d'histoire naturelle, Paris, France
- NCBS = National Centre for Biological Sciences, Bengaluru, India
- NHMW = Naturhistorisches Museum, Vienna, Austria
- NMPC = National Museum, Prague, Czech Republic
- SMNS = State Museum of Natural History, Stuttgart, Germany
- UASB = University of Agricultural Sciences, Bengaluru, India
- ZSI = Zoological Survey of India, Western Region, Pune, Maharashtra, India

Results

Taxonomy

- Order Coleoptera Linnaeus, 1758
- Superfamily Hydrophiloidea Latreille, 1802
- Family Hydrophilidae Latreille, 1802
- Subfamily Sphaeridiinae Latreille, 1802
- Tribe Coelostomatini Heyden, 1891
- Genus *Coelostoma* Brullé, 1835

Subgenera of *Coelostoma*

Mouchamps (1958) defined four subgenera of *Coelostoma* on the basis of the combination of three characters: (1) the pubescence on the mesofemora (with or without dense pubescence), (2) morphology of the abdominal apex (with or without stout setae) and (3) the morphology of the tarsal claws (simple or bifid, the latter in the subgenus *Hammacoelostoma* Mouchamps, 1958, not occurring in the Indian subcontinent). These characters have since then been successfully used to place all described species in

Table 1. Characters defining the subgenera of *Coelostoma* Brullé, 1935 as used in this study. Only the subgenera *Lachnocoelostoma* Mouchamps, 1958, *Coelostoma* s. str. and *Holocoelostoma* Mouchamps, 1958 occur in the Indian subcontinent.

Character	<i>Lachnocoelostoma</i>	<i>Coelostoma</i> s. str.	<i>Holocoelostoma</i>	<i>Hammacoelostoma</i>
Empodial setae	fine, hair-like	fine, hair-like	fine, hair-like	thick and strongly sclerotized (resembling an additional pair of massive spines between tarsal claws)
Mesofemur	with dense pubescence present on the whole surface or at least in the anterior part of the mesofemur (i.e., mesofemur can be largely bare in some species!)	completely without dense long pubescence, only with sparsely arranged short setae	completely without dense long pubescence, only with sparsely arranged short setae	with dense pubescence present on anterior two thirds
Abdominal ventrite I	with or without median carina	never with median carina	never with median carina	without median carina
Abdominal apex: stout setae	usually present, absent in few species	always absent	always present	absent or present
Abdominal apex: emargination	present or absent	always absent	present or absent	absent

subgenera (e.g., Hansen 1999). Characters (1) and (2), relevant for recognizing the subgenera occurring in India, were illustrated by Jia *et al.* (2014).

The study of the Indian *Coelostoma* revealed that the morphological diversity within the genus is much higher than expected, especially in the subgenus *Lachnocoelostoma*, with some species not fitting the combination of characters used by Mouchamps (1958). To deal with this problem, we are adapting the definition of the subgenera of *Coelostoma* in the way specified in Table 1, using five characters. The re-examination of *C. (Hammacoelostoma) afflatum* Knisch, 1922 revealed that the additional strongly sclerotized projections between the tarsal claws are in fact modified empodial setae, and not basal projections of the claws as suggested by Mouchamps (1958). Our concept narrows down the definition of *Coelostoma* s. str. and significantly widens the concept of *Lachnocoelostoma*. Reasons for that will be demonstrated in detail in the review of Indian *Lachnocoelostoma* (Sheth *et al.*, in prep.). The atypical species of *Lachnocoelostoma* (i.e., those having largely bare mesofemora or abdominal apex without stout setae) always differ from the subgenera treated in this paper in the presence of the abdominal median carina. The carina is absent in all *Coelostoma* s. str. and in all *Holocoelostoma*, including all species treated in this paper.

Key to Indian species of *Coelostoma* (s. str.)

1. Median lobe cylindrical, uniformly wide throughout; gonopore on its very apex (Figs 2D, 6J–K) ..
..... *C. lyratum* sp. nov.
- Median lobe more or less triangular, wider at the base than at the apex; gonopore subapical or basal (Fig. 2A–C, E–F) 2

2. Apex of the median lobe narrowly spatulate, gonopore basal (Figs 2F, 8J–K). Small species (Fig. 2F) *C. vividum* Orchymont, 1936
 - Apex of the median lobe not extremely narrow, gonopore subapical (Fig. 2A–C, E) 3
3. Median lobe very short and wide, gonopore very large (Figs 2D, 7J–K)
 - *C. vitalisi* Orchymont, 1923
 - Median lobe in form of narrow and elongate triangle (Fig. 2A–C) 4
4. Median lobe much longer than its basal struts, lateral sides of the median lobe concave. Apex of paramere strongly asymmetrical, with apical tooth-like projection (Figs 2C, 4J–K)
 - *C. fallaciosum* Orchymont, 1936
 - Median lobe only slightly longer than its struts, lateral margins of the median lobe straight. Apex of paramere more less symmetrical, without distinct tooth-like projection (Fig. 2A–B) 5
5. Aedeagus larger (0.7 mm), outer face of the paramere slightly concave in its apical third. Median lobe relatively wider at apex (Figs 2B, 5J–K) *C. nostocinum* sp. nov.
 - Aedeagus smaller (0.5 mm), outer face of the paramere continually arcuate, not concave subapically. Median lobe narrower at apex (Figs 2A, 3J–L) *C. aeneolum* Régimbart, 1903

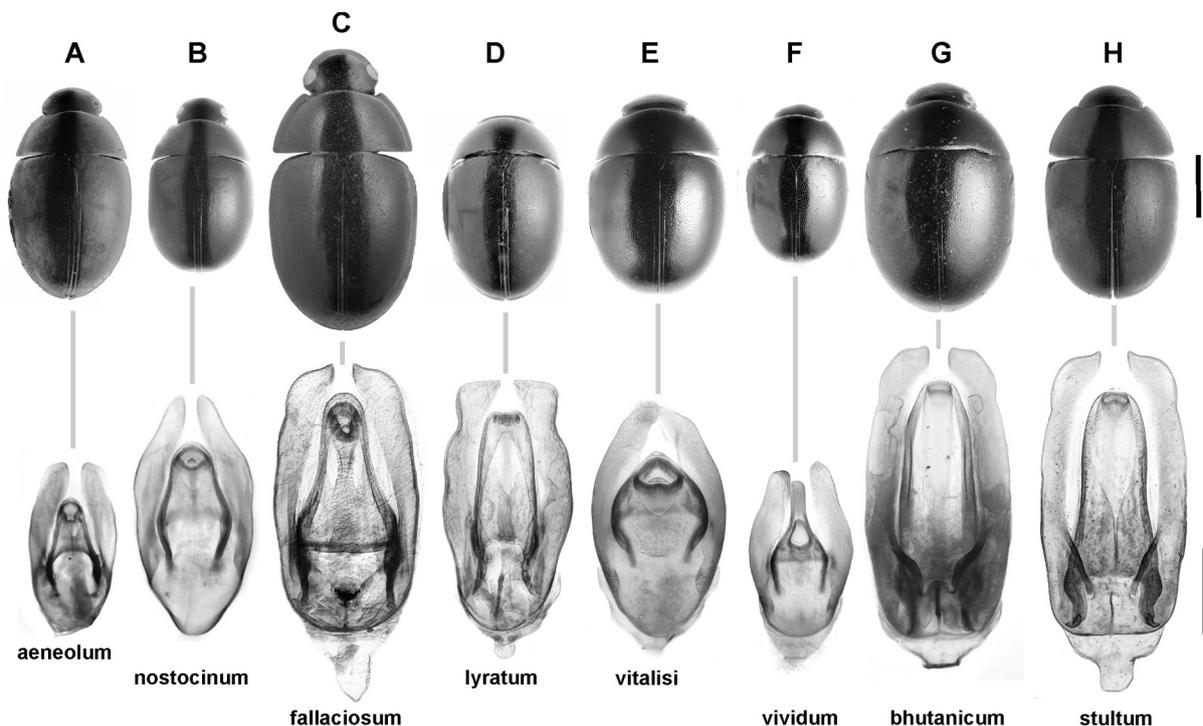


Fig. 2. Overview of *Coelostoma* Brullé, 1935 s. str. and *Holocoelostoma* Mouchamps, 1958 of the Indian subcontinent (habitus on the top, aedeagus on the bottom). – A–F. *Coelostoma* s. str. A. *C. aeneolum* Régimbart, 1903. B. *C. nostocinum* sp. nov. C. *C. fallaciosum* Orchymont, 1936. D. *C. lyratum* sp. nov. E. *C. vitalisi* Orchymont, 1923. F. *C. vividum* Orchymont, 1936. – G–H. *Holocoelostoma*. G. *C. bhutanicum* Jayaswal, 1972. H. *C. stultum* (Walker, 1858). All habitus figures and all aedeagi are to scale. Scale bars: habitus = 1 mm; aedeagus = 0.25 mm.

Key to Indian *Coelostoma* (*Holocoelostoma*)

1. Median lobe of the same width from base to apical fifth, in apical fifth distinctly narrowed; lateral margins of the median lobe strongly sclerotized, median lobe spoon-like when observed slightly laterally (Figs 2G, 9J–K) *C. bhutanicum* Jayaswal, 1972
- Median lobe widest at the base, gradually narrowing ca to the midlength, apical half narrowly parallel-sided, ca of the same width; lateral margins of the median lobe weakly sclerotized, median lobe not spoon-like when observed slightly laterally (Figs 2H, 10K–M)
..... *C. stultum* (Walker, 1858)

Coelostoma (s. str.) *aeneolum* Régimbart, 1903

Fig. 3A–M

Coelostoma aeneolum Régimbart, 1903: 337.

Coelostoma aeneolum – Zaitzev 1908: 403 (catalogue). — Knisch 1924: 110 (catalogue). — Orchymont 1928: 54 (catalogue).

Coelostoma (s. str.) *aeneolum* – Mouchamps 1958: 28 (assigned to *Coelostoma* s. str.). — Hansen 1999: 242 (catalogue).

Differential diagnosis

Coelostoma aeneolum resembles *C. nostocinum* sp. nov. and *C. fallaciosum* in having a narrowly triangular median lobe and the subapical gonopore. It can be distinguished from *C. fallaciosum* by parameres reaching much further than median lobe (in contrast to parameres only slightly longer than median lobe in *C. fallaciosum*), apex of the parameres more less symmetrically rounded (strongly asymmetrical and projecting into mesal ‘tooth’ in *C. fallaciosum*), the median lobe triangular with straight sides (sides clearly concave in *C. fallaciosum*) and much smaller aedeagus (ca 0.5 mm compared to 1.0 mm in *C. fallaciosum*). *Coelostoma aeneolum* is very similar to *C. nostocinum* sp. nov.; see under the latter species for differential characters and discussion.

Material examined

Lectotype (here designated)

INDIA • ♂; “MAHÉ, COTE DE MALABAR”; [11°42′0.09″ N, 75°31′59.96″ E]; [27 m a.s.l.]; “Juillet 1901” [Jul. 1901]; “M. Maindron leg.”; MNHN.

Paralectotype

INDIA • ♀; “CALICUT [Kozhikode], COTE DE MALABAR”; [11°15′38.85″ N, 75°46′49.48″ E]; [15 m a.s.l.]; “20–25 Juin 1901” [20–25 Jun. 1901]; “M. Maindron leg.”; MNHN.

The species was described based on an unspecified number of specimens deposited in MNHN. Both above specimens were found in coll. Régimbart in MNHN and their locality data agrees with the original description. We designate the male specimen here as a lectotype, to fix the identity of the species.

Other material

INDIA • 1 ♂; “Maharashtra, Bombay” [Mumbai]; [19°01′3.96″ N, 72°51′22.09″ E]; IRSNB.

Redescription

FORM AND COLOUR. Body length 4.6 mm, body width 2.6 mm (in both examined type specimens). Body oval in dorsal view, moderately convex in lateral view. Head black; pronotum and elytra uniformly dark

brown with slightly paler margins; ventral surface uniformly dark brown. Tarsi pale brown. Mouthparts and antennae yellowish, antennal club brown.

HEAD. Dorsal punctation dense, consisting of simple punctures without associated ridges; trichobothria present; surface between punctures smooth. Anterior margin of clypeus arcuate. Eyes large, interocular distance ca $3.3\times$ the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere moderately broad.

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin moderately bisinuate, posterolateral corners rectangular. Lateral margin with very indistinct sculpture; anterior and



Fig. 3. *Coelostoma* (s. str.) *aeneolum* Régimbart, 1903, lectotype. **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Frontal view. **D.** Thorax in ventral view. **E.** Dorsal punctation of head. **F.** Dorsal punctation of pronotum. **G.** Dorsal punctation of elytron. **H.** Abdominal ventrites. **I.** Detail of abdominal apex. **J–L.** Aedeagus. **J–K.** Lectotype, ♂ (MNHN) (J, ventral; K, dorsal). **L.** Non-type specimen from Mumbai, ♂ (IRSNB). **M.** Labels of the lectotype.

lateral margins with distinct bead not extending to posterior margin. Pronotal punctation sparser and finer than on head, consisting of simple punctures without associated ridges; surface between punctures smooth. Prosternum straight on anterior margin, carinate mesally, anterior portion of carina raised, producing tooth-like process seen laterally.

MESOTHORAX. Elytral punctation dense and moderately coarse, consisting of punctures without transverse ridges. Series of punctures absent. Sutural stria weakly impressed, present in apical half. Mesoventral plate $1.2 \times$ as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventricle.

METATHORAX. Metaventricle raised medially, posterior third and anterior portion of median elevation bare, remaining median surface with sparse regular setae; lateral portions densely pubescent. Anterior metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur and metafemur with sparsely arranged stout setae only.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite entire, without stout spines mesally.

AEDEAGUS (Fig. 3J–L). 0.4 mm long. Median lobe triangular, broad at base, tapering towards apex, bluntly rounded at apex; gonopore situated at apex, widely semicircular. Parameres longer than median lobe; narrow at base, rounded and slightly angulate at apex. Phallobase small, slightly wider than long.

Remarks

The species is only known from three historical specimens and the types had not been re-examined since the original description. We are here clarifying the identity of the species based on the examination of the types (see the redescription above) and an additional specimen. The species seems very rare, probably because of its distribution in lowland coastal areas from Maharashtra to Kerala, which are nowadays affected by high human population and high pollution. Additional research is needed to reveal whether the species is still present.

Biology

Unknown.

Distribution

Only known from coastal areas in northern Kerala (Mahé) and in Maharashtra (Mumbai).

Coelostoma (s. str.) *fallaciosum* Orchymont, 1936
Fig. 4A–K

Coelostoma fallaciosum Orchymont, 1936: 19.

Coelostoma (s. str.) *fallaciosum* – Hansen 1999: 244 (assigned to *Coelostoma* s. str.). — Hebauer 2002: 28 (faunistics); 2006: 8 (faunistics).

Differential diagnosis

Among Indian *Coelostoma* without pubescent mesofemora, *C. fallaciosum* may be recognized by its relatively large body size (resembling that of *C. stultum* and *C. bhutanicum*), simple abdominal apex

without emargination or stout setae (with emargination and stout setae in both latter species) and with a typical aedeagus with subapical gonopore and strongly asymmetrical apex of the paramere. In the morphology of male genitalia it also resembles *C. aeneolum*; see under that species for diagnosis.

Material examined

Holotype

INDONESIA • ♂; “B^r North Borneo, Mt. Marapok, Dent Province”; [1°01'15.25" N, 114°33'17.46" E]; [694 m a.s.l.]; “Collector G. leg.”; IRSNB.

Other material

INDIA • 2 ♂♂; “Uttar Pradesh, Fatepur Sikri” [Fatehpur Sikri]; [27°05'41.97" N, 77°40'4.89" E]; [174 m a.s.l.]; 21 Oct. 1997; J. Štastný leg.; NMPC.

NEPAL • 1 spec.; Annapurna, Pokhara, W of Phewa river + lake; [28°15'50.88" N, 83°58'18.66" E]; 800–850 m a.s.l.; 14–15 Oct. 2003; J. Schmidt leg.; NMPC.

Published records

NEPAL: Bheri Prov., Nepalgunj, 28°02'59" N 81°36'56" E (Hebauer 2002); Annapurna Prov., Pokhara, W of Phewa river and lake (Hebauer 2006).

Redescription

FORM AND COLOUR. Body length 5.6–6.4 mm (holotype 5.7 mm), body width 3.0–3.6 mm (holotype 3.3 mm). Body oval in dorsal view, moderately convex in lateral view. Head black, pronotum and elytra dark brown to black with slightly paler margins; ventral surface uniformly dark brown, abdomen with pale spot at sides of each ventrite; appendages paler distally; mouthparts and antennal club brown.

HEAD. Dorsal punctation moderately dense, consisting of simple punctures without associated ridges; surface between punctures smooth; few trichobothria present. Anterior margin of clypeus arcuate. Eyes large, interocular distance ca 4 × the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus, dark brown dorsally, sinuate on anterior margin. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere moderately broad.

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin almost straight, posterolateral corners rounded. Anterior and lateral margins with distinct bead not extending to posterior margin. Pronotal punctation moderately dense, slightly coarser than on head, consisting of simple punctures without associated ridges; surface between punctures smooth. Prosternum straight on anterior margin, weakly carinate mesally, anterior portion of carina not raised.

MESOTHORAX. Elytral punctation moderately dense and coarse, similar to that on pronotum, consisting of punctures without transverse ridges. Series of punctures absent. Sutural stria weakly impressed, present in apical two thirds. Mesoventral plate 1.1 × as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventrite.

METATHORAX. Metaventrite raised medially, median elevation bare, remaining median surface with sparse regular setae; lateral portions densely pubescent. Anterior metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur and metafemur with sparsely arranged short setae only.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite entire, without stout spines mesally.

AEDEAGUS (Fig. 4J–K). 1.0 mm long. Median lobe triangular, broad at base, tapering towards apex, bluntly rounded at apex; gonopore situated near apex, widely rounded. Parameres slightly longer than median lobe; pointed at apex, sinuate on outer margin. Phallobase small, slightly longer than wide.

Biology

Aquatic species, in Japan and Taiwan reported to inhabit shallow, well-vegetated pools (Liu *et al.* 2020; Nakajima *et al.* 2020). The biology of the specimens from the Indian subcontinent is unknown; all examined specimens were collected at light.

Distribution

A widespread species, so far recorded from Nepal (Hebauer 2002, 2006), northern India (this paper), Vietnam (Hansen 1999), southern China (Jia *et al.* 2014), Taiwan (Jia *et al.* 2014; Liu *et al.* 2020), Japan

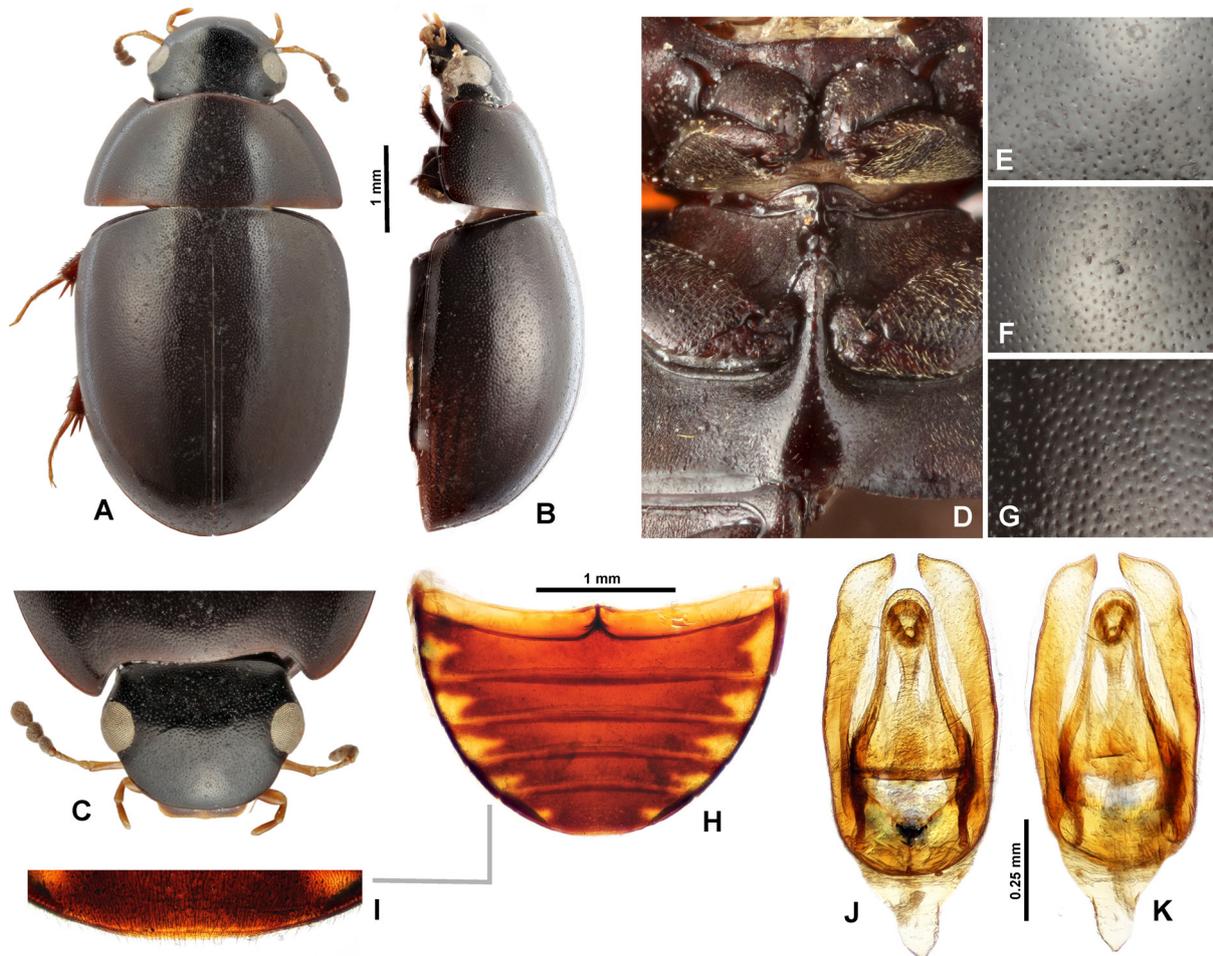


Fig. 4. *Coelostoma* (s. str.) *fallaciosum* Orchymont, 1936, ♂ specimen from India: Fatepur Sikri (NMPC). **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Head in dorsal view. **D.** Thorax in ventral view. **E.** Dorsal punctation of head. **F.** Dorsal punctation of pronotum. **G.** Dorsal punctation of elytron. **H.** Abdominal ventrites. **I.** Detail of abdominal apex. **J–K.** Aedeagus: ventral (J) and dorsal (K).

(Ishigaki and Iriomote Isl.; Hayashi 2008; Nakajima *et al.* 2020), Singapore (Hendrich *et al.* 2004), Borneo (Orchymont 1936) and Sumatra (Hansen 1999). First report for India.

Coelostoma (s. str.) *nostocinum* sp. nov.

[urn:lsid:zoobank.org:act:B069E8DC-6096-4292-B70D-93D6C5CB7337](https://zoobank.org/urn:lsid:zoobank.org:act:B069E8DC-6096-4292-B70D-93D6C5CB7337)

Fig. 5A–K

Differential diagnosis

Coelostoma nostocinum sp. nov. is characterized by smaller body size, by which it especially resembles *C. vividum*. Its male genitalia with the triangular median lobe easily distinguish it from all species except *C. fallaciosum* and *C. aeneolum*. The species may be distinguished from *C. fallaciosum* by its much shorter median lobe (compared to parameres) with straight lateral margins (concave in *C. fallaciosum*) and wider apex, and by the more or less symmetrically pointed apex of the paramere (strongly asymmetrical in *C. fallaciosum*). *Coelostoma nostocinum* sp. nov. is very similar to *C. aeneolum*, but may be distinguished from it by its (1) smaller body size (3.5–4.5 mm, compared to 4.6 mm in *C. aeneolum*), (2) larger aedeagus (0.7 mm, compared to 0.4 mm in *C. aeneolum*), (3) relatively longer apodemes of the median lobe (longer than half of the length of the apical triangular part of the median lobe, compared to much shorter than half the length in *C. aeneolum*) and (4) paramere distinctly concave on outer margin subapically and pointed apically (compared to evenly arcuate on whole outer margin and more less rounded apically in *C. aeneolum*).

Etymology

The species name refers to the finding of the holotype of this species in association with *Nostoc* Vaucher ex Bornet & Flahault (see Biology).

Material examined

Holotype

INDIA • ♂; “GOA province, 30 km S of MARGAO (Madgaon), Palolem env., INDIA 2002 exped; 15°00.47'N 74°01.56'E” [15°00'38.37" N, 74°01'23.76" E]; 0–20 m a.s.l.; 12–14 Aug. 2002; P. Šípek and M. Fikáček leg; found in *Nostoc*-like algae; NMPC.

Paratypes

INDIA – Goa • 11 specs; same collection data as for holotype; NMPC • 2 specs; same collection data as for holotype; BMNH • 1 spec; same collection data as for holotype; UASB 01923074 • 1 spec; same collection data as for holotype; ZSI • 3 specs; “30 km S of Margao, Palolem env.; 15°00.47' N, 74°01.56' E” [15°00'38.37" N, 74°01'23.76" E]; 0–20 m a.s.l.; 12–14 Aug. 2002; M. Fikáček and P. Šípek leg.; NMPC. – Maharashtra • 1 ♂, 33 specs; “4 km W of Lonavala, Bushi dam env.” [Bhushi dam]; [18°45'22.31" N, 73°24'32.95" E]; 500 m a.s.l.; 24–28 Oct. 2005; J. Bezděk leg.; at light; NMPC • 3 specs; same collection data as for preceding; SMNS • 1 ♂, 1 spec.; “4 km S of Lonavala, Bushi dam env.” [Bhushi dam]; [18°43'24.35" N, 73°23'49.43" E]; 500 m a.s.l.; 12–15 Oct. 2005; J. Bezděk leg.; NMPC • 1 spec.; same collection data as for preceding; NCBS BL020 • 2 ♂♂, 3 specs; Lonavala, 80 km E of Bombay; [18°45'21.96" N, 73°24'32.40" E]; [630 m a.s.l.]; 13 Sep. 1991; R. Schuh leg.; NHMW. – Karnataka • 1 spec.; Udipi distr., E of Bhatkal, Kollur; [13°51'48.71" N, 74°48'37.46" E]; [80 m a.s.l.]; 26–29 May 2006; Z. Kejval leg.; UASB 01923075. – Kerala • 6 specs; Cardamon Hills, 50 km NW of Pathanamhitta, Pambaiyar River; 9°25' N, 77°05' E; 300 m a.s.l.; 6–9 May 1994; Z. Kejval leg.; at light; NHMW • 1 spec.; same collection data as for preceding; NMPC.

Description

FORM AND COLOUR. Body length 3.3–4.5 mm (3.8 mm in holotype), body width 2.2–2.5 mm (2.4 mm in holotype). Body oval in dorsal view, moderately convex in lateral view. Head black, dark brown clypeus; pronotum and elytra uniformly dark brown to black; ventral surface pale to dark brown. Femora and tarsi yellowish brown, tibia dark reddish brown, tarsi pale brown. Mouth parts and antennae yellowish, antennal club brown.

HEAD. Dorsal punctation dense, consisting of simple punctures without associated ridges; trichobothria present; surface between punctures smooth. Anterior margin of clypeus non-arcuate. Eyes large, interocular distance ca $4.0\times$ the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere markedly wide.

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin moderately bisinuate, posterolateral corners rectangular. Anterior and lateral margins with distinct bead not extending to posterior margin. Pronotal punctation finer than on head, consisting of simple punctures

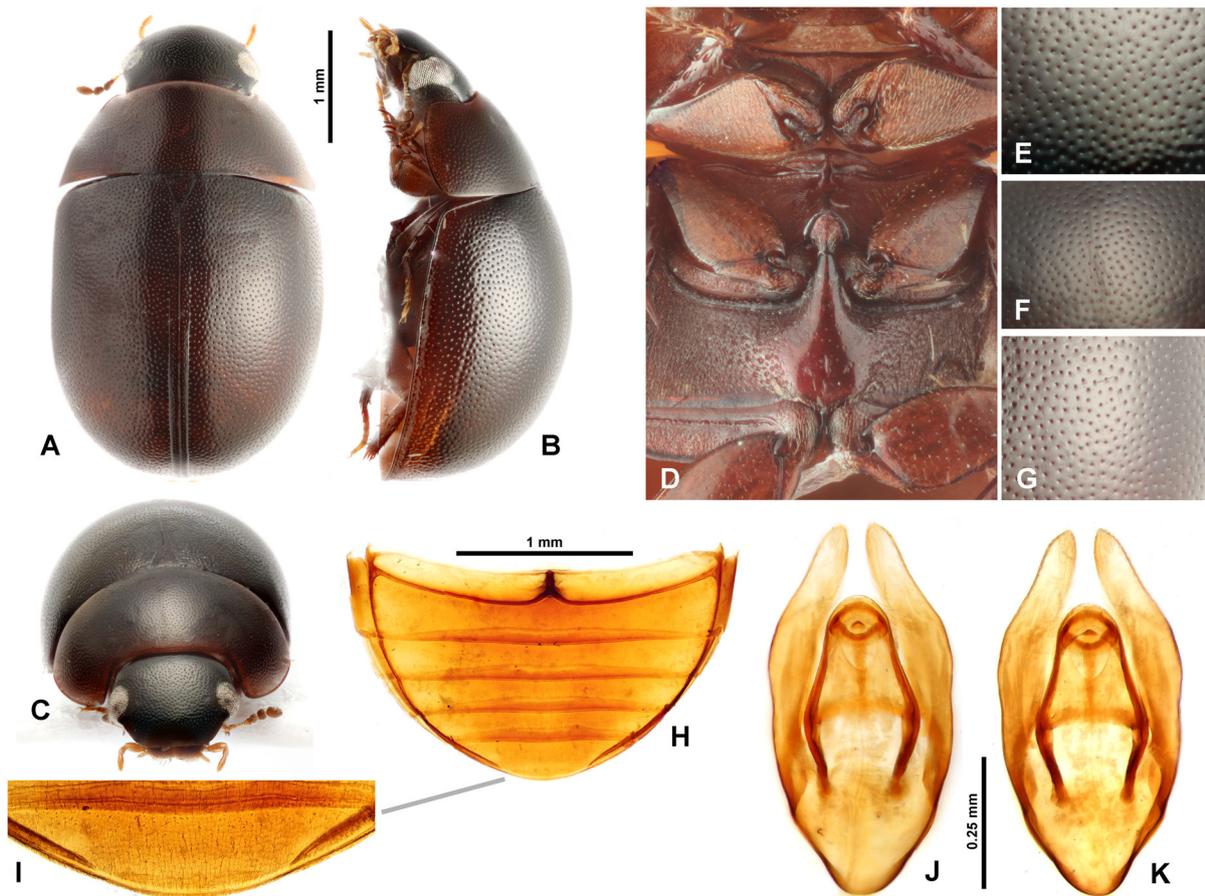


Fig. 5. *Coelostoma* (s. str.) *nostocinum* sp. nov. **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Frontal view. **D.** Thorax in ventral view. **E.** Dorsal punctation of head. **F.** Dorsal punctation of pronotum. **G.** Dorsal punctation of elytron. **H.** Abdominal ventrites. **I.** Detail of abdominal apex. **J–K.** Aedeagus: ventral (J) and dorsal (K). Photographs based on: A–G. Paratype from Lonavala, Bhushi dam (NMPC). H–K. Holotype, ♂ (NMPC).

without associated ridges; surface between punctures smooth. Prosternum nearly straight on anterior margin, gently carinate mesally.

MESOTHORAX. Elytral punctation dense and moderately coarse, consisting of punctures without transverse ridges. Weakly developed series of impressed punctures present along suture and laterally. Sutural stria well impressed, present in apical half, extends beyond middle; lateral elytral margins with sculpture. Mesoventral plate as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventrite.

METATHORAX. Metaventrite raised medially, completely glabrous on median elevation, lateral portions pubescent. Anterior metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur and metafemur with sparsely arranged short setae only.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite entire, without stout spines mesally.

AEDEAGUS (Fig. 5J–K). 0.7 mm long. Median lobe broad at base, slightly tapering towards widely rounded apex; gonopore situated at apex, widely semicircular. Parameres longer than median lobe; weakly arcuate on outer margin, narrowed in apical fourth; apex bluntly pointed; inner margin of parameres with long setae. Phallobase small, slightly wider than long.

Variation

Specimens from Maharashtra are slightly smaller than those from more southern areas. The aedeagus varies slightly in the shape of the parameres, the apical part of which is slightly wider in the specimens from Kerala; in all other aspects these specimens agree with those from Goa and hence we consider them conspecific.

Remarks

Coelostoma nostocinum sp. nov. and *C. aeneolum* are very similar in all characters including the morphology of the male genitalia, and both species seem to have very similar (and overlapping) distribution ranges. We were hence working with the hypothesis that they may be conspecific for some time, with the observed variation in body size and aedeagus morphology being an intraspecific variation. The examination of all available material, however, indicates that this is not the case, and that we really have two distinct morphotypes without intermediate characters: the species with larger body and smaller aedeagus with more or less rounded apices of parameres (*C. aeneolum*) and the smaller species with larger aedeagus with narrower and apically pointed paramere (*C. nostocinum* sp. nov.). Based on the material examined, both morphotypes are constant in the characters listed in the differential diagnosis across the distribution range (i.e., from Maharashtra to Kerala in both). For these reasons, we are treating them as separate species, with the smaller species described here as *C. nostocinum* sp. nov.

Biology

The specimens from Goa were collected under ‘balls’ of *Nostoc* blue-green algae growing on wet sandy places on rock cliffs at the sea coast. Specimens from Maharashtra were collected at light.

Distribution

Only known from the western coast of India and adjacent parts of the Western Ghats Mts, from Maharashtra to Kerala.

Coelostoma (s. str.) *lyratum* sp. nov.

[urn:lsid:zoobank.org:act:6E05380A-D3AA-410E-A974-D1CED984068A](https://zoobank.org/act:6E05380A-D3AA-410E-A974-D1CED984068A)

Fig. 6A–K

Differential diagnosis

The species is easily recognized based on its aedeagus which resembles those of *C. bhutanicum* and *C. stultum* in its apically situated gonopore and parallel-sided median lobe. In contrast to both latter species, the outer margin of the parameres in strongly bisinuate in *C. lyratum* sp. nov. (in contrast to a nearly continuously arcuate outer margin in *C. bhutanicum* and *C. stultum*) and the abdominal apex is simple, without emargination and stout setae.

Etymology

The species name refers to the lyriform shape of the aedeagus; adjective.

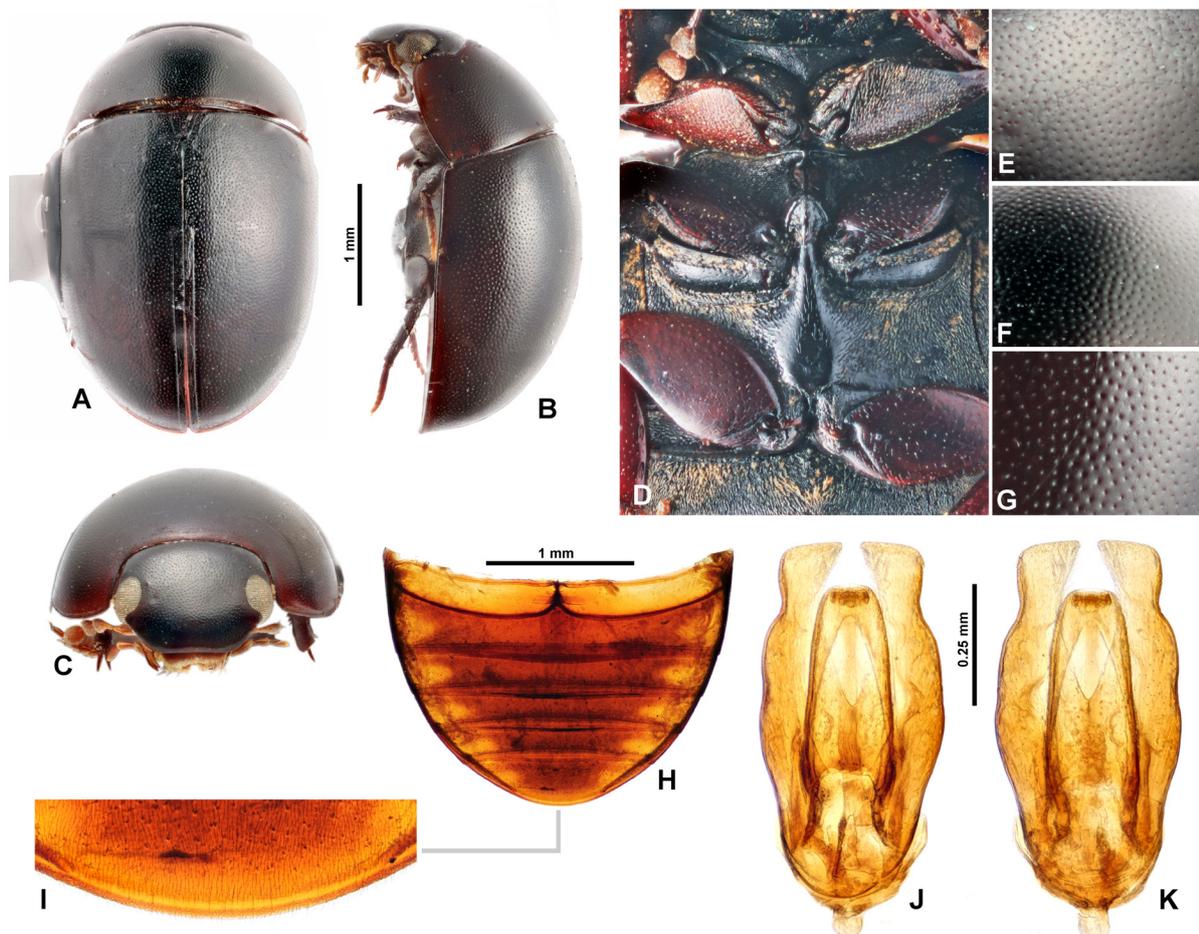


Fig. 6. *Coelostoma* (s. str.) *lyratum* sp. nov., holotype, ♂ (NMPC). **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Frontal view. **D.** Thorax in ventral view. **E.** Dorsal punctation of head. **F.** Dorsal punctation of pronotum. **G.** Dorsal punctation of elytron. **H.** Abdominal ventrites. **I.** Detail of abdominal apex. **J–K.** Aedeagus: ventral (J) and dorsal (K).

Type material

Holotype

INDIA • ♂; “Maharashtra, ca. 15 km of Savantvadi; 15°55'N 75°53'E” [15°55'3.72" N, 73°48'56.67" E]; ca 40 m a.s.l.; 22 May 2006; Z. Kejval leg.; riverside; NMPC.

Paratypes

INDIA • Maharashtra • 3 specs; same collection data as for holotype; NMPC • 2 specs; same collection data as for holotype; BMNH • 1 spec.; same collection data as for holotype; SMNS • 1 spec.; same collection data as for holotype; ZSI • 2 specs; same collection data as for holotype; NCBS-BL018–019 • 2 specs; same collection data as for holotype; UASB 01923068–69.

Description

FORM AND COLOUR. Body length 4.2–4.7 mm (holotype 4.5 mm), body width 2.7–3.1 mm (holotype 3.0 mm). Body narrowly oval in dorsal view, moderately convex in lateral view. Head black, reddish brown near clypeus and anterior to eyes; pronotum and elytra uniformly dark brown to black with slightly paler margins, ventral surface blackish brown, legs reddish brown. Mouthparts and antennae pale brown, antennal club brown.

HEAD. Dorsal punctation dense, consisting of simple punctures without associated ridges; trichobothria present; surface between punctures smooth. Anterior margin of clypeus arcuate, indistinctly emarginated medially. Eyes large, interocular distance ca 4.0 × the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere moderately broad.

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin moderately bisinuate, posterolateral corners rectangular. Anterior and lateral margins with distinct bead not extending to posterior margin. Pronotal punctation denser and finer than on head, consisting of simple punctures without associated ridges; surface between punctures smooth. Prosternum straight on anterior margin, weakly carinate mesally.

MESOTHORAX. Elytral punctation dense and moderately coarse, consisting of punctures without transverse ridges. Series of impressed punctures absent. Sutural stria impressed, present in apical two thirds. Mesoventral plate as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventrite.

METATHORAX. Metaventrite raised medially, median part sparsely pubescent except posterior third and anterior part, which are bare; lateral portions pubescent. Anterior metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur and metafemur with very sparsely arranged short setae only.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite entire, without stout spines mesally.

AEDEAGUS (Fig. 6J–K). 0.84 mm long. Median lobe of nearly the same width throughout; apex roundly cut off; gonopore situated at apex, widely semicircular. Parameres slightly longer than median lobe; heavily tri-sinuate on outer margin; apex acute at inner margin, rounded laterally. Phallobase small, slightly wider than long.

Biology

Unknown. The labels of the type specimens indicate that they were found at the riverside.

Distribution

Known from the type locality in southern Maharashtra.

Coelostoma (s. str.) *vitalisi* Orchymont, 1923
Fig. 7A–K

Coelostoma vitalisi Orchymont, 1923a: 418.

Coelostoma (s. str.) *vitalisi* – Orchymont 1925: 269 (faunistics); 1928: 57 (catalogue); 1936: 27 (faunistics). — Jia *et al.* 2017: 118 (faunistics).

Differential diagnosis

Coelostoma vitalisi is easy to recognize based on its aedeagus, with a very wide median lobe with a very large subapical gonopore. Thanks to the unique genital morphology, it cannot be confused with any other species of the genus.

Material examined

Holotype

Not examined.

Other material

INDIA • 1 ♂; “Assam, Kohora (= Kaziranga village), Green Reed Hotel; 27°35.93N, 93°26E” [26°35'21.81" N, 93°24'44.07" E]; [1000 m a.s.l.]; 16–18 Apr. 2008; Fikáček, Podskalská and Šípek leg.; at light; NMPC.

Published records

NEPAL: Narayani Sauraha, bank of Rapti River (Hebauer 2002; Jia *et al.* 2017); Seti distr., Bajhang, on the way from Chainpur to Sagu Bagar (Jia *et al.* 2017); valley of Rapti river, Jhawani (Jia *et al.* 2017); Narayani Prov., Sauraha SW Royal Chitwan Nat. Park (Hebauer 2002); Kathmandu, Baneshwar (Hebauer 2002). **INDIA:** **Uttarakhand:** Dehradun (Orchymont 1936). **Chhattisgarh:** ‘Barway’ [= Barway mission, Chainpur env., see Fikáček *et al.* 2012] (Orchymont 1925, 1936). **Bihar:** Pusa (Orchymont 1923b). **Jharkhand:** Mandar (Orchymont 1925). **Kerala:** ‘Calicut’ [= Kozhikode] (Orchymont 1936). **SRI LANKA:** without specified locality (Orchymont 1928, 1936) [specimens reported by Orchymont (1925) as *C. vitalisi* from India: West Bengal (‘Bengal’ and ‘Calcutta’) were found to belong to *C. vividum* by Orchymont (1936)].

Description

FORM AND COLOUR. Body length 4.0–4.9 mm, body width 2.5–2.9 mm. Body oval in dorsal view, moderately convex in lateral view. Head black; pronotum and elytra uniformly black to dark brown with slightly paler margins; ventral surface uniformly dark brown. Tarsi pale brown. Mouthparts and antennae yellowish, antennal club brown.

HEAD. Dorsal punctation dense, consisting of simple punctures, few punctures at posterior-most portion with associated ridges; trichobothria present; surface between punctures smooth. Anterior margin of clypeus gently arcuate. Eyes large, interocular distance ca 4.3 × the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus, sinuate

on anterior margin, brown. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere moderately broad.

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin moderately bisinuate, posterolateral corners rectangular. Lateral margin with very indistinct sculpture; anterior and lateral margins with distinct bead not extending to posterior margin. Pronotal punctation similar to that on head, consisting of simple punctures without associated ridges; surface between punctures smooth. Prosternum straight on anterior margin, very weakly carinate mesally, anterior portion raised, producing tooth-like process seen in lateral view.

MESOTHORAX. Elytral punctation dense and moderately coarse, similar to that on pronotum, consisting of punctures without transverse ridges. Series of punctures absent. Sutural stria impressed, present in apical half. Mesoventral plate $1.1 \times$ as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventrite.

METATHORAX. Metaventrite raised medially, posterior third and anterior portion of median elevation bare, remaining median surface with sparse regular setae; lateral portions densely pubescent. Anterior

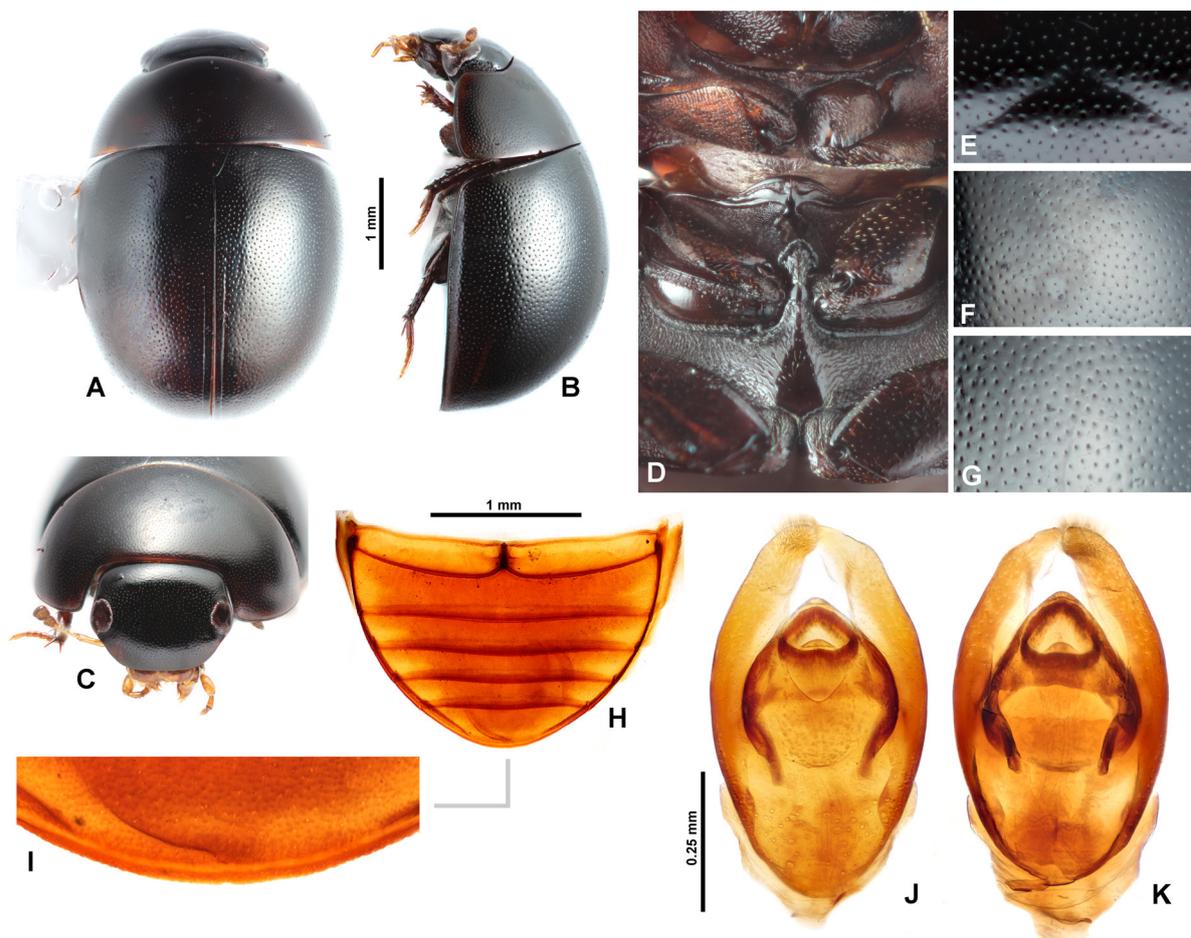


Fig. 7. *Coelostoma* (s. str.) *vitalisi* Orchymont, 1923, ♂ specimen from Assam: Kohora (NMPC). A. Dorsal habitus. B. Lateral habitus. C. Frontal view. D. Thorax in ventral view. E. Dorsal punctation of head. F. Dorsal punctation of pronotum. G. Dorsal punctation of elytron. H. Abdominal ventrites. I. Detail of abdominal apex. J–K. Aedeagus: ventral (J) and dorsal (K).

metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur with sparsely arranged stout setae only, metafemur with sparse pubescence.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite entire, without stout spines mesally.

AEDEAGUS (Fig. 7J–K). 0.75–0.85 mm long. Median lobe triangular, broad at middle, tapering towards apex; gonopore situated at apex, widely semicircular. Parameres longer than median lobe; rounded or obtusely pointed at apex. Phallobase small, slightly wider than long.

Biology

Aquatic species, Nakajima *et al.* (2020) reported it from shallow wetlands in lowland to hilly areas. Most specimens available in the collections were collected at light.

Distribution

Widespread species, known from Nepal (Jia *et al.* 2017), India (Orchymont 1925, 1936; this paper), Sri Lanka (Orchymont 1936), Cambodia, Thailand, Vietnam (Jia *et al.* 2017), Indonesia (Borneo, Java, Sumatra; Orchymont 1923a, 1925), Malaysia (Sabah; Orchymont 1925), Singapore (Orchymont 1925; Jia *et al.* 2014), southern China (Jia *et al.* 2014), Taiwan (Liu *et al.* 2020) and Japan (Minoshima 2017; Nakajima *et al.* 2020).

Coelostoma (s. str.) *vividum* Orchymont, 1936 Fig. 8A–K

Coelostoma vividum Orchymont, 1936: 28.

Coelostoma (s. str.) *vividum* – Jia *et al.* 2017: 118 (faunistics).

Differential diagnosis

Coelostoma vividum is easy to recognize due to its small body size and the aedeagus with the apically strongly narrowed median lobe.

Material examined

Paratype

INDONESIA • 1 ♂; “Bengealis” [Bengkalis]; [1°25′38.96″ N, 101°36′45.94″ E]; [40 m a.s.l.]; 1885; Maindron leg.; IRSNB.

Other material

INDIA – **Assam** • 1 ♂, 2 specs; “Kohora (= Kaziranga village), Green Reed Hotel; 27°35.93N 93°26E” [26°35′21.81″ N, 93°24′44.07″ E]; [1000 m a.s.l.]; 16–18 Apr. 2008; Fikáček, Podskalská and Šípek leg.; at light; NMPC. – **Meghalaya** • 1 ♂, 6 specs; W Garo Hills, Bagmara; 25°11.5 N, 90°38.5 E; ca 100 m a.s.l.; 15–21 May 1996; Jendek and Šauša leg.; NHMW.

BANGLADESH • 1 ♂; Dinajpur; [25°37′40.48″ N, 88°37′59.43″ E]; [41 m a.s.l.]; Oct. 1969; Barbe leg.; NMPC.

Published records

PAKISTAN: Khyber Pakhtunkhwa: Madyan (Jia *et al.* 2017). **NEPAL:** Mahakali distr., Kanchanpur Mahendranagar (Jia *et al.* 2017). **INDIA:** West Bengal: ‘Bengal’ (Orchymont 1936), Kolkata (Orchymont 1936).

Description

FORM AND COLOUR. Body length 3.4–4.1 mm, body width 2.1–2.3 mm. Body oval in dorsal view, moderately convex in lateral view. Head black; pronotum and elytra uniformly black to dark brown with slightly paler margins; ventral surface uniformly dark brown. Tarsi pale brown. Mouthparts and antennae yellowish, antennal club brown.

HEAD. Dorsal punctation dense, consisting of coarse simple punctures, a few punctures with associated ridges in posterior-most region; trichobothria present; surface between punctures smooth. Anterior margin of clypeus gently arcuate. Eyes large, interocular distance ca $4.0\times$ the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus, pale brown in coloration. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere moderately broad.

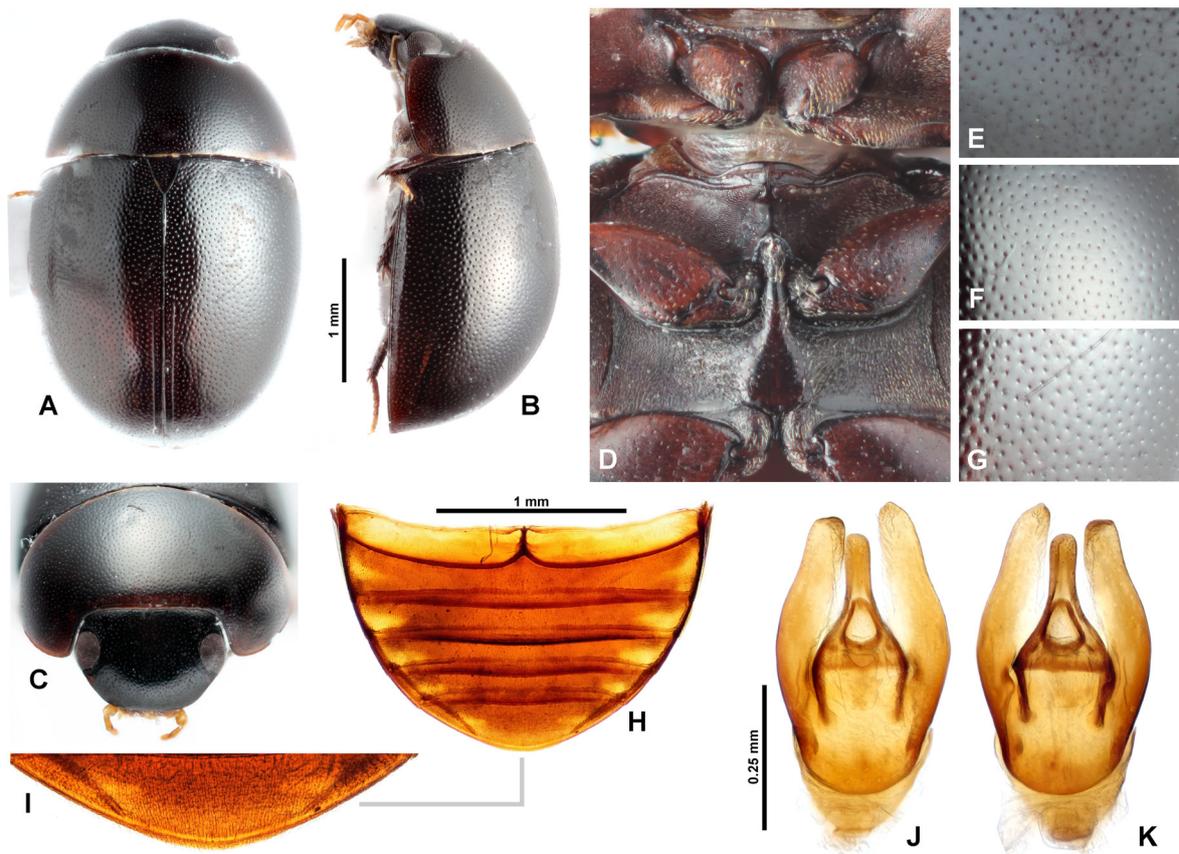


Fig. 8. *Coelostoma* (s. str.) *vividum* Orchymont, 1936, specimens from Assam: Kohora (NMPC). **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Frontal view. **D.** Thorax in ventral view. **E.** Dorsal punctation of head. **F.** Dorsal punctation of pronotum. **G.** Dorsal punctation of elytron. **H.** Abdominal ventrites. **I.** Detail of abdominal apex. **J–K.** Aedeagus: dorsal (J) and ventral (K).

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin moderately bisinuate, posterolateral corners rectangular. Lateral margin with very indistinct sculpture; anterior and lateral margins with distinct bead not extending to posterior margin. Pronotal punctation sparser and finer than on head, consisting of simple punctures without associated ridges; surface between punctures smooth. Prosternum straight on anterior margin, carinate mesally, anterior portion of carina raised, producing tooth-like process seen in lateral view.

MESOTHORAX. Elytral punctation dense and moderately coarse, consisting of punctures without transverse ridges. Series of punctures absent. Sutural stria impressed, present in apical half. Mesoventral plate 1.1 × as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventrite.

METATHORAX. Metaventrite raised medially, surface glabrous with sparse regular setae; lateral portions densely pubescent. Anterior metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur with sparsely arranged stout setae only; metafemur with sparse pubescence.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite entire, without stout spines mesally.

AEDEAGUS (Fig. 8J–K). 0.6 mm long. Median lobe triangular, broad at base, tapering towards narrowly spatulate apex; gonopore situated basally, widely semicircular. Parameres slightly longer than median lobe; broad, weakly pointed at apex, inner margin with setae. Phallobase small, slightly wider than long.

Biology

Unknown. Published specimens were all collected at light.

Distribution

Widespread species, so far recorded from northern Pakistan (Jia *et al.* 2017), Nepal (Jia *et al.* 2017), India (Orchymont 1936; this paper), Bangladesh (this paper), Cambodia (Jia *et al.* 2017), southern China (Jia *et al.* 2017) and Indonesia (Java, Sumatra, Borneo; Orchymont 1936).

Coelostoma (Holocoelostoma) bhutanicum Jayaswal, 1972

Fig. 9A–K

Coelostoma sulcata Pu, 1963: 77, **possible synonym** [needs confirmation, see comments below].

Coelostoma (Holocoelostoma) bhutanicum Jayaswal, 1972: 409.

Coelostoma (Holocoelostoma) bhutanicum – Hebauer 2002: 28 (faunistics).

Differential diagnosis

Coelostoma bhutanicum is easy to recognize from most other *Coelostoma* species by the apical gonopore and widely parallel-sided median lobe; in these characters it resembles only *C. stultum* and *C. lyratum* sp. nov. From *C. lyratum* sp. nov. it differs by the evenly arcuate outer face of the paramere and by the abdominal apex bearing a shallow emargination armed with stout setae. In both these characters it agrees with *C. stultum*, from which it is only recognizable by an examination of the male genitalia: the aedeagus of *C. bhutanicum* is more sclerotized and seemingly more ‘robust’ than that of *C. stultum* when examined quickly. The main difference is in the form of the median lobe, which has strongly

sclerotized lateral margins in *C. bhutanicum*. This causes the median lobe to be of nearly the same width from base to apical fifth, from which it abruptly narrows (in contrast, the median lobe is narrowing from base to ca midlength and is of more or less the same width in the apical half in *C. stultum*). The more sclerotized margins in *C. bhutanicum* also affect the 3D form of the median lobe, which is distinctly spoon-like (best seen when the aedeagus is slightly rotated when examined).

Material examined

Type material

Holotype not examined. [Types are deposited in the Zoological Survey in Kolkata but were not studied.]

Other material

NEPAL • 1 ♂; Bagmati, Sindhupalchok, Jarayetar-Dubhachaur; [28°1'45.43" N, 85°20'43.88" E]; 800–1600 m a.s.l.; 2 Jun. 1989; F. Hebauer determined as *C. stultum*; M. Brancucci leg.; NMPC.

INDIA – **Rajasthan [Rajasthan]** • 1 ♂, 1 ♀; Alwar district, 30 km N of Dausa, Gola-ka-bas village; 27°05'31" N, 76°18'47" E; 359 m a.s.l.; 24–28 Mar. 2004; P. Šípek and L. Šejnohová leg.; NMPC. – **Meghalaya** • 1 ♂, 1 ♀; W Garo Hills, Balphakram NP; [25°29'58.61" N, 90°18'57.16" E]; 300–500 m a.s.l.; 22–27 May 1996; Jendek and Šauša leg.; NHMW • 1 ♂; W Garo Hills, Bagmara; 25°11.5' N, 90°26.5' E; ca 100 m a.s.l.; 19–21 May 1996; Jendek and Šauša leg.; NHMW. – **Kerala** • 1 ♂; Cardamon Hills, 50 km NW of Pathanamhitta, Pambaiyar River; 9°25' N, 77°05' E; 300 m a.s.l.; 5–9 May 1994; Z. Kejval leg.; NHMW.

Published records

BHUTAN: Ganga lakha (Jayaswal 1972). **INDIA**: Uttarakhand: Nainital (Jayaswal 1972). Records published from Nepal by Hebauer (2002) need confirmation, as our examination of a few specimens identified by F. Hebauer revealed that he often confused *C. bhutanicum* with *C. stultum*.

Redescription

FORM AND COLOUR. Body length 4.7–5.8 mm, body width 2.8–3.5 mm. Body widely oval in dorsal view, moderately convex in lateral view. Head black; pronotum and elytra uniformly dark brown to black with slightly paler margins; ventral surface uniformly reddish brown. Tarsi pale brown. Mouthparts and antennae yellowish brown, antennal club brown.

HEAD. Dorsal punctation dense, consisting of simple punctures without associated ridges; trichobothria present; surface between punctures smooth. Anterior margin of clypeus arcuate. Eyes large, interocular distance ca 2.8× the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere moderately broad.

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin moderately bisinuate, posterolateral corners rectangular. Anterior and lateral margins with distinct bead not extending to posterior margin. Pronotal punctation slightly finer than on head, consisting of simple punctures without associated ridges; surface between punctures smooth. Prosternum straight on anterior margin, weakly elevated mesally, anterior portion of carina not very elevated.

MESOTHORAX. Elytral punctation dense and moderately coarse, consisting of punctures without transverse ridges. Series of impressed punctures absent. Sutural stria weakly impressed, present in apical half. Mesoventral plate as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventricle.

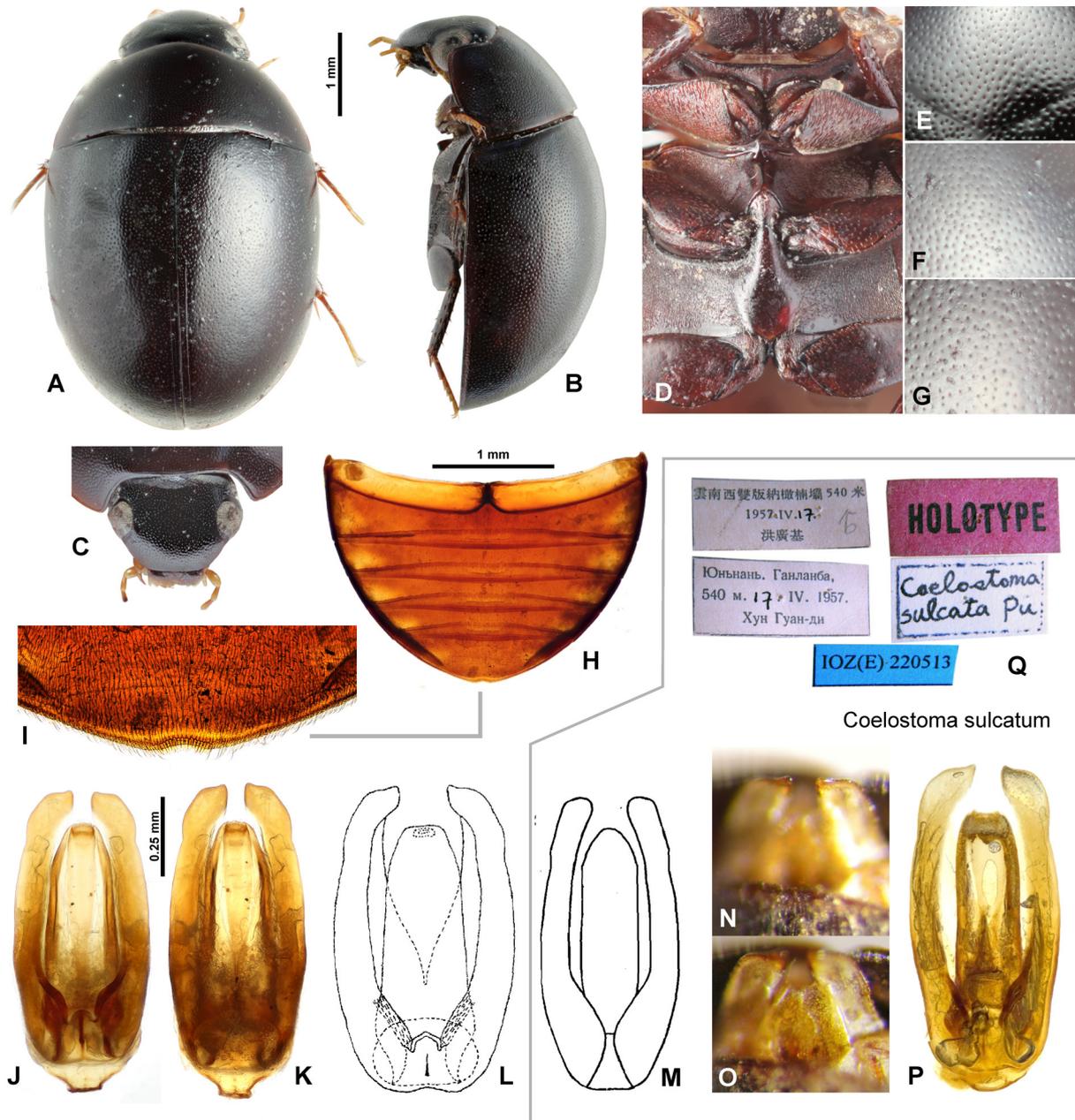


Fig. 9. *Coelostoma* (*Holocoelostoma*) *bhutanicum* Jayaswal, 1972 (A–L) and *C. (H.) sulcatum* Pu, 1963 (M–Q). A–K. *C. bhutanicum*, non-type specimen from India: Rajasthan, Alwar (NMPC). A. Dorsal habitus. B. Lateral habitus. C. Head. D. Thorax in ventral view. E. Dorsal punctation of head. F. Dorsal punctation of pronotum. G. Dorsal punctation of elytron. H. Abdominal ventrites. I. Detail of abdominal apex. J–K. Aedeagus: dorsal (J) and ventral (K). L. Illustration of the aedeagus of the paratype of *C. bhutanicum* by Jayaswal (1972). M. Aedeagus illustration from the description of *C. sulcatum* in Pu (1963). N–O. Apex of the aedeagus of the holotype of *C. sulcatum*. P. Aedeagus of the paratype of *C. sulcatum* from Yunnan: Jingdong. Q. Labels of the holotype of *C. sulcatum*.

METATHORAX. Metaventricle raised medially, posterior third and anterior of median elevation bare, lateral portions pubescent. Anterior metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur with sparsely arranged stout setae only; metafemur with very sparse pubescence.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite emarginate, with stout spines mesally.

AEDEAGUS (Fig. 9J–K). 1.0–1.1 mm long. Median lobe nearly parallel-sided, not widened basally, slightly narrowing in apical fifth; gonopore totally apical, widely oval in shape. Parameres longer than median lobe; apex rectangular at inner margin, not projecting inwards, rounded laterally. Phallobase small, wider than long.

Variation

The apical part of the median lobe is less narrowed in specimens from Taiwan (see Liu *et al.*, 2020), but otherwise the aedeagus morphology seems very constant across the range in this species.

Identity of *C. bhutanicum* and synonymies

The identity of this species was long unclear, and many taxonomists considered it as a possible synonym of *C. stultum*, although this opinion was never published because of the inaccessibility of the types. The comparison of the aedeagus of the specimens from northern India examined here with the drawing by Jayaswal (1972) leaves little doubt that both refer to the same species: Jayaswal's (1972) drawing (Fig. 9L) shows the typical shape of the median lobe having the same width along the whole length except for the apical fifth. The slightly wider form illustrated on Jayaswal's (1972) drawing is likely caused by the fact that the genitalia were slide-mounted.

Jia *et al.* (2014) illustrated the male genitalia of two specimens identified as *C. stultum* from China (from Guangdong and Xizang), which both clearly show the strongly sclerotized lateral margins of the median lobe and the shape of the median lobe corresponding to those in *C. bhutanicum*. This indicates that (1) Jia *et al.* (2014) mixed the two species, and *C. bhutanicum* clearly occurs in China, and (2) the status of *C. sulcatum* Pu, 1963 as a synonym of *C. stultum* proposed by Jia *et al.* (2014) is incorrect. *Coelostoma sulcatum* was described from specimens from Yunnan, Xishuanbanna (type locality) and Jindong, and the illustration by Pu (1963) shows the typical form of the median lobe present in *C. bhutanicum* (Fig. 9M). We hence suspect that *C. sulcatum* Pu, 1963 and *C. bhutanicum* Jayaswal, 1972 may refer to the same species. Martin Fikáček examined the types of *C. sulcatum* (the holotype from Xishuanbanna and a paratype from Jindong) briefly during his visit to Beijing in 2010 and took photographs of the holotype, with the abdominal apex showing a slightly protruding aedeagus (Fig. 9N–O), and of the completely dissected aedeagus of the paratype (Fig. 9P). The aedeagus of the paratype shows the median lobe with clearly sclerotized lateral margins, but it is rather narrow and not abruptly narrowing at the apex as it is typical for *C. bhutanicum*; this may be because the aedeagus is slightly deformed by dehydration. The apex of the aedeagus of the holotype shows the typical shape of the parameres present in both *C. bhutanicum* and *C. stultum* but absent from the illustration by Pu (1963) and also clearly shows the narrowing apex of the median lobe, further indicating that the shape of the median lobe of the paratype may be a deformation. The dissection of the holotype, remounting the aedeagus of the paratype or the examination of fresh material from Xishuanbanna would be necessary to understand the identity of *C. sulcatum* correctly and to confirm its synonymy with *C. bhutanicum*, which we are hypothesizing here. This synonymy would affect the nomenclature, since *C. sulcatum* would become a valid name and *C. bhutanicum* its junior synonym. However, we refrain from proposing the formal synonymy until the

identity of *C. sulcatum* can be completely clarified, in order to prevent even more confusion about the species concepts within the subgenus *Holocoelostoma*.

Biology

Aquatic species; in Taiwan, the specimens were collected at the sides of ponds (among plant roots) and of running water (under stones and in mud) (Liu *et al.* 2020). The specimens examined by us were likely collected at light.

Distribution

Due to the confusion of this species with *C. stultum*, the distribution of *C. bhutanicum* requires more study. The occurrence is so far confirmed in Bhutan, Nepal and northern India (Jayaswal 1972, this paper), in China (based on photographs provided by Jia *et al.* 2014), in Taiwan (Liu *et al.* 2020) and Japan (Watanabe & Minoshima 2020).

Coelostoma (Holocoelostoma) stultum (Walker, 1858)

Fig. 10A–M

Hydrobius stultus Walker, 1858: 209.

Coelostoma stultum – Zaitzev 1908: 404 (catalogue). — Knisch 1924: 113 (catalogue).

Coelostoma (Holocoelostoma) stultum – Orchymont 1923b: 2 (faunistics); 1928: 56 (catalogue); 1936: 17 (faunistics). — Mouchamps 1958: 3 (transfer to *Holocoelostoma*). — Satô 1979: 49 (faunistics). — Hebauer 2000: 6 (faunistics); 2002: 31 (faunistics); 2006: 8 (faunistics). — Darilmaz & Ahmed 2015: 10 (faunistics). — Jia *et al.* 2017: 118 (faunistics).

Differential diagnosis

Large species, easy to recognize from all other *Coelostoma* species except *C. bhutanicum* by the combination of the widely parallel-sided median lobe with apical gonopore and emarginate abdominal apex with stout setae. From *C. bhutanicum* it may be only recognized by the morphology of the median lobe of the aedeagus, which is wide basally, gradually narrowing to ca midlength and more or less of the same width in apical half. In contrast to *C. bhutanicum*, *C. stultum* does not have strongly sclerotized lateral margins of the median lobe and the median lobe is not spoon-like in form.

Material examined

Lectotype (here designated)

SRI LANKA • ♀; “Ceylon”; [7°52'23.80" N, 80°46'18.52" E]; [243 m a.s.l.]; BMNH.

Other material

INDIA – **Uttar Pradesh** • 2 ♂♂; Fatapur Sikri [Fatehpur Sikri]; [27°5'41.97" N, 77°40'4.89" E]; [174 m a.s.l.]; 31 Oct. 1997; J. Šťastný leg.; NMPC. – **Rajasthan** • 1 ♂, 28 specs; Bharatpur, Keoladeo National Park and around; 27°12.42' N, 77°30.48' E; 220 m a.s.l.; 31 Aug.–5 Sep. 2002; M. Fikáček and P. Šípek leg.; NMPC • 3 specs; same collection data as for preceding; NCBS-BL022–024 • 3 specs; same collection data as for preceding; UASB 01923080–82 • 2 specs; same collection data as for preceding; ZSI • 1 ♂, 3 specs; Bharatpur; [27°12'54.67" N, 77°30'10.80" E]; [180 m a.s.l.]; 11 Aug. 1989; A. Riedel leg; NHMW. – **Goa** • 1 ♂; “30 km S of Margao (= Madgaon), Palolem env.; 15°00.47' N, 74°01.58' E” [15°0'38.37" N, 74°1'23.76" E]; 0–20 m; 12–14 Aug. 2002; P. Šípek and M. Fikáček leg.; NMPC. – **Assam** • 1 ♂, 1 ♀; “Kohora (Kaziranga village) at Green Reed hotel; 26°35' N, 93°26' E” [26°35'21.81" N, 93°24'44.07" E]; “160 m” [1000 m a.s.l.]; 16–18 Apr. 2008; Fikáček, Podskalská and Šípek leg.; at light; NMPC. – **Meghalaya** • 1 ♂; W Garo Hills, Balphakram NP; 25°11' N, 90°51' E;

300–500 m a.s.l.; 22–27 May 1996; Jendek and Šauša leg.; NHMW • 1 ♂; W Garo Hills, Bagmara; 25°11.5' N, 90°38.5' E; ca 100 m a.s.l.; 18–21 May 1996; Jendek and Šauša leg.; NHMW.

SRI LANKA • 1 ♂; Colombo; [6°55'40.52" N, 79°51'39.79" E]; [13 m a.s.l.]; BMNH.

Published records

All published records of *C. stultum* from the Indian subcontinent need re-examination, as they very likely include misidentified *C. bhutanicum*.

Description

FORM AND COLOUR. Body length 3.8–5.2 mm, body width 2.6–3.3 mm. Body oval in dorsal view, moderately convex in lateral view. Head black; pronotum and elytra uniformly dark brown; ventral surface uniformly reddish brown. Tarsi pale brown. Mouthparts and antennae yellowish brown, antennal club brown.

HEAD. Dorsal punctation dense, consisting of simple punctures without associated ridges; trichobothria present; surface between punctures smooth. Anterior margin of clypeus arcuate. Eyes large, interocular distance ca 3.3 × the width of one eye in dorsal view; eye emarginate anteriorly. Labrum moderately sclerotized, largely exposed anterior of clypeus. Antenna with 9 antennomeres, club loosely segmented. Second maxillary palpomere moderately broad.

PROTHORAX. Pronotum bisinuate anteriorly, anterolateral corners obtuse; posterior margin moderately bisinuate, posterolateral corners rectangular. Anterior and lateral margins with distinct bead not extending to posterior margin. Pronotal punctation sparser and finer than on head, consisting of simple punctures without associated ridges; surface between punctures smooth. Prosternum slightly projecting mesally on anterior margin, carinate mesally, anterior portion of carina very weakly elevated.

MESOTHORAX. Elytral punctation dense and moderately coarse, consisting of punctures without transverse ridges. Series of impressed punctures present along suture and laterally. Sutural stria weakly impressed, present in apical half. Mesoventral plate as long as wide, arrowhead-shaped, bluntly pointed anteriorly, posteriorly widely attached to metaventrite.

METATHORAX. Metaventrite raised medially, posterior third and anterior of median elevation bare, lateral portions pubescent. Anterior metaventral process narrowly projecting between mesocoxae; posterior process bifid. Wings well-developed (macropterous).

LEGS. Profemur with dense pubescence except in apical fifth; mesofemur with sparsely arranged stout setae only; metafemur with very sparse pubescence.

ABDOMEN. All ventrites densely pubescent. First ventrite without carina. Posterior margin of last ventrite emarginate, with stout spines mesally.

AEDEAGUS (Fig. 10K–M). 0.8–1.0 mm long. Median lobe broad at base, slightly tapering towards apex; gonopore situated at apex but still directed dorsally, widely oval in shape. Parameres slightly longer than median lobe; apex rectangular at inner margin, not projecting inwards, rounded laterally. Phallobase small, wider than long.

Variation

The form of the median lobe differs slightly between the examined specimens from India and Sri Lanka and those from Taiwan and Japan (see Liu *et al.* 2020), but in all cases the median lobe is widest at the

base and narrowed ca at mid-length. Additional studies are needed to understand whether this variation may represent a geographic variability of the species.

Lectotype designation

On the request to loan the type specimens from the Walker collection at BMNH, we received two specimens, both considered as syntypes. Both are females, but each of them belongs to a different species: the specimen labelled as cotype belongs to the subgenus *Holocoelostoma* based on the emarginated abdominal apex and mesofemora lacking dense pubescence; it agrees externally in all details



Fig. 10. *Coelostoma (Holocoelostoma) stultum* (Walker, 1858). **A.** Dorsal habitus. **B.** Lateral habitus. **C.** Head. **D.** Thorax in ventral view. **E.** Dorsal punctation of head. **F.** Dorsal punctation of pronotum. **G.** Dorsal punctation of elytron. **H.** Abdominal ventrites. **I–J.** Detail of abdominal apex. **K–M.** Aedeagus: dorsal (K) and ventral (L–M). **N.** Labels of the lectotype. Specimens: A–I, K–L. Non-type specimens from Uttar Pradesh, Fatehpur Sikri, ♂ (NMPC). J, N. Lectotype, ♀ (BMNH). M. Non-type specimen, ♂, from Sri Lanka: Colombo (BMNH).

with a male specimen from Colombo, the genitalia of which are illustrated on Fig. 10M. The second specimen, labelled as type, has an emarginate abdominal apex and densely pubescent mesofemora, and hence belongs to the subgenus *Lachnocoelostoma*. To fix the current concept of *C. stultum* and of *Holocoelostoma* (of which *C. stultum* is the type species), we are therefore designating the first specimen as the lectotype.

Biology

Aquatic species; in Japan and Taiwan it inhabits vegetation-rich places with muddy bottoms, typically ponds, rice fields and river sides (Liu *et al.* 2020; Nakajima *et al.* 2020).

Distribution

Coelostoma stultum is reported as a very widespread species, extending from the Arabian Peninsula (Fikáček *et al.* 2010) to Japan (Hayashi 2008) and New Guinea (Hebauer 2001) (see Hansen 1999 for a summary), also recorded from the Mascarene Islands and Madagascar (Hebauer 2006). This distribution

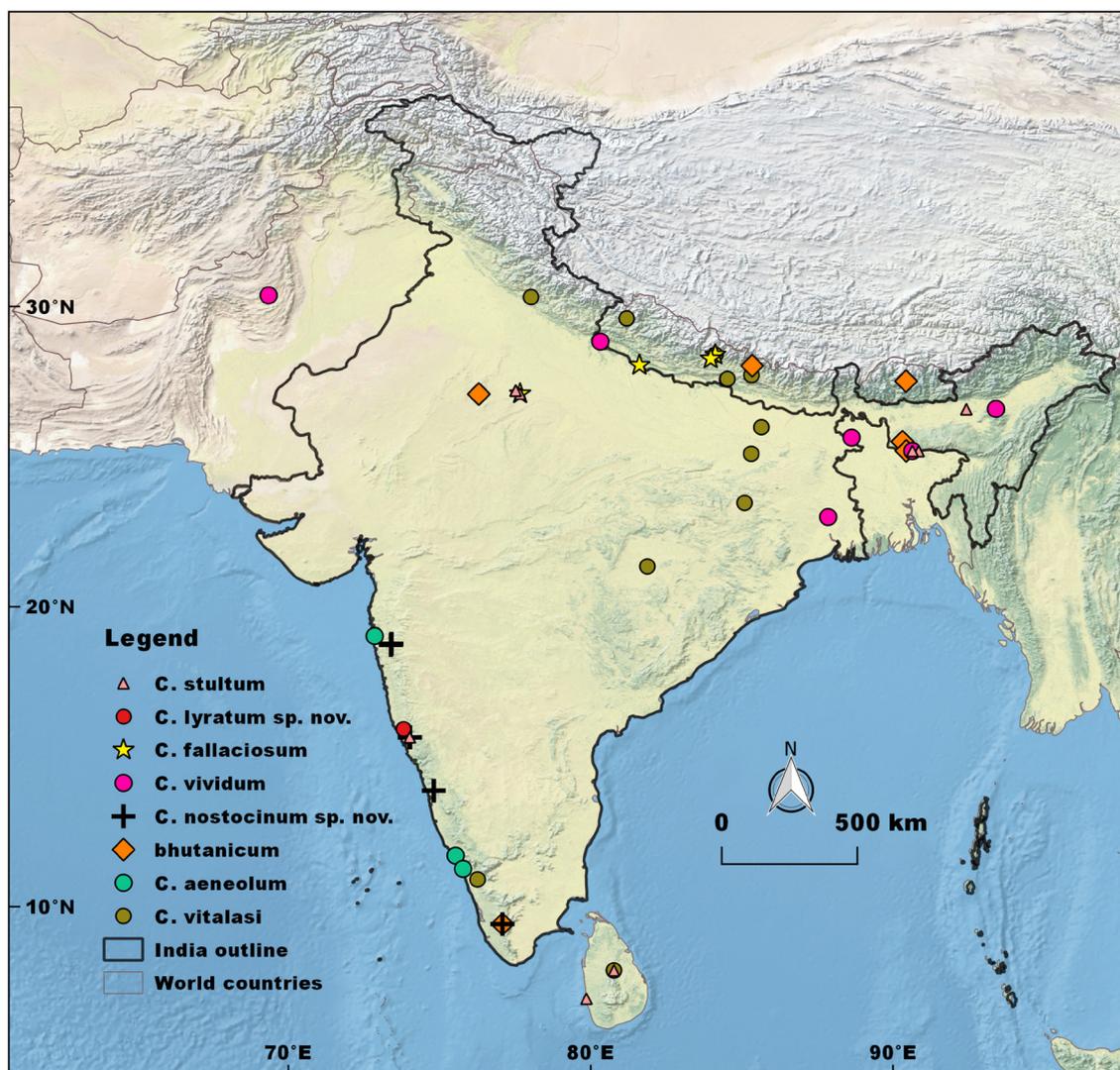


Fig. 11. Known distribution of the *Coelostoma* s. str. and *Holocoelostoma* species in the Indian subcontinent.

is, however, surely partly based on misidentified specimens of *C. bhutanicum*, and needs revision. Based on the material examined for this study and published illustrations of male genitalia, we may confirm the species to occur in the following countries at present: United Arab Emirates (Fikáček *et al.* 2010), India (this paper), Sri Lanka (Walker 1858, this paper), Taiwan (Liu *et al.* 2020) and Japan (Hayashi 2008).

Discussion

The species diversity of the subgenera *Coelostoma* (s. str.) and *Holocoelostoma* in the Indian subcontinent is rather low (6 and 2 species, respectively), with 5 species being moreover very widespread across the whole Oriental Region (Fig. 11). In this respect the fauna of the Indian subcontinent corresponds, e.g., to the fauna of China, where 5 species of *Coelostoma* s. str. and two species of *Holocoelostoma* occur, all of them being widespread species (Jia *et al.* 2014, 2017; this paper). In contrast to the Chinese fauna, three species of the Indian subcontinent seem to be more local and likely endemic to the western coast of India (*C. aeneolum*, *C. nostocinum* sp. nov. and *C. lyratum* sp. nov.). The relatively low species diversity of *Coelostoma* (s. str.) and *Holocoelostoma* in the Oriental Region seems to contrast with the available data on the subgenus *Lachnocoelostoma*, which contains a high number of species, many of which are local endemics (e.g., Jia *et al.* 2014, 2017, 2019; Liu *et al.* 2020). Habitat preferences of *Coelostoma* (s. str.) and *Holocoelostoma* species may be partly responsible for this pattern: all species of these two subgenera for which habitat data are available inhabit lowland standing waters. The only known exception is the finding of the above-described *C. nostocinum* sp. nov. in growths of *Nostoc* blue-green algae not associated with a nearby aquatic environment. In contrast, available data on the species of *Lachnocoelostoma* indicate a much wider spectrum of habitats, including the sides of running waters and wet rocks (Jia *et al.* 2014; Liu *et al.* 2020). Previous studies on aquatic beetles indicated that species of standing (lentic) waters tend to have larger ranges than species of running (lotic) waters (e.g., Ribera & Vogler 2000). Available data would indicate a similar pattern for Oriental *Coelostoma*, although further studies are needed to test this assumption.

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Supplementary File

SM.01. List of specimens examined in DarwinCore format (.xls file).