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Groundwater amphipods (Crustacea, Malacostraca) of India, with description of three new cavernicolous species

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Abstract

Stygofaunistic surveys of peninsular India yielded, among others, three new cavernicolous amphipod taxa: *Orientogidiella reducta* gen. n., **sp. n.** in the Borra caves of Andhra Pradesh state, *Bogidiella hindustanica* **sp. n.** (Bogidiellidae) and *Indoniphargus subterraneus* **sp. n.** (Austroniphargidae) in the Kapiladevi caves of Telangana state. The new genus, *Orientogidiella* **gen. n.**, is proposed to accommodate all the hitherto known species of the *Bogidiella indica*-group. This paper gives an illustrated description of the three new species together with their taxonomic affinities. A new record of *O. indica* comb. n., from the Guthikonda caves in Andhra Pradesh is provided as well. The structure of the *Indoniphargus* mandible is revisited with scanning electron microscopy (SEM) and revealed a poorly known flexible structure on the molar process which could be useful for phylogenetic purposes. The species diversity and geographic distribution of the Indian stygobiotic amphipods are briefly reviewed.

Key words: Amphipoda, *Bogidiella*, *Indoniphargus*, *Orientogidiella* new genus, SEM, taxonomy, caves

Introduction

The freshwater subterranean domain of India, which is vast (3 287 263 km^2) and highly diversified, has remained de facto *terra incognita* for stygofauna till recently (Ranga Reddy 2018). As for amphipods, *Indoniphargus indicus* (Chilton, 1923) is the only species known until the mid-1980s (Botosaneanu 1986). The essential taxonomic reports belong to two distinct time periods: historical (Chilton 1923; Stephensen 1931; Straškraba 1967) and modern (Holsinger *et al*. 2006; Messouli *et al*. 2007; Senna *et al*. 2013; Sidorov *et al*. 2016). Also, Dudgeon (1999) and Nesemann *et al*. (2004) referred to the Indian Amphipoda in their faunistic reports. To date three bogidiellid species, viz. *Bogidiella indica* Holsinger, Ranga Reddy, and Messouli, 2006, and *Bogidiella totakura* Senna, Mugnai, and Ranga Reddy, 2013, occur in bore wells along the coastal belt of the Rivers Krishna and Godavari in Andhra Pradesh state, *Eobogidiella venkataramani* Sidorov, Katz, Taylor, and Chertoprud, 2016, in a spring-fed habitat in Karnataka state and a putatively crangonyctoid *Kotumsaria bastarensis* Messouli, Holsinger, and Ranga Reddy, 2007, in Kotumsar Cave in the east-central state of Chhattisgarh. Also the gammaroid *Indoniphargus indicus*, which inhabits various groundwater habitats (e.g., springs, well water, and a mine pit) is present in the north-eastern states of Bihar, West Bengal and Odisha. At the same time, some related invertebrate groups of stygobionts such as Syncarida and Copepoda are better studied and a number of recent reports update the stygofaunistic lists of India (Ranga Reddy 2018; see also Williams 1986) and also certain faunistic investigations have been done on marine interstitial groups of amphipods of the neighboring insular territories (Coineau & Rao 1972; Wells & Rao 1987; Vonk & Jaume 2014). Even such a relatively poor taxonomic list of the groundwater amphipods of continental India sheds significant light on their as yet ambiguous historical origin.

Recent faunistic studies of three limestone caves, viz. the Borra, Guthikonda and Kapiladevi caves located in the central and south-central regions of continental India, have yielded three new stygomorphic amphipod crustaceans, which are described and illustrated herein. Of the two new bogidiellid species, *Bogidiella* *hindustanica* **sp. n.** is attributed to the *lindbergi*-group, while *Orientogidiella reducta* **gen. n.**, **sp. n.**, the second member of the *indica*-group, is placed in the newly proposed genus *Orientogidiella* **gen. n.** The third new species belongs to the poorly known mesogammarid genus *Indoniphargus* and is described herein as *Indoniphargus subterraneus* **sp. n.** The affinities of the new species with its allied groups are clarified by a comprehensive discussion of its peculiar morphology.

Material and methods

Subterranean amphipods were collected from three different caves in central and southeastern India (Fig. 1) by the Karaman-Chappuis method (Chappuis 1942) in May/June 2013 and July 2014. Samples were preserved in ca. 70% ethanol, dissected using a dissecting microscope Lomo MBS-9 and mounted on microscope slides in polyvinyl lactophenol (PVL) and methylene blue stain (Sigma-Aldrich Company, Inc.); dissected appendages were then covered with a coverslip and edged by clear nail polish. Prior to dissection, body length from the base of antenna 1 to the base of telson was measured. All the pertinent morphological structures were drawn using a Carl Zeiss NU-2 compound microscope equipped with a drawing device, as modified by Gorodkov (1961). Mouthparts used for scanning electron microscopy (SEM) were dehydrated in acetone and air-dried overnight, and sputter-coated with chromium before being photographed with a Carl Zeiss Merlin field emission scanning electron microscope. Following the Treatise on Zoology (Bellan-Santini 2015), the terms 'article' and 'segment' are used to refer to the articulated parts of appendages and body segmentation, respectively. The term 'defining angle' (or alternatively 'palmar angle') of the gnathopod propodi refers to the angle formed at the end of the palm and beginning of the posterior margin or the point at which the tip of the dactylus closes on the propodus (Birstein 1941; Holsinger 1974). In the present paper we abide by the Bousfield's classification system (Bousfield 1977, 1978), which was partly reflected in Takhteev *et al*. (2015), and believing that without a comprehensive discussion and accurate verification of the modern "Senticaudate concept" (Lowry & Myers 2013) cannot be accepted with due responsibility (d'Udekem d'Acoz & Verheye 2017; Myers & Lowry 2018). A geographical map, with location of the sampling sites, was constructed with open source software Generic Mapping Tools, GMT 4.5.14. The description given here is based on the type series, and the material examined is deposited in the Muséum national d'Histoire naturelle, Paris, France (prefix MNHN).

Systematics

Class Malacostraca Latreille, 1802

Order Amphipoda Latreille, 1816

Superfamily Bogidielloidea Hertzog, 1936

Family Bogidiellidae Hertzog, 1936

Orientogidiella, new genus

Type species. *Bogidiella indica* Holsinger, Ranga Reddy, and Messouli, 2006, here designated.

Generic diagnosis. Amphipods with obvious troglomorphic traits (anophthalmy and depigmentation), slender habitus, small head, well-developed but irregularly rounded inter-antennal lobe. [1]***Antenna I longer than antenna II,*** about 33–35% as long as body. Antenna II lacking aesthetascs. Mandibles well-developed, each with strong incisor, lacinia mobilis and spine row; molar process reduced and with short setae; palp 3-articulate, distal article narrow, bearing 1 apical seta. Outer plate of ***maxilla I*** with 6 or 7 apical serrate spines; inner plate bearing 2–4 apical plumose/naked setae; ***palp 2-articulate (normal) or 1-articulate (reduced)***, bearing 2 apical setae. Both

1. Core diagnostic features are indicated in bold-italic style.

plates of maxilla II sparsely setose with naked setae. Other mouthparts (labrum, paragnath and maxilliped) normal, without obvious peculiarities. Gnathopods relatively small, with prominent propodi; palmar angles of both gnathopods indistinct but with mid-palmar spines; propodi with stiff, tiny notched setae along inner and outer faces of palmar margin; dactyli with shallow serration accompanied by thin setae on inner face, and nail indistinctly demarcated. Coxal plates shallow (wider than deep), plates V–VII indistinctly lobate. ***Pereopod V short***, about 70% as long as pereopod VI and 35% as long as pereopod VII, ***with stocky carpus (article 5) armed with conspicuous groups of strong spines***; pereopod VI armed similar to pereopod V. Coxal gills present on pereonites II–VI. ***Pleopods I–III*** similar, ***without inner rami. Second and/or first uropod sexually dimorphic; inner ramus with apical modified spine in males.*** Uropod III and telson typical of bogidiellids.

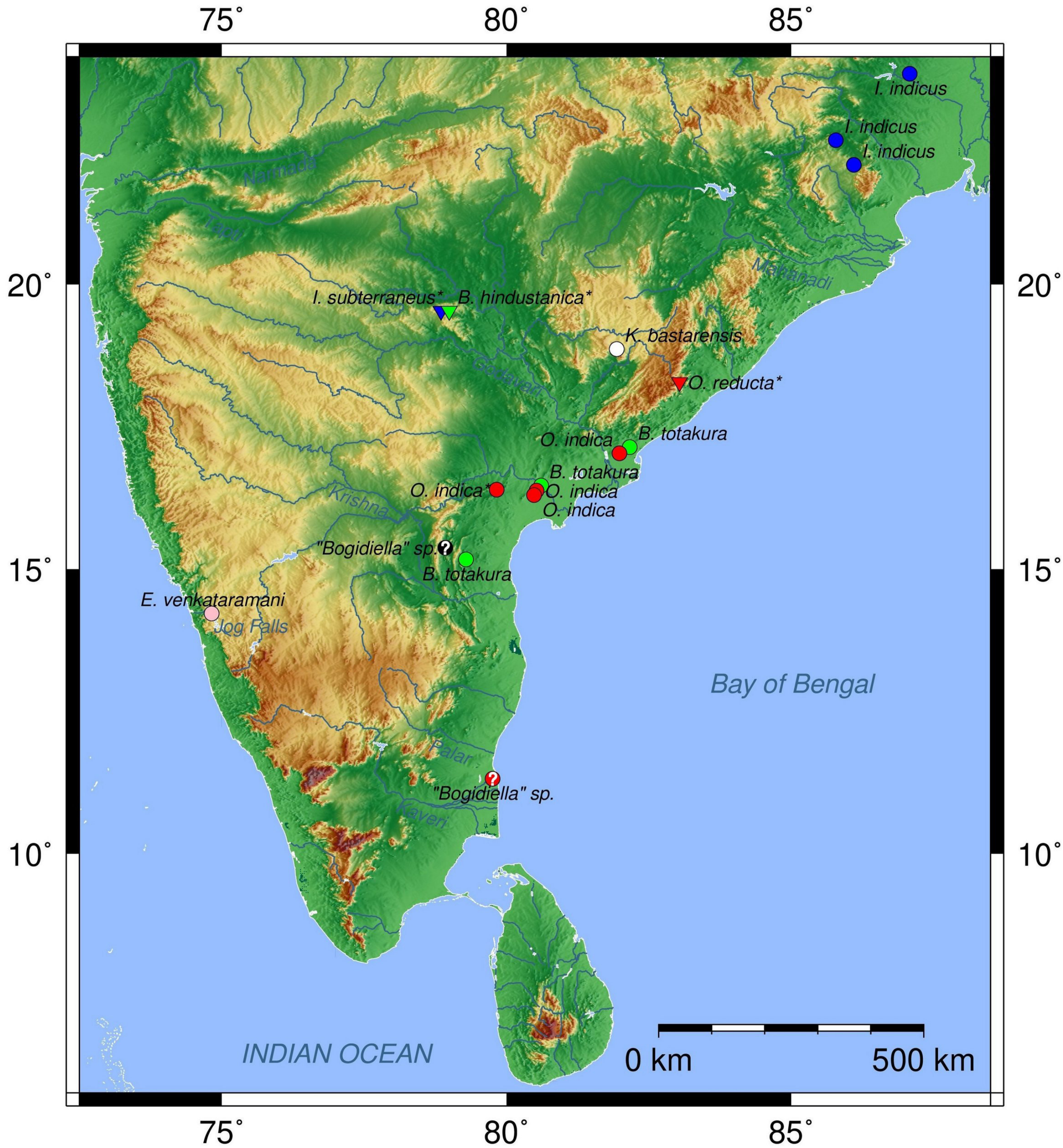

FIGURE 1. Height map of India showing geographic distribution of subterranean amphipods. Question mark (?) indicates collections of undescribed specimens of *Bogidiella* sp. reported in Holsinger *et al*. (2006). Asterisk (*) indicates new sample sites.

Etymology. The generic epithet *Orientogidiella* is derived from the combination of *Orient* (from Latin noun, *Oriens*) meaning the East with '*gidiella*' a part of the closely related genus *Bogidiella*. Gender feminine.

Composition and geographic distribution. Both *Orientogidiella indica* (Holsinger, Ranga Reddy, and Messouli, 2006) comb. n. and *Orientogidiella reducta* **sp. n.** inhabit the freshwater subterranean environment of the southeastern Indian peninsula.

Remarks. In a previous publication, Sidorov *et al*. (2016), being of the opinion that *Bogidiella indica* belonged to the *niphargoides*-group, had expressed doubts about the reliability of the morphological features proposed by Holsinger *et al*. (2006: 53), i.e. reckoning the special structural features of pereopod V for designating the *indica*-group (group E). However, having carried out a comparative morphological analysis of 114 described bogidiellid species in 37 genera, and in particular for *B. indica* (the former monotypic representative of the *indica*-group) versus *Orientogidiella reducta* **gen. n.**, **sp. n.**, described herein, we agree with the rationale of the taxonomic criteria suggested by Holsinger *et al*. (2006) for the *indica*-group of species. Based on the structurally unique pereopod V of this group, we propose here a new genus, *Orientogidiella* **gen. n.**, to accommodate both species. This taxonomic decision warrants a new combination for nomenclatural consistency: *Orientogidiella indica* (Holsinger, Ranga Reddy, and Messouli, 2006) comb. n.

Orientogidiella **gen. n.** is distributed in the coastal belt along the Eastern Ghats (Ghats orientales) at altitudes ranging from ca. 19 to 710 m above sea level. Taking into account the Chidambaram specimen of *Bogidiella* sp. sensu Holsinger *et al*. (2006), which belongs to the same genus, the distribution of *Orientogidiella* **gen. n.** extends from 18° N l. towards the south 11° N l. exclusively along the present coastline, but not extending deeper than 100 km into the interior of the continent (see also discussion in Holsinger *et al*. 2006). Although, we could not confirm our findings with molecular data, we are of the opinion that the species of *Orientogidiella* **gen. n.**, sharing unique phenotypic features, inhabit a common territory along the east coast of India for about 1000 km.

***Orientogidiella reducta*, new species**
Figures 2A, 3–5

Diagnosis. Slender, small-sized amphipods of typical bogidiellid habitus (sexual dimorphism pronounced, i.e., males slightly larger than females; uropods I and II sexually dimorphic with inner rami bearing 1 modified apical spine each in males); coxal plates shallow (wider than deep); posterodistal corners of pleonal plates I–III acute; antenna I longer than antenna II; accessory flagellum of antenna I reduced, 1-articulate; molar of mandible greatly reduced; palp of maxilla I reduced, 1-articulate; propodus of gnathopod I distinctly larger and stouter than that of gnathopod II; pereopods V and VI relatively short (especially pereopod V) with dense row of fine setae on anterior margin of merus (article IV) and with stocky carpus (article V) armed with conspicuous groups of strong spines; pereopods II–VI with coxal gills. Large males 5.5–6.5 mm, largest female 5.0 mm.

Material examined. Holotype MNHN-IU-2018-47. INDIA: ♂ 5.5 mm, Borra caves, cave-pool sediments, 18.280278, 83.038611, elevation ca. 705 m, Andhra Pradesh state, coll. Shabuddin Shaik, 17th June 2013. Paratypes MNHN-IU-2018-48: 2 ♂♂ measuring 6.5 mm each, 3 ♂♂ measuring 6.0 mm each, 1 ♂ 5.5 mm, ca. 3.5 mm fragment, 1 ♀ 5.0 mm, oostegites undeveloped; same data as for holotype.

Etymology. The specific epithet *reducta* (Latin) is an adjective, meaning 'reduced'.

Description of holotype MNHN-IU-2018-47. GENERAL BODY MORPHOLOGY (Figs 2A, 3A, 5A, B, F). *Body* unpigmented (whitish in color), smooth, setose with fine setae. *Head* longer than deep and longer than first pereon segment; rostrum indistinct, interantennal lobe irregularly rounded apically; eyes absent. *Pleonal plates I–III* lacking setae/spines on ventral margins; posterior margins convex, bearing 2 or 3 thin setae; posterodistal corners acute. *Telson* subquadrate with apical margin roundly convex, width to length ratios 1:0.6, bearing 2 strong, notched spines, accompanied by 3 penicillate setae subapically. ANTENNAE (Figs 2A, 3B, C). *Antenna I* about 35% of body length; primary flagellum of 12 articles, each article with 2–6 setae, aesthetascs present on 10 distal articles; ratios of peduncular articles 1–3 1:0.6:0.3; proximal article of peduncle with 2 simple spines on ventral margin; accessory flagellum small, 1-articulate. Ratio of lengths of antenna I to antenna II is 1:0.8; flagellum of *antenna II* of 5 articles, last one minute, each of other articles sparsely setose; peduncular article 4 slightly longer than article 5; flagellum ca. 30% shorter than peduncle (articles 4+5); last 2 peduncular articles with short spines and setae; gland cone short. MOUTH PARTS (Figs 3D–I). *Labrum* subtrapezoidal, as long as broad, epistome broadly roundish. Inner lobes of *paragnath* absent; outer lobes closely spaced, apices somewhat narrowly rounded and finely setose; mandibular process narrow. *Left mandible*: incisor with 5 teeth, lacinia mobilis consisting of 2 finely denticulate plates of similar size; row of 4 densely plumose spines (1 of them long) between lacinia and molar process; molar vestigial, conical, bearing 3 plumose spines. *Right mandible*: incisor with 5 teeth, lacinia mobilis with 5 teeth, row of 4 plumose spines (1 of them long) between lacinia and molar process; molar similar to that of left mandible; mandibular palp article 2 about 25% longer than article 3; palp article 1 without seta, article 2 with 2 long setae on inner margin; distal article narrow, with 1 long seta on apex. *Maxilla I* palp reduced, 1-articulate, with 2 long setae of equal length on apex (palps symmetrical); outer plate with 7 serrate spines; inner plate with 2 plumose setae. *Maxilla II* inner plate broader than outer one, with 4 apical setae of varying size; outer plate bearing 4 simple setae apically. *Maxilliped* outer plate short, evenly rounded apically, with 2 naked sub-apical spines and 2 long lateral setae in distal part; inner plate broad, with 2 short apical spines (1 of them finely serrate) and 1 stiff naked seta, 1 seta located medially on small pedestal; palp 4-articulate; article 2 longest, expanded, distinctly convex on inner margin, with 11 long simple setae in 2 rows along inner margin; article 3 narrow, bearing 2 sets of long setae apically and on medial face; article 4 about as long as preceding article, slightly curved and tapering distally, with 1 dorsal seta and 2 setae at base of nail; inner margin pubescent, nail sharply pointed, 0.25× length of pedestal. Lateralia with 15 strong, pectinate spines. COXAL PLATES AND GILLS (Figs 2A, 4A–G). *Coxal plates I–VII* wider than long, free, not overlapping one another, coxa VI largest; coxal plates V–VII semicircular, narrow posteriorly, bearing 1 stiff seta. *Coxal gills* oblong, stalked on coxae II–VI. GNATHOPODS I AND II (Figs 2A, 4A, B). *Gnathopod I* basis short, broadest medially, with 1 short seta on distoposterior corner; merus with 4 stiff setae on distoposterior margin, posterior surface spinose; carpus triangular, with 2 setae of equal length on narrowly rounded spinose distoposterior lobe; propodus prominent, swollen, ca. 1.5× longer than broad, palmar margin slightly convex, nearly 1.5× longer than posterior margin, palmar angle indistinct, armed with 3 strong spines and 1 long seta; anterior margin with 1 seta, and a group of 2 setae anterodistally; palm armed with 12 stiff, tiny notched setae along inner and outer faces; dactylus falcate, about 50% length of propodus, with 3 shallow serrations, accompanied by thin 1 seta on inner face and 2 short setae on outer face, demarcation of nail indistinct. *Gnathopod II* basis sublinear, with 1 short seta on distoposterior corner; ischium posterior surface spinulose with 1 posterodistal seta; merus with 1 stiff posterodistal seta; carpus sub-triangular, with 16 thin subequal setae on broadened, spinulose ventral lobe, 1 set of long setae distally on medial face; propodus small, nearly 0.3× shorter than propodus of gnathopod I; palmar margin straight, shorter than posterior margin; palmar angle distinct, armed with 2 strong spines and 1 long seta; anterior margin with 1 seta, anterodistal group with 3 setae; palm armed with 2 stiff, tiny notched setae, accompanied by 2 long setae along inner and outer faces; dactylus similar to that of gnathopod I. PEREOPODS (Figs 2A, 4C-G): lacking lenticular organs. *Pereopods III–IV* subequal, bases fusiform (especially PIII), each with 1 stiff seta on anterodistal margin; dactyli ca. 0.4× length of corresponding propodi. *Pereopod V* very short, only about 33% length of pereopod VII and 70% length of pereopod VI; basis broad, 0.5× broad as long, posterior margin with 3 notched spines and 1 seta; merus with a dense row of fine setae anteriorly; carpus (article 5) short and stocky, armed with conspicuously strong lateral spines; propodus (article 6) longer and narrower than carpus, with 5 apical spines; dactylus (article 7) 0.4× length of corresponding propodus. *Pereopod VI* length 0.3× body length; basis broad, length to width is 1:0.5; posterior margin with 3 notched spines and 1 seta; anteriorly 3 notched spines and 2 setae; merus armed like that of pereopod V; carpus armed more profusely than that of pereopod V; propodus with 5 lateral and 4 apical spines; dactylus about 0.33× length of corresponding propodus. *Pereopod VII* ca. 45% longer than pereopod VI, basis subrectangular, ca. 50% longer than wide, both anterior and posterior margins bearing notched spines; carpus longer than merus; propodus with 1 group of 3 short spines and 1 long stiff seta apically; dactylus ca. 40% length of corresponding propodus. PLEOPODS AND UROPODS (Figs 2A, 5A–E). *Pleopods I–III* subequal; peduncular articles linear, in ratios 1:1:0.8, with 2 retinacula each; inner ramus absent; outer ramus 3-articulate, fringed with long, plumose setae at distal end of each article. *Uropod I* peduncle without basofacial spine; with 2 dorsolateral spines and distally with 1 very strong dorsomedial spine; exopodite to endopodite length 0.8:1; endopodite length 0.6× peduncle; rami straight, each armed with 4 strong apical spines (1 of them simple, much larger); endopodite with 1 modified apical spine (large, bowed, tapered to sharp point, with tiny serration on upper surface). *Uropod II* peduncle with 1 dorsolateral spine and 1 strong dorsomedial spine distally; exopodite to endopodite length 0.8:1; endopodite a little shorter than peduncle; rami straight, each armed with 4 spines apically (1 of them simple, much larger) and endopodite with 1 modified sub-apical spine. *Uropod III* (single appendage was found separately in vial): long, with peduncle only about half length of rami, armed with 2 notched spines apically; rami subequal, armed with singly inserted 4 or 5 lateral and 3 apical spines (1 of them long).

Variation. Not observed.

Sexual dimorphism. Female 5.0 mm long, oostegites (brood plates) weakly developed, very small and present on pereopods II–V (non-setose in the material examined); uropods I and II lacking modified spines; in all other characters similar to male.

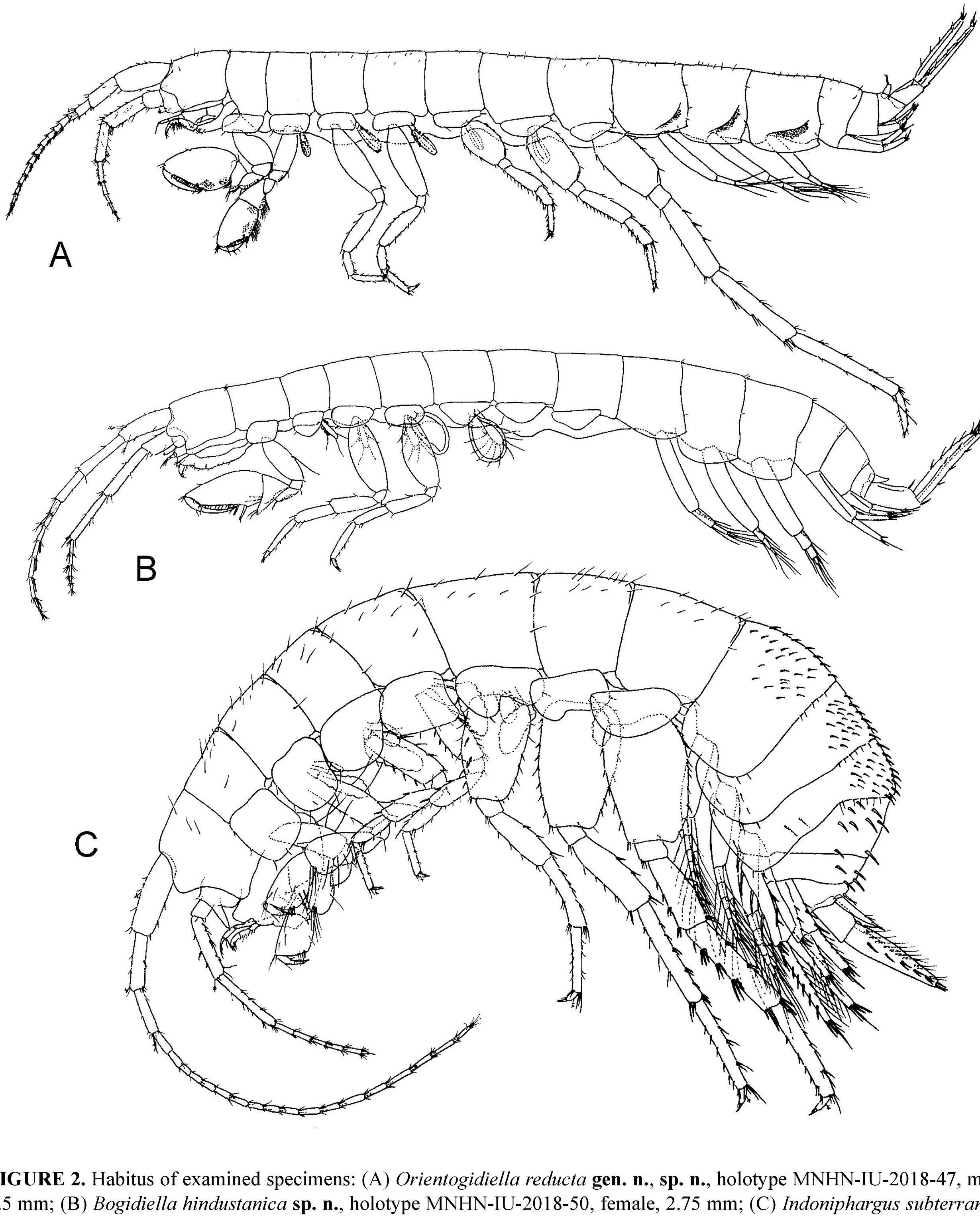

FIGURE 2. Habitus of examined specimens: (A) *Orientogidiella reducta* **gen. n., sp. n.**, holotype MNHN-IU-2018-47, male, 5.5 mm; (B) *Bogidiella hindustanica* **sp. n.**, holotype MNHN-IU-2018-50, female, 2.75 mm; (C) *Indoniphargus subterraneus* **sp. n.**, holotype MNHN-IU-2018-52, female, 5.2 mm.

Distribution and ecology. *Orientogidiella reducta* **gen. n., sp. n.** is known only from its type locality (see Fig. 1). A bathynellacean syncarid, *Habrobathynella borraensis* Ranga Reddy, Shaik, and Totakura, 2014, was also collected from the same locality (Ranga Reddy *et al*. 2014). Interestingly, clusters of some extremely small eggs (or cysts?) were found under each of the pleonal or epimeral plates in the so-called "epimeral pockets" (used here as a conditional name for the cavity between lower free margin of epimera and the lateral margin of abdomen; see Fig. 5A).

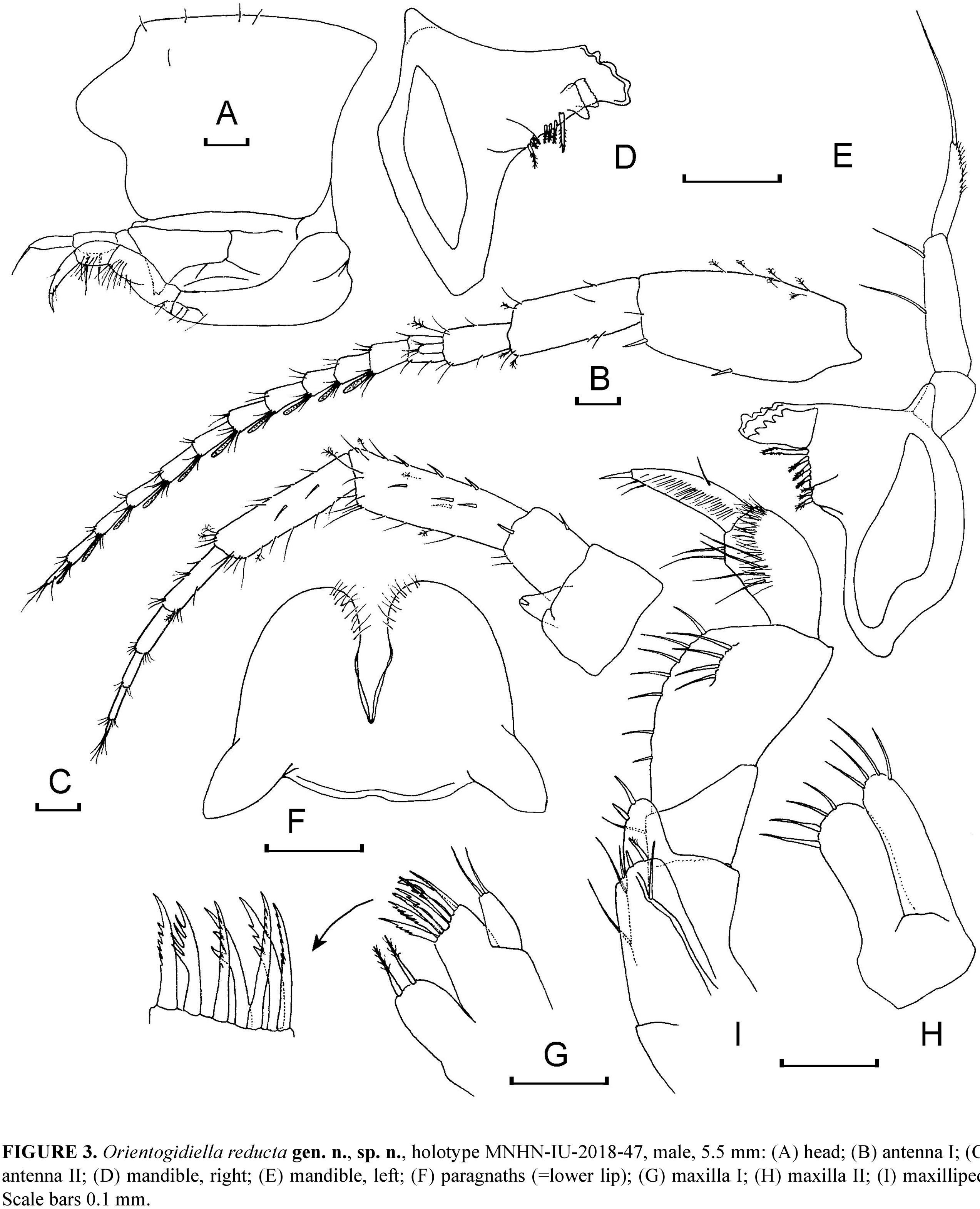

FIGURE 3. *Orientogidiella reducta* **gen. n.**, **sp. n.**, holotype MNHN-IU-2018-47, male, 5.5 mm: (A) head; (B) antenna I; (C) antenna II; (D) mandible, right; (E) mandible, left; (F) paragnaths (=lower lip); (G) maxilla I; (H) maxilla II; (I) maxilliped. Scale bars 0.1 mm.

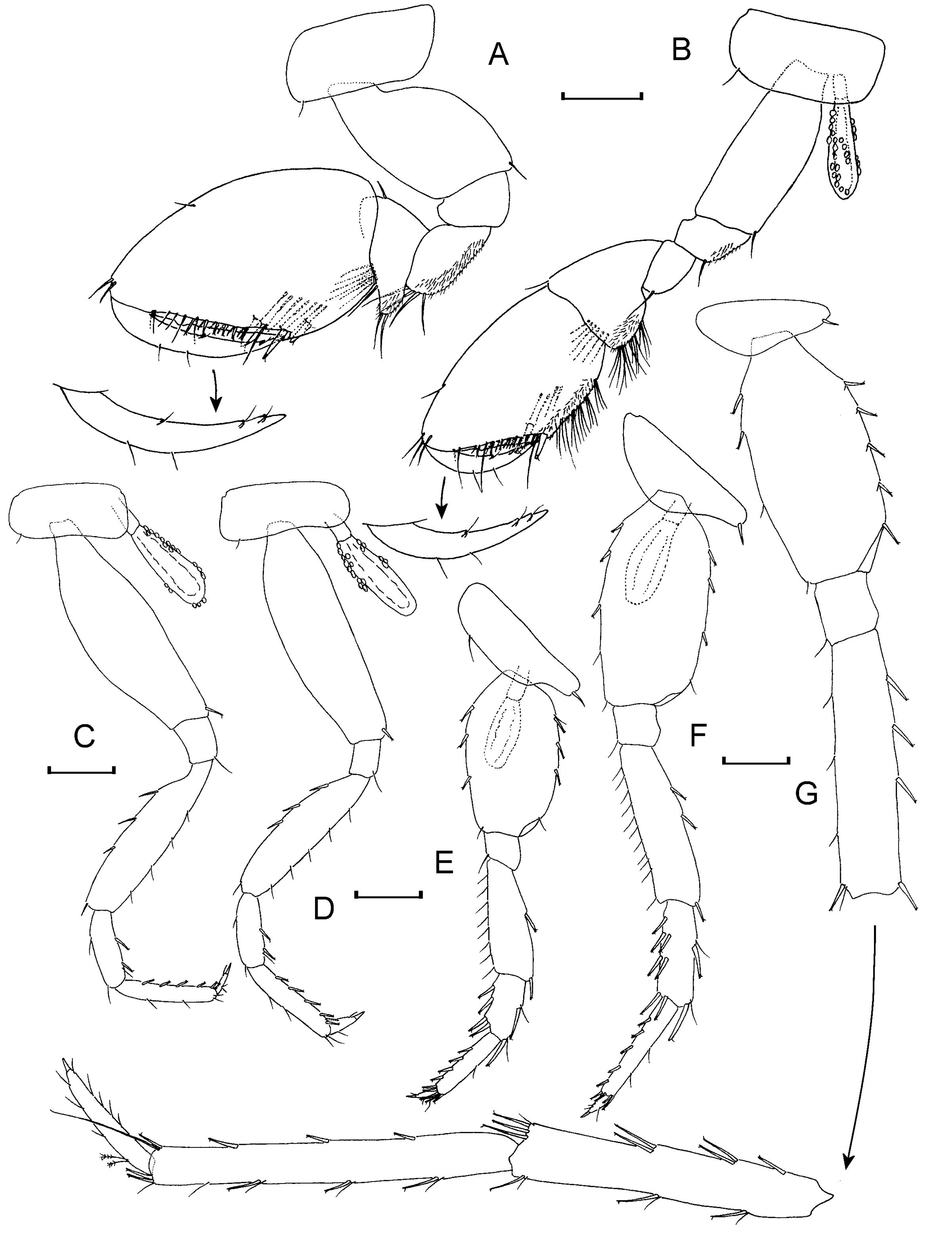

FIGURE 4. *Orientogidiella reducta* **gen. n., sp. n.**, holotype MNHN-IU-2018-47, male, 5.5 mm: (A) gnathopod I; (B) gnathopod II; (C) pereopod III; (D) pereopod IV; (E) pereopod V; (F) pereopod VI; (G) pereopod VII. Scale bars 0.2 mm.

Remarks. *Orientogidiella reducta* **gen. n., sp. n.** most closely resembles *O. indica* (Holsinger *et al*. 2006) comb. n., but can be distinguished from the latter by (character states of *O. indica* comb. n. in parentheses): palp of maxilla I reduced, 1-articulate (normal, 2-articulate); inner lobes of paragnath absent (present); defining angle of gnathopod II armed with 2 strong spines and 1 long seta (spines absent); merus (article 4) of pereopods V and VI with dense row of fine setae on anterior margin (bearing 4 or 5 spines); posterodistal corners of pleonal plates I–III acute (corners of plates I and II indistinct, sub-rounded, plate III acute); and inner ramus of uropod II in males bearing 1 modified spine (modified spines absent).

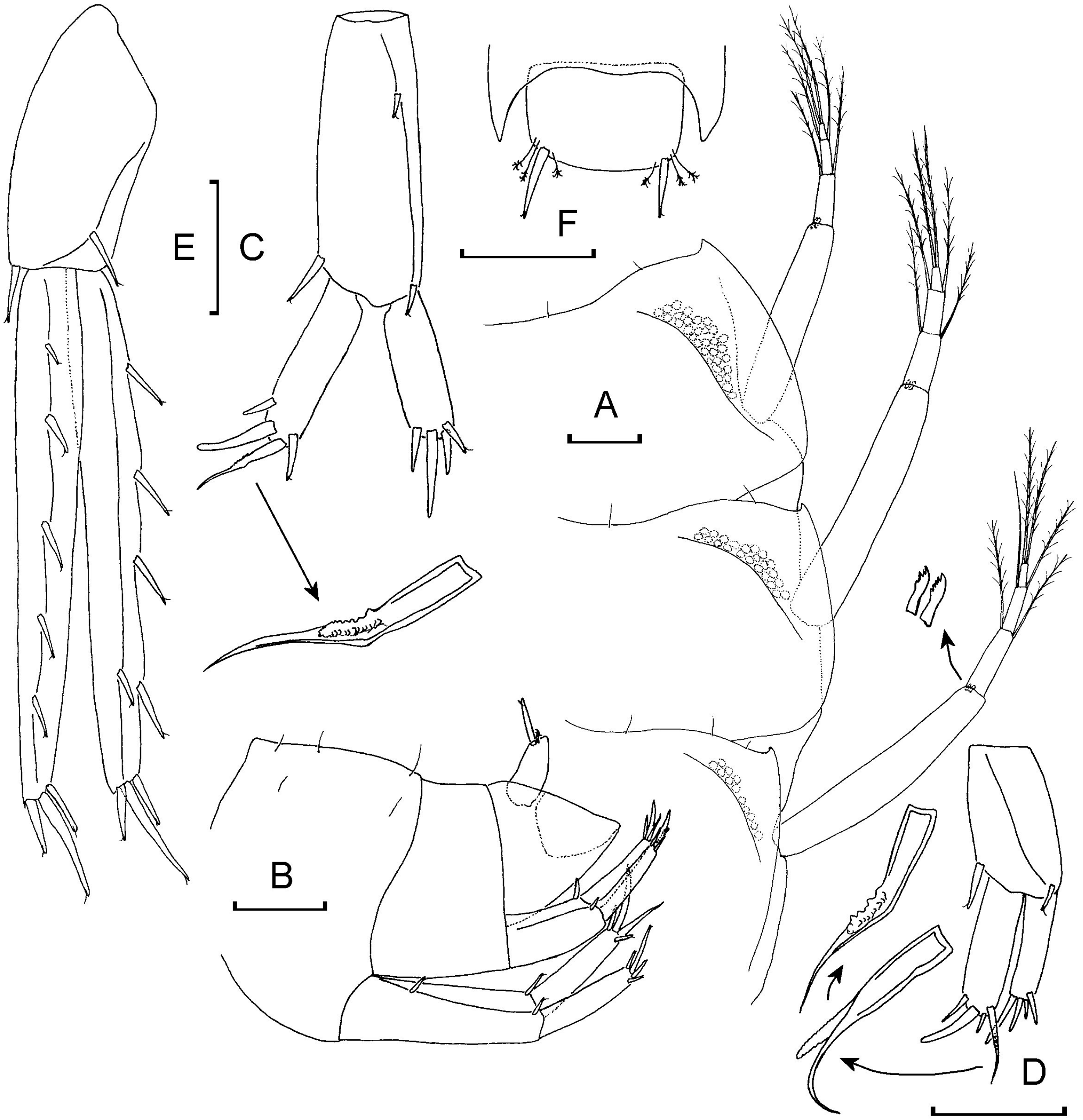

FIGURE 5. *Orientogidiella reducta* **gen. n., sp. n.**, holotype MNHN-IU-2018-47, male, 5.5 mm: (A) pleonal plates I–III and pleopods I–III; (B) urosome; (C) uropod I; (D) uropod II; (E) uropod III; (F) telson. Scale bars 0.2 mm.

Orientogidiella indica (Holsinger, Ranga Reddy, and Messouli, 2006), new combination

Bogidiella indica Holsinger, Ranga Reddy, and Messouli, 2006: 45, Figs 1–5.

Distribution. Previously recorded from three water-wells in Andra Pradesh state of the southeastern India (Holsinger *et al*. 2006) (see Fig. 1).

New record. INDIA: nine specimens MNHN-IU-2018-49: 3 ♀♀ measuring 3.5 mm each, oostegites undeveloped, 3 ♀♀ measuring 3.25 mm each, oostegites undeveloped, 2 ♂♂ measuring 2.75 mm each, ca. 1.5 mm fragment, Guthikonda caves, cave-pool sediments, 16.395112, 79.827492, elevation 160 m, Andhra Pradesh state, coll. Shabuddin Shaik, 6th June 2014.

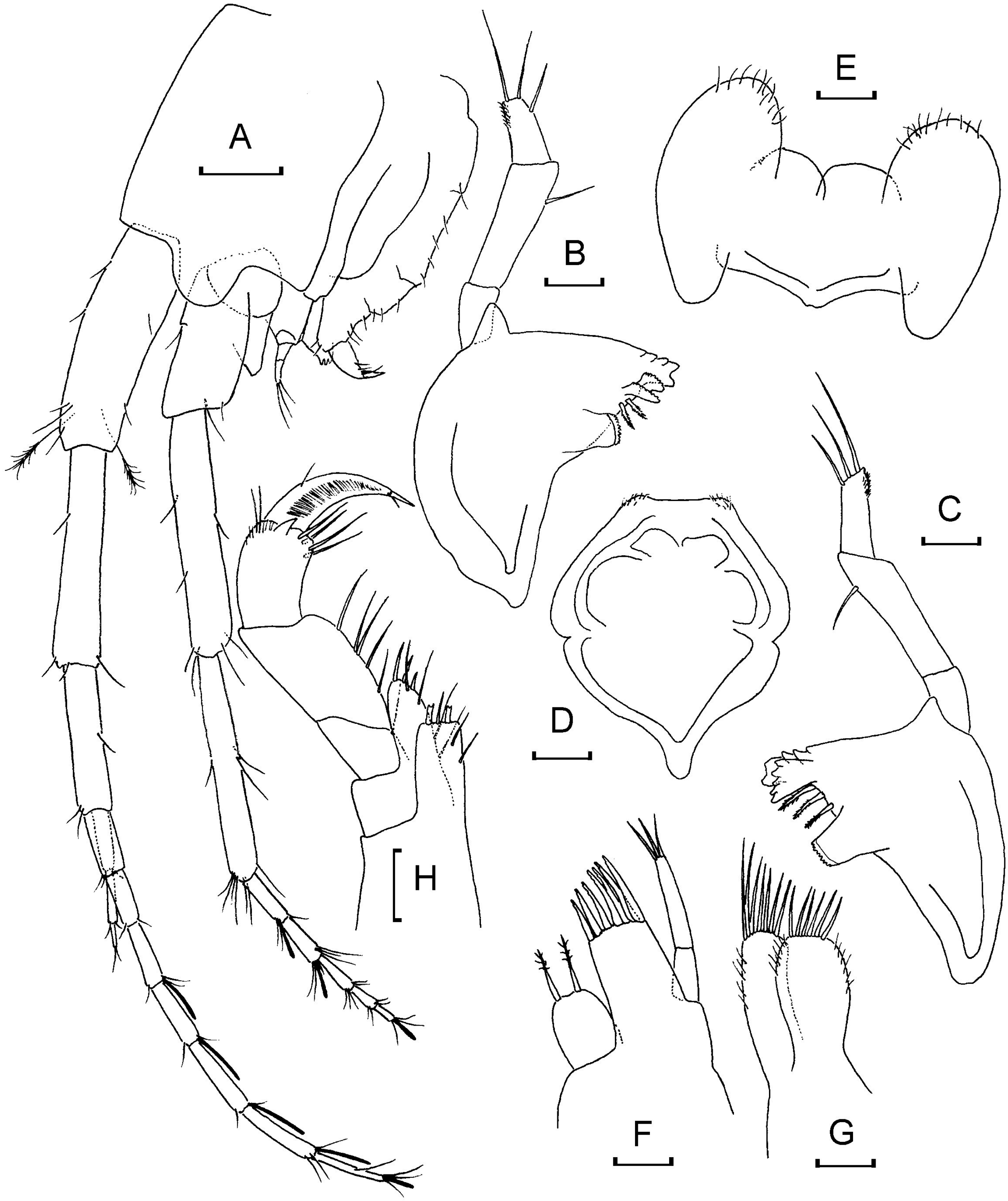

FIGURE 6. *Bogidiella hindustanica* **sp. n.**, holotype MNHN-IU-2018-50, female, 2.75 mm: (A) head and antennae; (B) mandible, right; (C) mandible, left; (D) labrum (=upper lip); (E) paragnaths (=lower lip); (F) maxilla I; (G) maxilla II; (H) maxilliped. Scale bars 0.1 mm.

Remarks. Specimens from the Guthikonda caves agree well with the original description in all essential characters, but a couple of them are at variance: (1) maxilla I outer plate with 7 instead of 6 spines, but their serrate nature is close to the original description (in Holsinger *et al*. 2006, p. 47); (2) gnathopods I and II in both sexes with two shallow dentations on inner face of dactyli accompanied by a thin seta each (similar to those in *O. reducta* **sp. n.**); specimens from the Guthikonda caves reached maturity at a smaller body size: largest males 2.75 mm, largest females 3.25–3.5 mm.

Genus *Bogidiella* Hertzog, 1933

Bogidiella hindustanica, new species

Figures 2B, 6–8

Diagnosis. Slender, small-sized amphipod of typical bogidiellid habitus (sexual dimorphism unknown); distinguished by shallow coxal plates (wider than deep); posterodistal corners of pleonal plates I–III sub-acute; antenna I longer than antenna II; accessory flagellum of antenna I long, 3-articulate; mandibular molar well-developed; maxilla I palp normal, 2-articulate; propodi of both gnathopods almond-shaped, propodus of gnathopod I somewhat large; pereopods V and VI normal; coxal gills present on pereopods IV and V (observed on a damaged specimen). Largest female 2.75 mm.

Material examined. Holotype MNHN-IU-2018-50. INDIA: ♀ ca. 2.75 mm, oostegites developed, setose, Kapiladevi caves, cave-pool sediments, 19.532333, 78.995028, elevation 324 m, Telangana state, coll. Shabuddin Shaik, 12th May 2013. Paratypes MNHN-IU-2018-51: 1 broken ♀ ca. 2.75 mm, oostegites developed, setose, 3 juveniles, ca. 1.5 mm fragment; same data as for holotype. Accompanying fauna: *Indoniphargus subterraneus* **sp. n.** (Amphipoda: Austroniphargidae) described below.

Etymology. The specific epithet *hindustanica* (Latin) is an adjective, derived from the historical toponym, Hindustan, for the Indian subcontinent. Gender feminine.

Description of holotype MNHN-IU-2018-50. GENERAL BODY MORPHOLOGY (Figs 2B, 6A, 7D, 8A, E, I). *Body* unpigmented, smooth. *Head* as long as first pereon segment; rostrum indistinct, interantennal lobe evenly rounded apically; eyes absent. *Pleonal plates I–III* with sub-acute posterodistal corners and with single seta on posterior margin each, ventral margin of plates unarmed. *Telson* subquadrate, narrowed apically, with apical margin straight, bearing 2 tiny setae apically. ANTENNAE (Figs 2B, 6A). *Antenna I* ca. 40% of body length; primary flagellum of 7 articles, each article with 2 or 3 setae, aesthetascs present on each of 5 distal articles; ratios of peduncular articles 1–3 1:1:0.6; proximal article of peduncle with a few thin setae on ventral margin; accessory flagellum long, 3-articulate. Ratio of lengths of antenna I to antenna II is 1:0.77; flagellum of *antenna II* with 5 articles, each article sparsely setose, articles 1, 2 and 5 bearing slender semitransparent, rod-like structures (probably aesthetascs); peduncular article 4 slightly longer than article 5; flagellum 60% shorter than peduncle (articles 4+5); last 2 peduncular articles with sparse setae; gland cone not markedly elongate. MOUTH PARTS (Figs 6B–H). *Labrum* roundish, epistome produced. Inner lobes of *paragnath* well developed, outer lobes broadly spaced, sparsely setose apically; mandibular process narrow. *Left mandible*: incisor with 5 teeth, lacinia mobilis consisting of 2 finely denticulate plates of similar size; 2 or 3 densely plumose spines between lacinia and molar process; molar produced and triturative. *Right mandible*: incisor with 5 teeth, lacinia mobilis with 5 teeth, a row of 3 densely plumose spines between lacinia and molar process; molar similar to that of left mandible; mandibular palp article 2 about twice as long as palp article 3; proximal palp article without seta; article 2 with 1 seta on inner margin; distal article truncated, with 3 long unequal setae on apex, and numerous fine setae near lateral margin on distal half of article. *Maxilla I* palp 2-articulate, with 3 long setae of equal length on apex (palps symmetrical); outer plate with 7 finely pectinate spines; inner plate with 2 faintly plumose setae. *Maxilla II* inner plate broader than outer one, with 6 apical setae; outer plate with 7 long setae of varying size apically. *Maxilliped* outer plate evenly rounded apically, with 3 long, simple apical spines and 2 stiff setae on lateral face, and 2 long lateral setae in distal part; inner plate with 2 bifid apical spines and 1 stiff naked seta, 2 setae located on ventral face; palp 4-articulate; palp article 2 longest, nearly straight on outer margin, slightly convex on inner margin, with a row of 5 long, simple setae along inner margin; article 3 0.7× as long as article 2, with sharply pointed cuticular projection distally and bearing a set of 4 long, stiff setae in ventrodistal position and 2 thin setae in dorsodistal position; article

4 longer than preceding article, distinctly curved and tapering distally, with 1 dorsal seta, and 1 seta at base of nail, inner margin pubescent, nail sharply pointed, 0.25× length of pedestal. COXAL PLATES, OOSTEGITES AND GILLS (Figs 2B, 7A, D). *Coxal plates I–VII* wider than long, without overlapping one another; coxa V largest; coxal plates V–VII progressively smaller posteriad, sub-triangular, plates V and VI bearing 1 stiff seta each posteriorly. *Oostegites* (brood plates) small, progressively larger posteriad, linear, setose with long setae on pereopods II–V. *Coxal gills* ovate, stalked on coxae IV and V. GNATHOPOD I (GII missing) (Figs 2B, 7A). *Gnathopod I*, basis oblong, broadest medially, with 1 long seta on posterior margin; merus with 2 stiff setae on distoposterior margin, posterior surface densely spinose; carpus triangular, with 2 setae of equal length on pointed spinose distoposterior lobe; propodus oblong, about 2.0× longer than broad, palmar margin slightly convex, 3.0× longer than posterior margin, palmar angle indistinct, armed with 3 strong spines and 1 long seta; anterior margin with 1 seta, and a group of 3 setae anterodistally; palm armed with 9 or 10 stiff, tiny notched setae along inner and outer faces; dactylus falcate, about 60% length of propodus, with 2 notches accompanied by thin seta on inner face, demarcation of nail indistinct. PEREOPODS III and IV (PV through PVII missing) (Figs 2B, 7B, C): lacking lenticular organs; structurally similar, bases rather long, fusiform, and each with 2 setae on distal margin; dactyli about 0.3× length of corresponding propodi. PLEOPODS AND UROPODS (Figs 2B, 8B–H). *Pleopods I–III* subequal; peduncular articles linear, in ratios of ca. 0.9:1.0:0.9, with 2 retinacula each; inner rami reduced, 1-articulate, shorter than basal width of article 1 of outer ramus; outer ramus 3-articulate, fringed with long, plumose setae at distal end of each article. *Uropod I* peduncle without basofacial spine and with 1 dorsomedial spine; exopodite as long as endopodite; endopodite length 0.5× peduncle; rami straight, each ramus armed with 3 spines apically (1 of them much larger, sword-shaped). *Uropod II* peduncle with 1 dorsomedial spine distally; exopodite to endopodite length 0.7:1.0; endopodite as long as peduncle; rami straight, each ramus armed with 3 or 4 spines apically (1 of them much larger, sword-shaped). *Uropod III* long, with peduncle twice shorter than rami, armed with 2 notched spines on apex; endopodite with 5 singly inserted spines along outer margin and 3 long, sharply pointed apical spines; exopodite with 5 singly inserted notched spines along margins and 6 apical spines (2 of them much larger, sword-shaped).

Variation. No morphological variation was observed in two damaged adult female specimens of the same body length. Three probably juvenile females measuring ca. 1.1–1.5 mm in body length and without clearly visible oostegites (brood plates) were found in the material examined. The specimens showed no ontogenetic variation in the morphology of appendages except for palms of both gnathopods (see Figs 7E, F) being poorly armed, and articles more profusely covered with minute bristles. Further, the study of these juvenile specimens leaves no doubt that *B. hindustanica* **sp. n.** has normal pereopods V and VI and so cannot be assigned to *Orientogidiella* **gen. n.**

Sexual dimorphism. Males unknown.

Distribution and ecology. *Bogidiella hindustanica* **sp. n.** is known only from its type locality (see Fig. 1).

Remarks. *Bogidiella hindustanica* **sp. n.** is assigned to the *lindbergi*-group (group D, which contains species for which sexually dimorphic characters are unknown, see Koenemann & Holsinger 1999), and to this group we also attribute *B. totakura* Senna *et al*., 2013 because the sexual dimorphism of this species remains still enigmatic. *Bogidiella hindustanica* **sp. n.** closely resembles *B. totakura* in possessing the following features: normal pereopods V and VI; 3-articulate accessory flagellum on antenna I; broad mandibular molar and almost similar form and armature of mandibular palps; and uropods I and II rami with 3 or 4 apical spines (1 of them much larger, sword-shaped). *B. hindustanica* **sp. n.** can, however, be distinguished from the latter species by (character states of *B. totakura* in parentheses): pleopods I–III inner rami reduced, 1-articulate (inner rami absent); and entire apical margin of telson has 2 minute setae (apical margin notched, bearing 2 large spines).

?Superfamily Crangonyctoidea Bousfield, 1973

Family Austroniphargidae Iannilli, Krapp, and Ruffo, 2011 sensu Iannilli *et al*. (2011)
Genus *Indoniphargus* Straškraba, 1967

Indoniphargus subterraneus, new species
Figures 2C, 9–12

Diagnosis. Stocky, small-sized amphipod of typical austroniphargid habitus (sexual dimorphism marked, i.e., males smaller than females, dorsal surface weakly spinose, gnathopods and uropod II sexually dimorphic); remarkably shallow coxal plates III and IV (posterior excavation of coxal plate IV indistinct); antenna II shorter than antenna I, with long gland cone; body of mandibles large, with well-developed palp, molar process with transverse ribs and strong, pectinate spiniform seta ("damper seta"); gnathopods I and II dissimilar in size and armament; carpus of both gnathopods (article 5) elongate and swollen, posterior margins of articles covered with fine soft hairs; pereopods III–VII relatively short and spinose, pereopod VI longest; thoracic segments covered with fine hairs dorsally, but abdominal segments spiny; posterodistal corners of pleonal plates I–III roundish; telson deeply cleft, 2 apical spines on either lobe; coxal gills of pereopods II–VI stalked. Largest male 4.0 mm, female 5.2 mm.

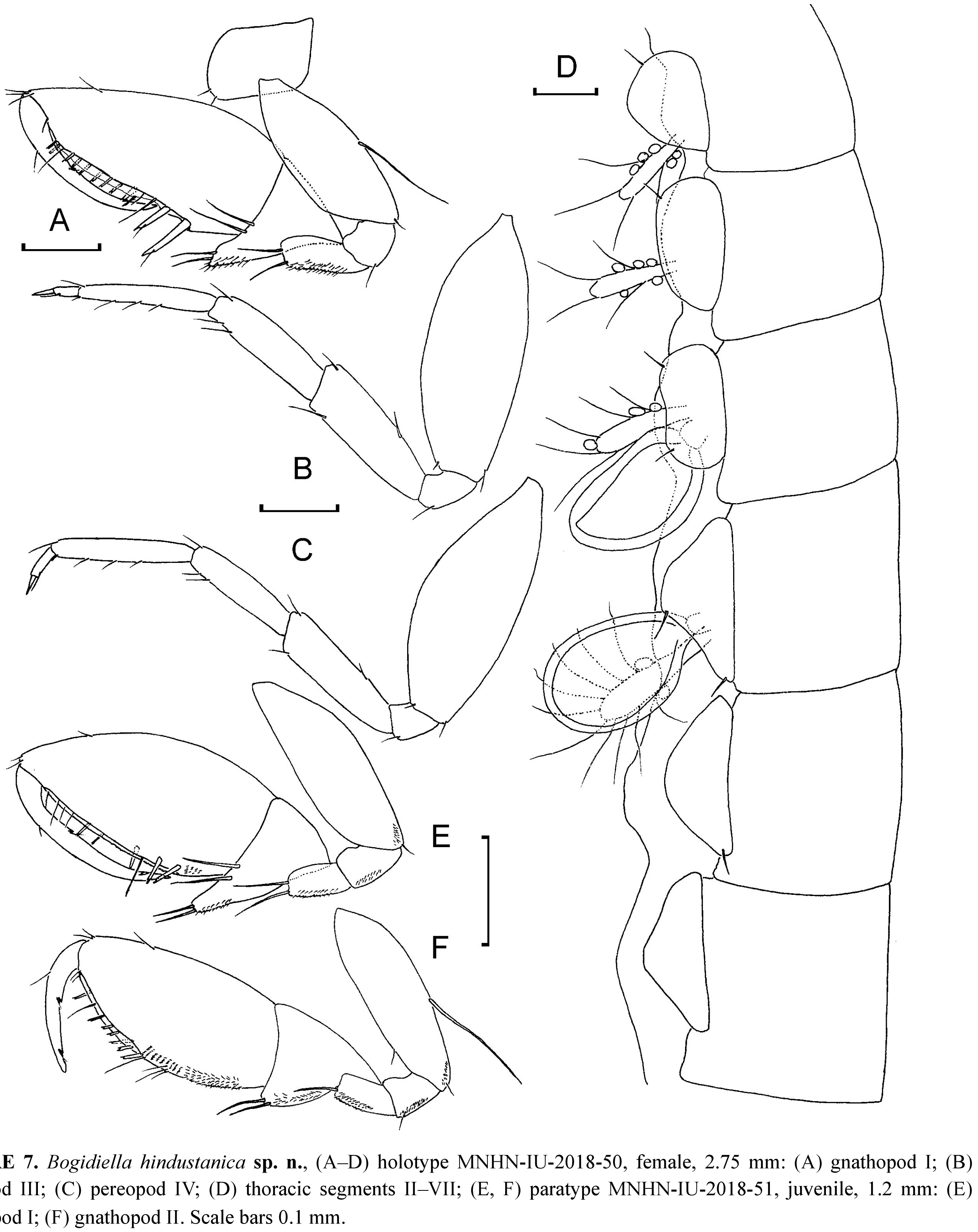

FIGURE 7. *Bogidiella hindustanica* **sp. n.**, (A–D) holotype MNHN-IU-2018-50, female, 2.75 mm: (A) gnathopod I; (B) pereopod III; (C) pereopod IV; (D) thoracic segments II–VII; (E, F) paratype MNHN-IU-2018-51, juvenile, 1.2 mm: (E) gnathopod I; (F) gnathopod II. Scale bars 0.1 mm.

Material examined. Holotype MNHN-IU-2018-52. INDIA: ♀ 5.2 mm, oostegites developed, non-setose, Kapiladevi caves, cave-pool sediments, 19.532333, 78.995028, elevation 324 m, Telangana state, coll. Shabuddin Shaik, 12th May 2013. Paratypes MNHN-IU-2018-53: 2 ♂♂ measuring 4.0 mm each, 5 juveniles; same data as for holotype. Accompanying fauna: *Bogidiella hindustanica* **sp. n.** (Amphipoda: Bogidiellidae) described above.

Etymology. The specific epithet *subterraneus* (Latin) is an adjective, meaning 'underground'. Gender masculine.

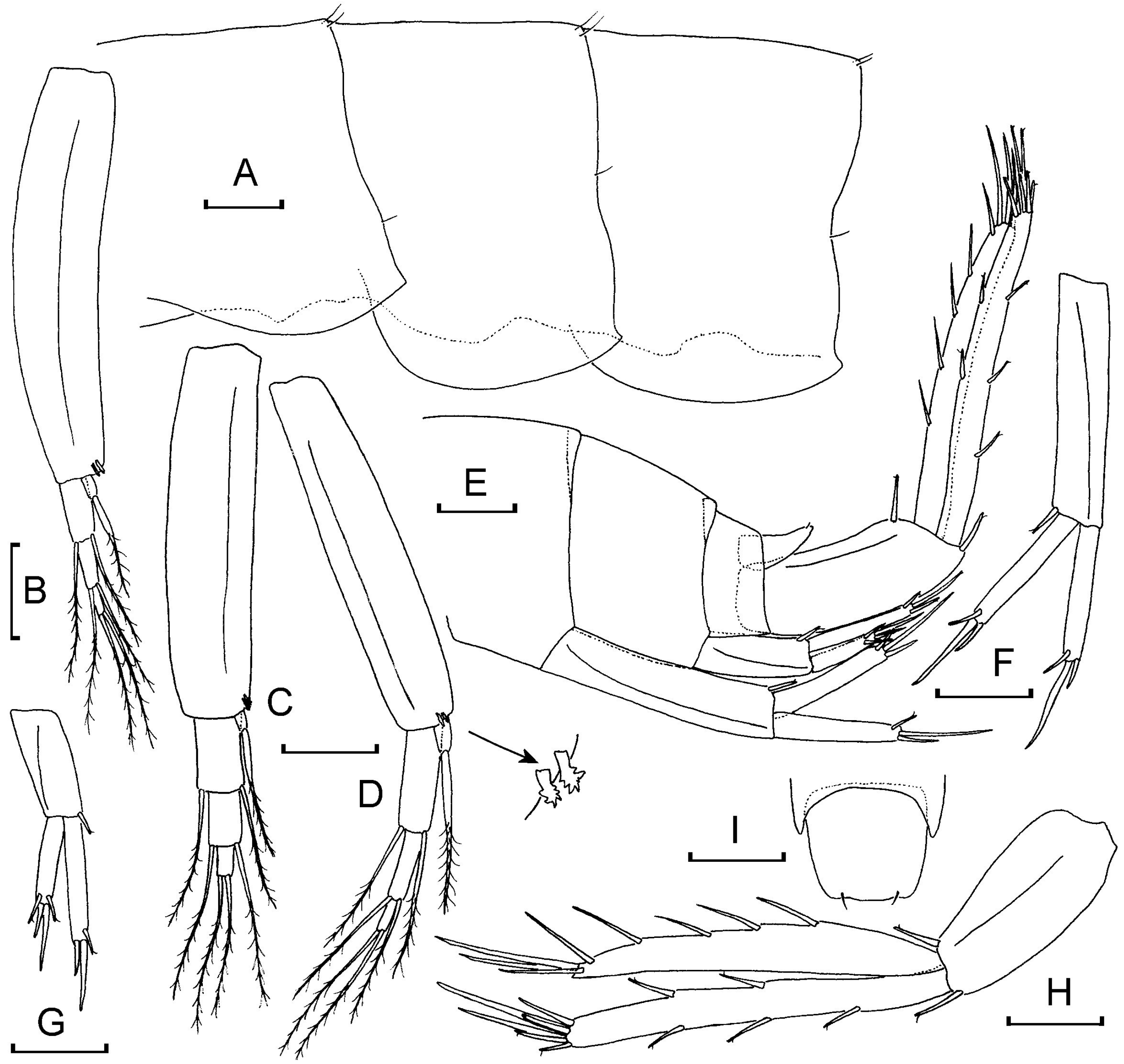

FIGURE 8. *Bogidiella hindustanica* **sp. n.**, holotype MNHN-IU-2018-50, female, 2.75 mm: (A) pleonal plates I–III; (B–D) pleopods I–III; (E) urosome; (F) uropod I; (G) uropod II; (H) uropod III; (I) Telson. Scale bars 0.1 mm.

Description of holotype MNHN-IU-2018-52. GENERAL BODY MORPHOLOGY (Figs 2C, 9A, 11A, H). *Body* whitish, semitransparent in preserved specimens, stout, lacking dorsal cuticular elements, but densely covered with thin setae and curved spines. *Head* as long as first pereon segment; rostrum indistinct; interantennal lobe rounded, inferior antennal sinus shallow; eyes absent. *Pleonites* and *urosomites* bearing stiff, curved and distally notched setae on dorsal surface; urosome segments distinct; urosomite I bearing 2 strong spines on ventral margin. *Pleonal plates I–III* with roundish posterodistal corners, each bearing 2 or 4 notched spines; 5–7 stiff notched setae on posterior margin; ventral margins of plates unarmed; plates II and III with lateral groups of spines.

Telson about 0.25× longer than broad, deeply cleft; lobes tapered distally, bearing 2 apical notched spines each. ANTENNAE (Figs 2C, 9B, C). *Antenna I* ca. 55% of body length, and 2.0× longer than antenna II; ratios of peduncular articles 1–3 1:0.7:0.5, article 1 with a few notched spines on ventral margin; primary flagellum with 18 articles, each article with 2-4 short setae, aesthetascs present on each of 12 distal flagellar articles; accessory flagellum short, 2-articulate. *Antenna II* (flagellum short due to some malformation): gland cone long; peduncular article 5 longer than article 4, both articles bearing sparse notched spines along dorsal and ventral margins; flagellum about 30% shorter than peduncle (articles 4+5), consisting of 6 articles with sparsely covered thin setae; calceoli absent. MOUTH PARTS (Figs 9D–K). *Labrum* sub-quadrate with fine setae on apex. *Paragnath* outer lobes rounded, mandibular process narrow, inner lobes absent. *Mandibles* sub-equal: right mandible incisor process with 6 teeth, lacinia mobilis consisting of 2 finely denticulate plates of similar size, and a row of 4 serrate spines between lacinia and molar; triturative molar process bearing strong, pectinate spiniform seta (see Fig. 12) at upper distal corner and opposite short, plumose gnathobasic seta; incisor of left mandible with 7 teeth, lacinia mobilis with 5 teeth; a row of 4 serrate spines between lacinia and molar process; molar similar to that of right mandible; mandibular palp article 2 twice as long as palp article 3; proximal palp article without setae; article 2 with a group of 4 plumose setae on subterminal margin; distal article short, with a group of 10 E-setae (1 of them very long) on distal half. *Maxilla I* inner plate narrow, with 2 plumose setae, outer plate with 9 multi-toothed spines (first two of them bifid); palp relatively long, both asymmetric; distal palp article with 6 strong spines and 1 simple seta each on apical and sub-apical margins (left maxilla I, Fig. 9H); or 4 finely plumose setae (right maxilla I, Fig. 9I). *Maxilla II* with both plates narrow, apical margin of outer plate with 24 simple setae of varying size and occurring in 2 rows; inner plate lacking oblique row of setae but bearing 1 long, plumose seta apicomedially and 16 short simple setae in 2 rows on apical margin. *Maxilliped*: inner plate oblong, narrow, with 3 strong spines and 2 naked setae apically, 4 plumose setae on inner ventral face; outer plate sub-ovoid, with a row of 6 strong, knife-like spines and 3 groups of paired simple setae along outer margin; palp article 2 sub-linear, with a row of about 10 thin setae along inner ventral face and 1 elongate apicolateral seta; article 3 narrow, with a subtle pubescent bulge on posterodistal lobe, 3 long setae on distal margin, and a row of 4 long simple setae medioventrally; article 4 (distal) shorter than article 3, curved, with 1 dorsal seta and 2 setae at base of nail; inner margin pubescent, nail slender, sharply pointed and slightly shorter than pedestal. COXAL PLATES, OOSTEGITES AND GILLS (Figs 2C, 10A–G). *Coxal plates I–IV* dissimilar in shape being somewhat square or rectangular, slightly overlapping one another, and each with a sparse row of short setae along ventral margin; *coxal plates V* and *VI* with distinct anterior lobes, posterior margin bearing 1 seta each; *coxal plate VII* rather large, semilunar, with 2 setae on posterior margin; each of plates II–VI bearing single coxal gill each with long stalk. Sternal gills absent. *Oostegites II–V* not well developed. GNATHOPODS I AND II (Figs 2C, 10A, B). *Gnathopods* almost similar, subchelate, but gnathopod II somewhat larger than gnathopod I; surface of posterior margins with peculiar patches of pilosity; basis (article 2) with 2 short setae on anterior and 3 long setae on posterior margins; carpus (article 5) stout, sub-triangular, anterior angle bearing 1 seta, 2 groups of long, stiff setae on subventral margin; propodus (article 6) sub-rectangular, bearing a group of 3 setae on antero-distal corner, 1 or 3 long setae along on subventral margin; palm twice shorter than posterior margin, somewhat oblique and beveled, with cutting margin rugous, palmar margin with 2 short setae along outer and inner faces, palmar angle indistinct but armed with 4 distally notched spines along with 2 long setae; dactylus strong, crescent-shaped, nail long, 0.4× of total length of dactylus, 1 seta on anterior margin, inner margin smooth, with a group of setules. PEREOPODS (Figs 2C, 10C–G). *Pereopods III* and *IV* sub-similar, without any obvious peculiarities; bases narrow, with short, stiff setae on both margins. *Pereopods V−VII* sub-similar; length ratios 5:6:7 is 0.7:1.0:0.9. *Pereopod VI* length 0.5× body length. Bases of pereopods V–VII narrowed distally, posterior margins slightly expanded, but postero-distal lobes indistinct; marginal serration with short, stiff notched setae posteriorly and with 6–10 notched spines anteriorly; merus, carpus and propodus strongly spinose, especially in pereopod VII; dactyli relatively short, about 0.3× of propodus length, inner margin with 1 stiff seta at hinge. PLEOPODS AND UROPODS (Figs 2C, 11B–G). *Pleopods I–III* sub-equal, each with 2 coupling setae (retinacles); peduncular articles naked; outer rami larger, with 7–8 articles each, inner rami slender, consisting of 5 articles, both rami fringed with long, plumose setae. *Uropod I* heavily spinose with strong, curved, distally notched spines; protopodite with 4 robust, basofacial spines, 5 dorso-lateral spines, 5 dorso-medial setae and 1 very large corner spine; endopodite as long as protopodite, each with 3 spines on outer margin, accompanied by short plumose setae; exopodite as long as endopodite, bearing 5 spines along lateral margin; rami fringed with long plumose setae on inner margins and armed with 5 spines apically and sub-apically (one of them very large).

Uropod II exopodite 0.2 as long as protopodite and slightly shorter than endopodite; protopodite and rami armed sub-similar to those of uropod 1. *Uropod III* parviramus/dispariramus; endopodite vestigial, scale-like, 50% of as protopodite length, fringed with 1 medial and 1 apical plumose setae; exopodite 1-articulate, 0.6 as long as protopodite, with 5 sets of distally notched spines on outer margin and with a dense row of 10 plumose setae accompanied by 2–3 short spines along inner margin and 3 distally notched apical spines.

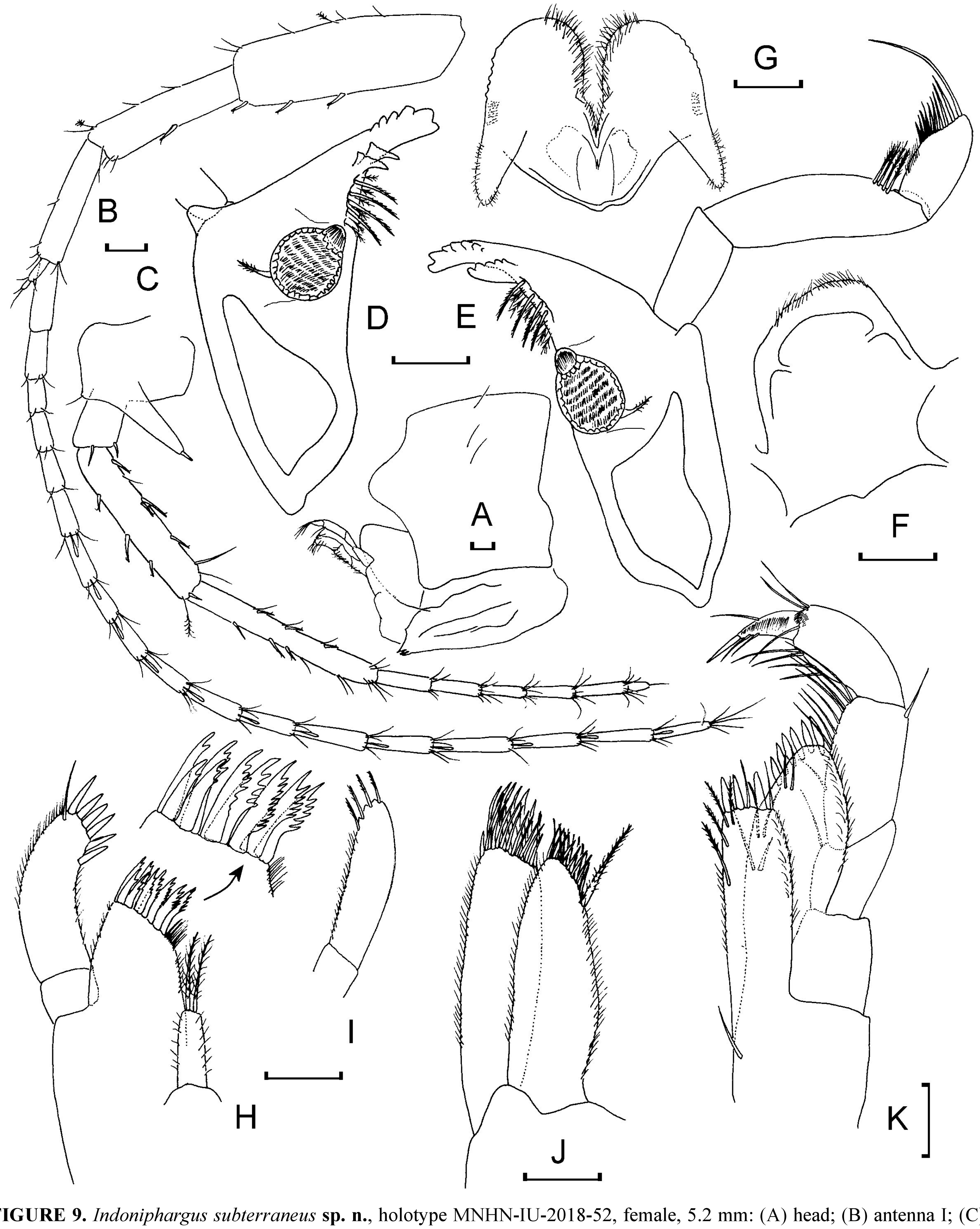

FIGURE 9. *Indoniphargus subterraneus* **sp. n.**, holotype MNHN-IU-2018-52, female, 5.2 mm: (A) head; (B) antenna I; (C) antenna II; (D) mandible, right; (E) mandible, left; (F) labrum (=upper lip); (G) paragnaths (=lower lip); (H) maxilla I, left; (I) palp of right maxilla I; (J) maxilla II; (K) maxilliped. Scale bars 0.1 mm.

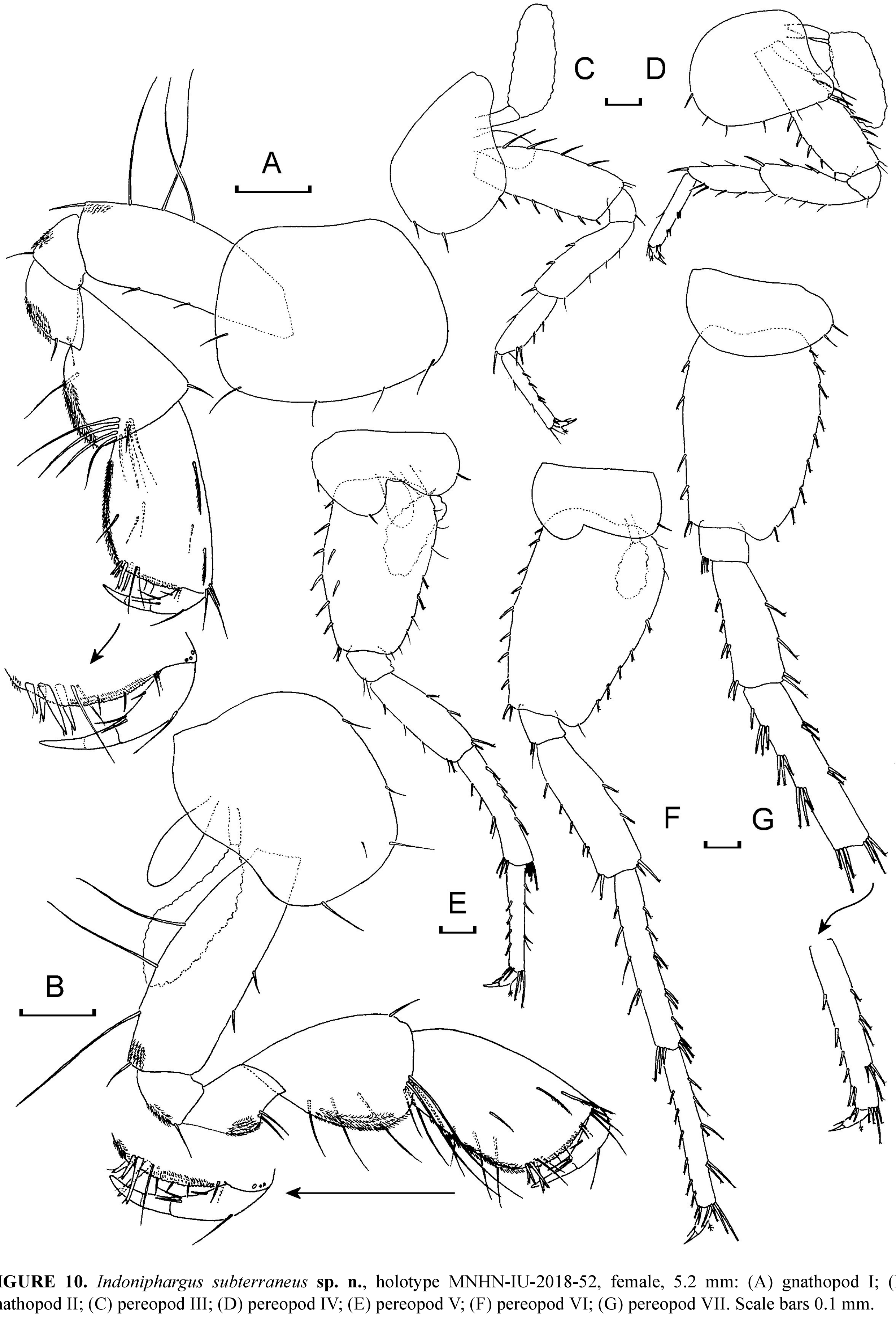

FIGURE 10. *Indoniphargus subterraneus* **sp. n.**, holotype MNHN-IU-2018-52, female, 5.2 mm: (A) gnathopod I; (B) gnathopod II; (C) pereopod III; (D) pereopod IV; (E) pereopod V; (F) pereopod VI; (G) pereopod VII. Scale bars 0.1 mm.

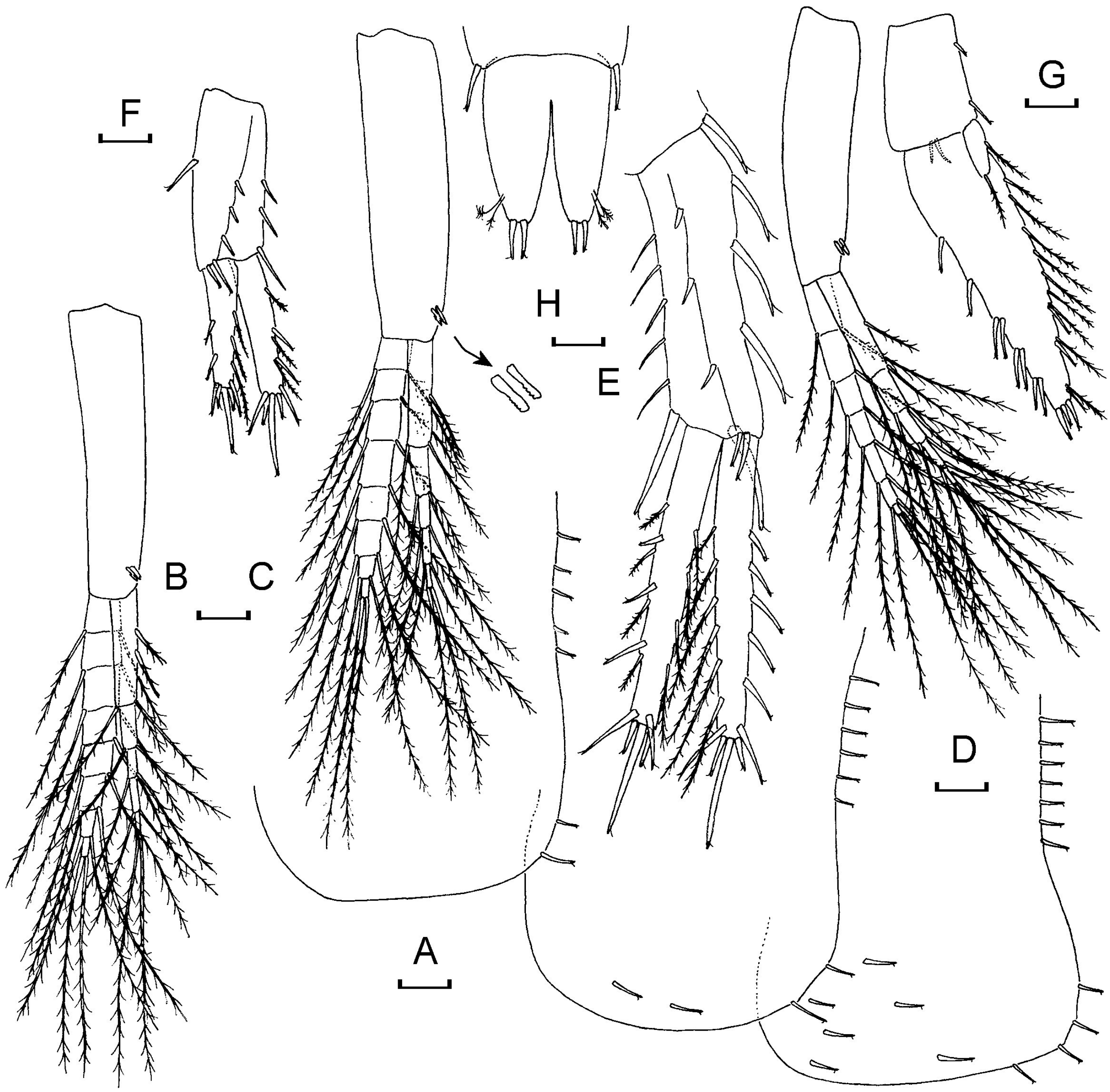

FIGURE 11. *Indoniphargus subterraneus* **sp. n.**, holotype MNHN-IU-2018-52, female, 5.2 mm: (A) pleonal plates I–III; (B–D), pleopods I–III; (E) uropod I; (F) uropod II; (G) uropod III; (H) telson. Scale bars 0.1 mm.

Variation. Not observed.

Sexual dimorphism. Two damaged, apparently subadult males, both without antennae, some pereopods differing from those of female, and habitus smaller and more slender and sparsely covered with spines and setae; gnathopods sub-similar, gnathopod propodi with a clearly emergent palmar angle and bearing only 2 mid-palmar spines; peduncle of uropod II heavily armed bearing 3 additional groups of paired spines on ventral face.

Distribution and ecology. *Indoniphargus subterraneus* **sp. n.** is known only from its type locality (see Fig. 1).

Remarks. An enigmatic *I. indicus* (Chilton, 1923) collected in a coalmine and springs of north-eastern India (Fig. 1) was reported in several previous publications (see Straškraba 1967), which has now necessitated a comparative study of this species with *I. subterraneus* **sp. n.** First of all, it must be underscored that the differences observed by us, though not numerous, are indeed significant. A distinctive feature of *I. indicus* is the clear reduction in the size of coxal plates, which is typical of stygomorphic forms; also, *I. subterraneus* **sp. n.** can be distinguished from *I. indicus* mainly by the following features (character states of *I. indicus* in parentheses): gland cone of antenna II long, tip reaching about half of peduncular article 4 (short, not reaching); posterodistal corners

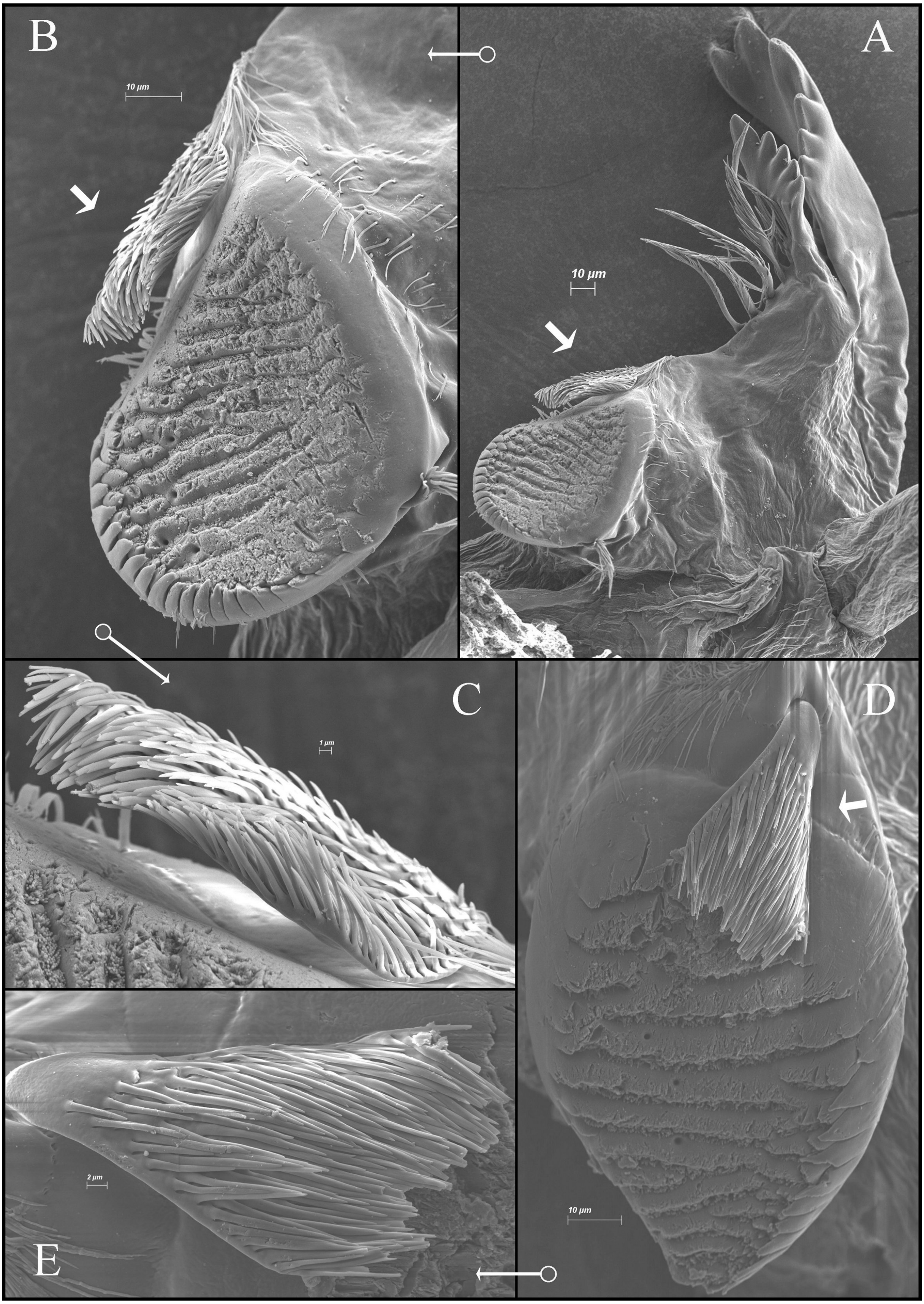

FIGURE 12. Scanning electron micrographs of mandibles of *Indoniphargus subterraneus* **sp. n.**, holotype MNHN-IU-2018-52, female, 5.2 mm: (A) right mandible, anterior part; (B) molar process of the same mandible, lateral view; (C) surface of a pectinate "damper seta" (detail from Fig. 12B); (D) molar process of left mandible, median view; (E) surface of a pectinate "damper seta" (detail from Fig. 12D).

of pleonal plates roundish (rectangular), and telson without dorsolateral spines (with 2 spines). At the same time, we must admit that some features of *I. indicus* (e.g., number of spines on outer plate of maxilla I, absence of the oblique row facial setae on maxilla II, mittenform propodi of gnathopods, a number of retinacles, etc.) are somewhat different from those mentioned in the previous publications, thus warranting a more detailed morphological study of the species. Further, we propose to treat the genus *Indoniphargus* Straškraba, 1967, as belonging to the family Austroniphargidae Iannilli, Krapp, and Ruffo, 2011 sensu Iannilli *et al*. (2011) (see Discussion below).

Discussion

The history of the taxonomic position of the monotypic genus *Indoniphargus* is rather confusing. Originally, Chilton (1923) tentatively placed *indicus* in the genus *Niphargus* on the basis of a diagnosis compiled by Stebbing (1906, p. 405). Later, Stephensen (1931) gave a detailed re-description of this species, justifying it as an addition to the genus *Neoniphargus* Stebbing, 1899. After re-examining the Australian *Neoniphargus*, Straškraba (1964) differed with this viewpoint, because he presumed it to be a distinct genus that is more closely related to the Japanese *Eoniphargus* Uéno, 1955; and some time later, Straškraba himself (1967) proposed a new genus *Indoniphargus* for *indicus*, suggesting its origin along with the distant *Neoniphargus*-*Eoniphargus* group from a common littoral ancestor, which inhabited the shallow areas in the Western Pacific. A decade later, Bousfield (1977), when erecting the family Neoniphargidae (family group 3) for the heterogeneous groups of apomorphic and mainly epigean crangonyctoideans of antiboreal freshwaters, provisionally included ?*Indoniphargus* here. Thereafter, Barnard & Karaman (1980), while unraveling Bousfield's amphipod system, suggested that *Indoniphargus* needs to be removed from crangonyctids and transferred to the eriopisellid-group of Melitoidea (Hadzioidea), but it would perhaps have been better if *Eoniphargus* had been shifted to the gammarids (see also Bousfield 1982, p. 262). Still later, Williams & Barnard (1988) revised the taxonomy of freshwater crangonyctoid amphipods of Australia and removed *Indoniphargus* from the Neoniphargidae on the premise that 'as a crangonyctoid because…has basofacial spines on the peduncle of uropod 1' . In the World amphipod checklist by Barnard & Barnard (1983), *Indoniphargus* is briefly characterized with an obvious contradiction as a genus 'with the facies of certain crangonyctids or Oriental gammarids' , and placed it in the section "E. *Melita* (Melitidae), sub-section 2a. *Eriopisella*-group". Around the same time, Barnard & Karaman (1983) suggested that the affinities of *Indoniphargus* lie with the Australian crangonyctoids, but may also be with a geographically closer marine relative, and in Stygofauna Mundi (Botosaneanu 1986), *Indoniphargus* was putatively named by Williams (1986) as belonging to (melitid?). Stock & Jo (1990) thoroughly clarified relationship between *Eoniphargus* and *Indoniphargus*, suggesting a combination of characters that are a sufficient proof for a non-crangonyctid lineage of the Oriental group. A little later, Holsinger (1994) analyzed the global biodiversity patterns of the subterranean amphipods and assigned the Indian species to the *Eoniphargus/Indoniphargus* group, stating that taxonomic affinities of these groups are unclear. Then, Tomikawa *et al*. (2007) re-described the type species of *Eoniphargus* (*E. kojimai* Uéno, 1955) and transferred it to the Mesogammaridae, reinforcing the morphological data with DNA phylogeny and expressing the opinion that *Indoniphargus* could potentially be also a mesogammarid. In the work devoted to taxonomy of the Madagascan amphipods, Iannilli *et al*. (2011) did not specifically discuss the identity of *Indoniphargus*, but explained in detail the rationale behind the family Austroniphargidae, which was originally created for the endemic subterranean groups of Madagascar. Finally, the most recent work devoted to the description of a rather aberrant Brazilian cavernicolous mesogammarid (Fišer *et al*. 2013) provides itemized comparison of *Indoniphargus* with its relatives.

During morphological investigation of the Kapiladevi specimens of *I. subterraneus*, we observed certain poorly known characters that appear to be significant for reappraising the taxonomic position of the genus *Indoniphargus*: (1) ***small, curved abdominal spines*** that are extensively covering the dorsolateral surface of pleosomal and urosomal segments constitute a rather remarkable feature that does not occur in other known amphipods. So, *Indoniphargus*, according to Straškraba (1967, p. 128), is reminiscent of Schellenberg's (1931) gammarid genera of "Sectio spinosa", but in our opinion such a similarity is extremely superficial because the spines are spread over a vast area in sub-symmetrical spots on both sides; (2) posterior margins of ***gnathopods I and II possess pilosity patches*** densely covered with microseta. This feature together with the characteristic shape and structure of the same gnathopods is indeed shared by a number of amphipod groups such as the Madagascan Austroniphargidae sensu Iannilli *et al*. (2011) and the Australian neoniphargids (Williams & Barnard 1988; Bradbury & Williams 1997); (3) molar process of the mandible is stout and the surface is equipped with transverse ribs, bearing ***'pectinate spine-seta' at upper corner***, and the mandibular palp also has a characteristic structure and armament, particularly article 2 has a compact group of setae and article 3 is short, bearing only a multiple group of E-setae (lacking A-, B-, C- and D-setae). The above-listed features, in our opinion, vividly characterize an unusual construction of mandibles. The structural details of the mandibles, particularly the "pectinate spine-seta" of the molar, are well depicted for *I. indicus* when it was first treated by Stephensen (1931, pp. 16–17), and subsequent references (see Vigna Taglianti 1972, p. 45; Daneliya 2011, p. 42) could be useful in figuring out the essential morphology. Apparently, something distinctly similar to the same structure but not indicated in the original text-descriptions is depicted in the Madagascan spring austroniphargid *Dussartiella madegassa* Ruffo, 1979 (Ruffo 1979) (currently Dussartiellidae of Allocrangonyctoidea in "Senticaudate concept") and in the Brazilian cavernicolous mesogammarid *Potiberaba porakuara* Fišer, Zagmajster, and Ferreira, 2013 (see Fišer *et al*. 2013). This pectinate spine structure (termed here "damper seta") in SEM-images appears as a movable flat paddle, apparently with smooth ventral face and pectinate (cristate) from above. By judging the location and shape of the "damper seta" and its clearly visible but somewhat damaged terminal part (Fig. 12), we are of the opinion that this structure probably serves as an absorber, preventing excessive friction of the surfaces of both molars against each other, thus reducing their premature abrasion, and/or serves to clean the surface of the opposite molar from sticking food particles. This structure seems to be rather widely represented in Amphipoda in varied shapes (see also Mayer *et al*. 2012, p. 273).

A number of important morphological features inherent in Madagascan Austroniphargidae sensu Iannilli *et al*. (2011) were either not sufficiently well described or undue importance has been attached to them. For example, in Iannilli *et al*. (2011) the surfaces of the molar processes of mandibles are drawn schematically which makes it difficult for us to do a detailed comparative morphological analysis of mouthparts. The character states of urosomal segments (coalesced/non-coalesced) are over-emphasized in the diagnoses of the Madagascan families by Lowry & Myers (2012, 2013), and the same is the case in various other groups of amphipods as well (Bousfield 1983). We are of the opinion that such a segmental abnormality is not a taxonomically significant family-level criterion. It is likely that this feature results from chromosomal mutation or incorrect expression of homeotic genes (*Hox* series), which indeed appeared independently in a number of distant lineages (Averof & Patel 1997; Dohle *et al*. 2004). Similarly, we should not place too much emphasis on such troglomorphisms as terete body, elongation of appendages (Delić *et al*. 2016), reduction of coxal plates and palpi of mouthparts (for example, see a very impressive situation with Bogidiellidae). So, in this sense, we believe that there is absolutely no need to create several families within the separate Madagascar biogeographic region, exposing the endemic taxa to taxonomic inflation.

In addition to the above-mentioned features we would like to determine the core characteristics of austroniphargid-group, in which we consider the genus *Indoniphargus* Straškraba, 1967 to have a place, by the following characters: abdominal segments distinctly spiny; antenna I longer than antenna II, calceoli absent; mandibles with strong body and molar process; gnathopods sub-similar, with pilosity; pereopods III–VII spiny; sternal gills absent; uropod III with reduced inner ramus; and telson longer than broad; palpi of mouth parts and pleopod rami considerably reduced in a number of species, and urosomal segments either fused or separate (partial coalescence may be observed). In our opinion, *Indoniphargus* is incompatible with Mesogammaridae (heterogeneous group with obscure biogeography) mostly due to the incongruous gnathopods and uropods, notwithstanding these two taxa are related to the "gammarid stem" rather than to a crangonyctid-paramelitid group. Since there is not shown a clear availability of a consimilar "damper seta" for the related malagasian groups, we tentatively decide that *Indoniphargus* occupies an intermediate position within Austroniphargidae sensu Iannilli *et al*. 2011, but it is rather close to *Sandro*, differing from the latter mainly in the morphology of paragnaths, pleopods and uropod III. These two genera probably contain species with the largest set of obvious plesiomorphies.

The existing views on the origin of the highly endemic fauna of Madagascar seem varied. Consensual validation, however, is partly reflected in the checklists compiled for this territory (Rémillet 1973; Kayo *et al*. 2012). Following intensified researches aimed at understanding the groundwater fauna, the emerging new information sheds further light on the post-Gondwanan distribution of groundwater crustaceans (Williams 1986; Ranga Reddy 2011, 2018; Ranga Reddy *et al*. 2014). *Indoniphargus* and closely similar groups apparently originated from a common putative ancestor which inhabited desalinated shallow areas in palaeo-Madagascar and palaeo-India[1] prior to break-up about 90–85 My ago (Ashwal *et al*. 2017).

Conclusion

The subterranean waters of the Indian sub-continent contains 5 genera and 8 species of stygomorphic amphipods assigned to the 3 different families. The taxonomic structure supports an unique amphipod fauna with derivatives from the Indo-Madagascan austroniphargid genus *Indoniphargus* (*I. indicus*, *I. subterraneus* **sp. n.**), the cosmopolitan and diverse bogidiellid genera *Bogidiella* (*B. totakura*, *B. hindustanica* **sp. n.**), *Eobogidiella* (*E. venkataramani*) and *Orientogidiella* **gen. n.** (*O. indica*, *O. reducta* **sp. n.**) and a rather unique monotypic genus *Kotumsaria* (*K. bastarensis*), putatively classified as a crangonyctid.

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