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Two new stygobiotic species of *Elaphoidella* (Crustacea: Copepoda: Harpacticoida) with comments on geographical distribution and ecology of harpacticoids from caves in Thailand

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Abstract

Elaphoidella thailandensis **sp. nov.** and *E. jaesornensis* **sp. nov.**, collected during an investigation of cave-dwelling copepod fauna in the northern part of Thailand, are described and figured herein. The new species were collected from pools filled by percolating water from the unsaturated zone of a karstic aquifer in Phitsanulok and Lampang Provinces, respectively. *Elaphoidella thailandensis*, from Tham Khun cave, is distinguished from its congeners by the two-segmented endopod of pediger 1, the absence of endopod on pediger 4, and the setal formula 4, 5, 6 for the distal exopodal segment of pedigers 2–4. *Elaphoidella jaesornensis*, from Tham Phar Ngam cave, is distinguished from its most closely related species, *E. namnaoensis* Brancelj, Watiroyram & Sanoamuang, 2010, by the armature formula of the endopod of pedigers 2–5. The geographical distribution and ecology of Harpacticoida from Thai caves is also presented.

Key words: karstic caves, zoogeography, Southeast Asia, stygobiont, subterranean

Introduction

The genus *Elaphoidella* Chappuis, 1929 is distributed worldwide, with more than 200 known species (for a complete list see Wells 2007). They inhabit various habitats in both epigean and hypogean environments throughout different zoogeographic regions. The genus is characterized by a large number of stygobiotic taxa (Boxshall & Defaye 2008; Mori & Brancelj 2008; Galassi *et al*. 2009). Many of them are common in percolating water from unsaturated karstic habitats (i.e. epikarst) in the temperate zone (Brancelj 2009).

In the past, information on the species of *Elaphoidella* from Southeast Asia was limited and sporadic. Chappuis (1928) reported three new species from Java: *E. bromeliacola* (Chappuis, 1928) collected from phytotelmata (water bodies held by plants) of *Colocasia glabra* Banks ex Gaertn, *Pandanus* sp. (Pandanaceae); *E. malayica* (Chappuis, 1928) from phytotelmata of *Billbergia pyramidalis* (Sims) Lindl (Bromeliaceae); and *E. javaensis* (Chappuis, 1928) from moist moss. Three years later, Chappuis (1931) reported eight *Elaphoidella* species from phytotelmata of *C. glabra* and from a thermal spring in Java and Sumatra: *E. grandidieri* (Guerne & Richard, 1893), *E. bidens* (Schmeil, 1894), *E. longipedis* Chappuis, 1931, *E. thienemanni* Chappuis, 1931, *E. similis* Chappuis, 1931, *E. cornuta* Chappuis, 1931, *E. elegans* Chappuis, 1931 and *E. intermedia* Chappuis, 1931. Considering their ecology, only *E. intermedia* could be considered as a potentially subterranean species, while the rest of the species are epigean, living in phytotelmata or in surface water. However, during recent investigations of caves in Thailand it appears that they are frequently found in epikarst, where they have viable populations (Watiroyram, pers. observ.). From this point of view they can be considered as stygophilic taxa with very wide ecological tolerance (pers. observ. of the authors). Apart from the already listed species from the Indonesian islands, there are more records from research expeditions to Vietnam and Thailand. Borutzky (1967) described a second subterranean species, *E. vietnamica* Borutzky, 1967, from a cavern water reservoir in Vietnam. A third

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subterranean species, *E. margaritae* was found in Thailand by Pesce and Apostolov in 1985 (Pesce & Apotolov 1985). Overall, 12 *Elaphoidella* species were reported from Southeast Asia before 1985.

The study of stygobiotic harpacticoid copepods has been greatly neglected in Thailand. Up to date, four species have been found in two different types of aquifers. The first species, *Elaphoidella margaritae* Pesce & Apostolov, 1985, was described from a well (i.e. porous aquifer) in Phuket Province (Pesce & Apotolov 1985). Since then, no information related to freshwater stygobiotic Harpacticoida was available until 2007, when Apostolov (2007) reported *Onychocamptus mohammed* (Blanchard & Richard, 1891) from Thailand. Unfortunately, Apostolov (2007) omitted any comment on the locality where the species was found as well as on its ecology.

Later on, *Elaphoidella namnaoensis* Brancelj, Watiroyram & Sanoamuang, 2010, the first stygobiotic taxon from karstic aquifers was described from Tham Yai Nam Nao cave in Nam Nao National Park, Phetchabun Province, Northern Thailand (Brancelj *et al.* 2010). In the same year, *Asiacaris dispar* Cottarelli, Bruno & Berera, 2010, the second species from a porous aquifer, was described from the gravel bank of a river on Pha-ngan Island in the Gulf of Thailand (Cottarelli *et al*. 2010).

The purpose of this paper is to describe two new species of *Elaphoidella* collected from an epikarstic habitat. In addition, a brief discussion about the current information on the presence of other freshwater Harpacticoida collected between 2007 and 2011 from caves in the northern part of Thailand is provided.

Material and methods

Samples from individual pools on the floor of caves' galleries, filled exclusively by percolating water (for details see site description), were collected and filtered by means of special sampling equipment (Brancelj & Culver 2005) with additional sampling by hand net and plankton net in some cases. In all cases, samples were filtered through a mesh size of 100 µm. Samples were stored in plastic bottles immediately after sampling, and formaldehyde was added to a final concentration of 4%. In the laboratory, animals were sorted under a stereomicroscope and stored in 70% alcohol. Before dissection, specimens were placed in a 1:10 v/v solution glycerol and 70% alcohol, which were replaced within one hour by pure glycerol. Specimens were dissected at 1000x magnification under an Olympus SZH-2 stereomicroscope.

The material is deposited at the Natural History Museum (NHMUK), and at the Museum of Khon Kaen University, Thailand (KKU-COP), and at one of the authors (L. S.) collection at Khon Kaen University (KKU).

All appendages and body ornamentation were examined under a magnification of 1000x. All drawings, except for the female/male habitus, were made at the same magnification (1000x), with a drawing tube mounted on an Olympus compound microscope (BHS 40). The final versions of the drawings were made using the CorelDraw 12.0 graphic program. For permanent slides, all body parts were placed in a drop of glycerol on a microscope slide, covered by a cover glass, and sealed with nail polish. The following abbreviations are used throughout the text and figures: Endp, endopod; Exp, exopod; Exp/Endp-1, proximal segment; Exp/Endp-2, middle segment; Exp/Endp-3, distal segment; P1–P5, pedigers 1–5; A, aesthetasc. The nomenclature and descriptive terminology follows that proposed by Huys & Boxshall (1991).

Taxonomic account

Order Harpacticoida Sars, 1903

Family Canthocamptidae Sars, 1906

Genus *Elaphoidella* Chappuis, 1929

Elaphoidella thailandensis sp. nov.

(Figs. 1–5)

Etymology. *Elaphoidella thailandensis* **sp. nov.** is named after Thailand, where it was found for the first time. The name is a noun composed from the name Thailand, and the Latin suffix –ensis, denoting a place (meaning: "from Thailand").

Type locality. Tham Khun Cave is located in Ban Chomphu Nuea, Chomphu Subdistrict, Noen Maprang District (Phitsanulok Province, Northern Thailand). The coordinates of the entrance are: 16° 39′ 55.8″ N, 100° 39′ 14.6″ E, 140 m above sea level. The cave is about 50 m long, represented by one horizontal gallery, 1 to 3 m high. Its water bodies directly depend on precipitation during rainy season (May–October) and persist throughout the year; there is no other subterranean water inside. Part of the cave is dimly lighted due to the large entrance hole. Leaf litter and other organic matter can easily be transported into the cave either by wind through the entrance or by gravity and water flow through fissures in the roof. Water dripping from the ceiling was collected directly in several jars (volume 1–3 L) left there by visitors, who attend a Buddha statue in the cave, which is situated 10 m from the entrance. In addition to the jars, in their vicinity, there are 5–10 small pools (volume of 50 mL to 1 L) also filled by dripping water. Specimens of the new species were collected from epikarstic drips in the two jars and four small pools. On the collecting date (13 August 2010), water temperature was 25.8 °C, pH 8.0, and a conductivity of 320 μS cm^{-1} for the jar which animals were selected as the type specimens.

Material examined. Holotype: adult female, completely dissected and mounted on a slide: NHMUK 2011.2089. Allotype: adult male, completely dissected and mounted on a slide: NHMUK 2011.2090. Paratypes: three females with egg sacs and two males (stored in 70% alcohol): NHMUK 2011.2091–2095; two females with egg sacs and one male (stored in 70% alcohol): KKU-COP-2011-002. All material collected by S. Watiroyram, 13 August 2010.

Description. Female. Body length, measured from anterior margin of rostrum to posterior end of caudal rami, 510–540 µm (mean = 520 µm, n = 5); elongated, subcylindrical, depigmented. Thoracic somites, genital double-somite, abdominal somites with several rows of dorsal spinules (Fig. 1A). Naupliar eye absent. Rostrum small, fused to cephalothorax. Cephalothorax smooth, with four pairs of sensilla and without integumental windows. Posterior margins of thoracic and abdominal somites dorsally serrated. Thoracic somites with one (3rd) or two pairs (1st & 2nd) of dorsal sensilla. Genital double-somite wider than long, without trace of division between genital and third urosomites, with two pairs of dorsal sensilla and row of strong spinules along ventrodistal margin, interrupted in middle (Fig. 1B). Genital complex (Fig. 1B) with single large copulatory pore, copulatory duct bell-shaped; paired seminal receptacles well developed. Fourth urosomite with ventrolateral row of robust spinules along distal margin, interrupted in middle; with pair of dorsal sensilla. Fifth urosomite with continuous row of ventral spinules along distal margin; with one pair of dorsal sensilla. Anal somite with large anal operculum. The latter with 10–11 rounded teeth (outer most teeth on each side forming triangular flattened plate with round tip curved outwards), not reaching distal end of anal somite; flanked by pair of sensilla and with median row of tiny spinules between the latter (Fig. 1C). Four (exceptionally five or six) strong and robust ventral spinules, decreasing in length from innermost; near inner basal corner of each ramus (Fig. 1B).

Caudal ramus (Fig. 1A–C) approximately conical, about 1.5 times as long as wide, with well-developed dorsal keel; rami slightly divergent. Inner margin with several strong lateral spinules; distal margin with row of strong ventral spinules. Each ramus with 7 setae; seta I very small, ventral to seta II; setae II, III, VI and VII bare; anterolateral seta (II) inserted at about proximal third of caudal ramus; posterolateral seta (III) as long as setae II, VI, and VII and all approximately as long as caudal ramus; outer terminal seta (IV) about three times as long as caudal ramus, unipinnate, without breaking plane; inner terminal seta (V) long, distal two-thirds pinnate, fracture plane not visible; inner terminal seta (VI) thin; dorsal seta (VII) thin, inserted close to inner distal corner of ramus.

Antennule (Fig. 2A) relatively short, eight-segmented, not reaching posterior margin of cephalothorax (Fig. 1A). Aesthetasc on fourth segment cylindrical, with rounded tip and reaching slightly beyond tip of antennule. Second aesthetasc on terminal segment long and slim. Setal formula as follows: 1, 8, 5, 2+A, 1, 3, 2, 7+A. All setae thin and bare. No surface ornamentation.

Antenna (Fig. 2B) robust, with allobasis; one-segmented Exp and Endp. Allobasis with one thin seta and few spinules on the middle of outer margin. Exp with two apical smooth and two subapical unipinnate setae. Endp with two strong, sharp outer spines accompanied by several strong, shorter spinules of different lengths; three geniculate and one normal seta, and one strong and sharp spine on distal end of segment.

Mandible (Fig. 2C) short and robust, with two strongly chitinized teeth on gnathobase; with short, smooth seta at dorsal corner and dorsal pore. Mandibular palp two-segmented; one seta on proximal segment (basis) and four setae on distal segment (endopod). All setae thin and bare.

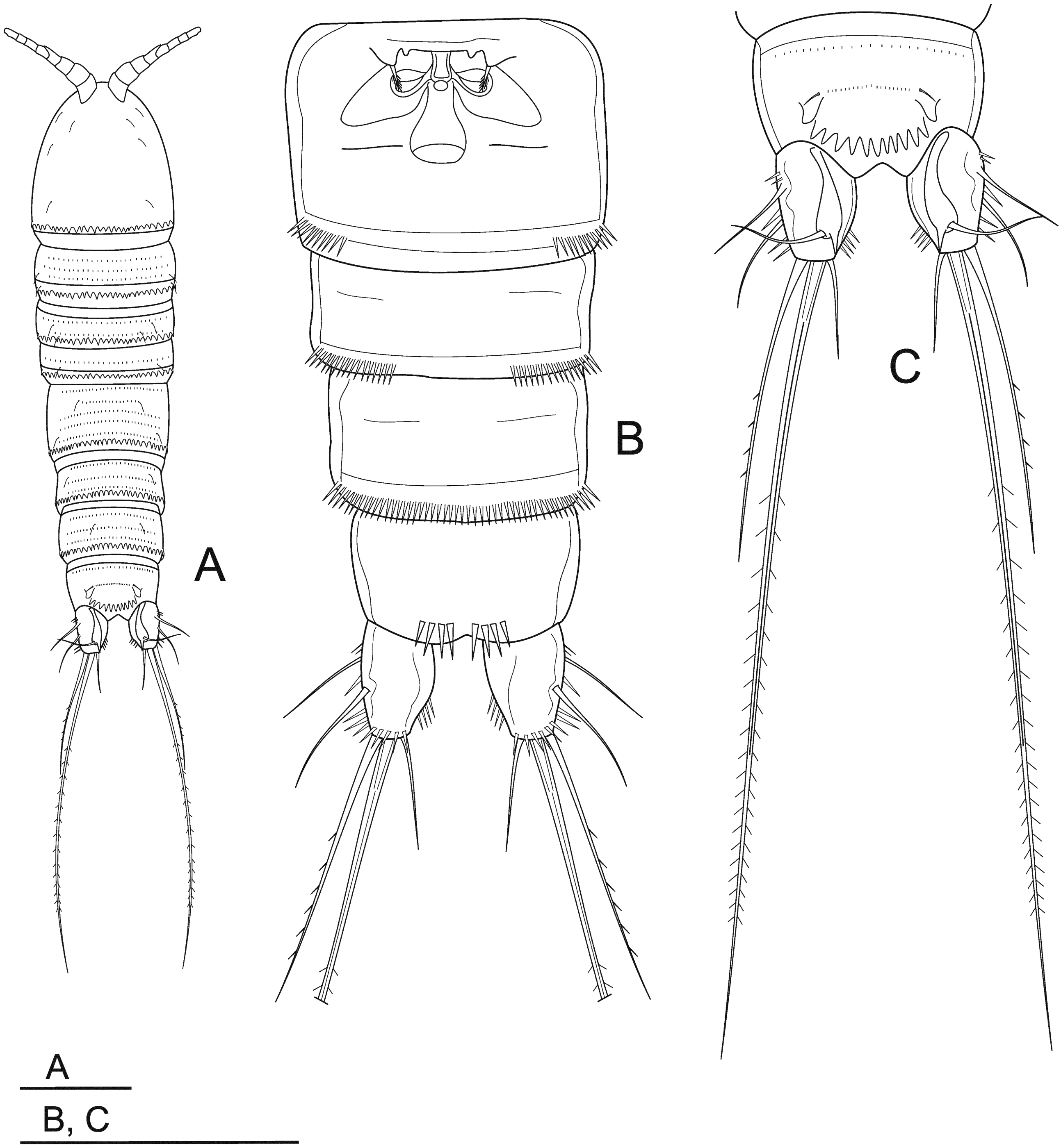

FIGURE 1. *Elaphoidella thailandensis* **sp. nov.**, female (holotype): A, habitus, dorsal view; B, genital double-somite, abdominal somites, and anal somite, ventral view; C, anal somite and caudal rami, dorsal view. Scale bars = 100 µm.

Maxillule (Fig. 2D) composed of robust praecoxa, coxa, and basis. Praecoxal arthrite with six strong apical spines and bare seta on anterior surface. Coxa with cylindrical endite bearing pinnate seta. Basal endite with two smooth and one pinnate setae. Endp and Exp represented by three thin, smooth setae at about half-way the outer margin.

Maxilla (Fig. 2E) two-segmented, composed of syncoxa and allobasis. Syncoxa with rows of outer spinules and two endites; proximal endite with two short pinnate setae, distal endite with two short pinnate setae and one longer, smooth seta. Allobasis drawn out into strong serrate claw with one accompanying seta. Endp represented by three smooth setae.

Maxilliped (Fig. 2F) three-segmented, composed of syncoxa, basis, and one-segmented Endp. Basis 2.5 times as long as wide, with about 20 outer spinules equal in length; with a short, smooth proximal seta. Endp drawn out into strong, acutely curved claw; slightly longer than basis and ornamented with several spinules in distal half; accessory armature represented by short seta at base of endopodal claw.

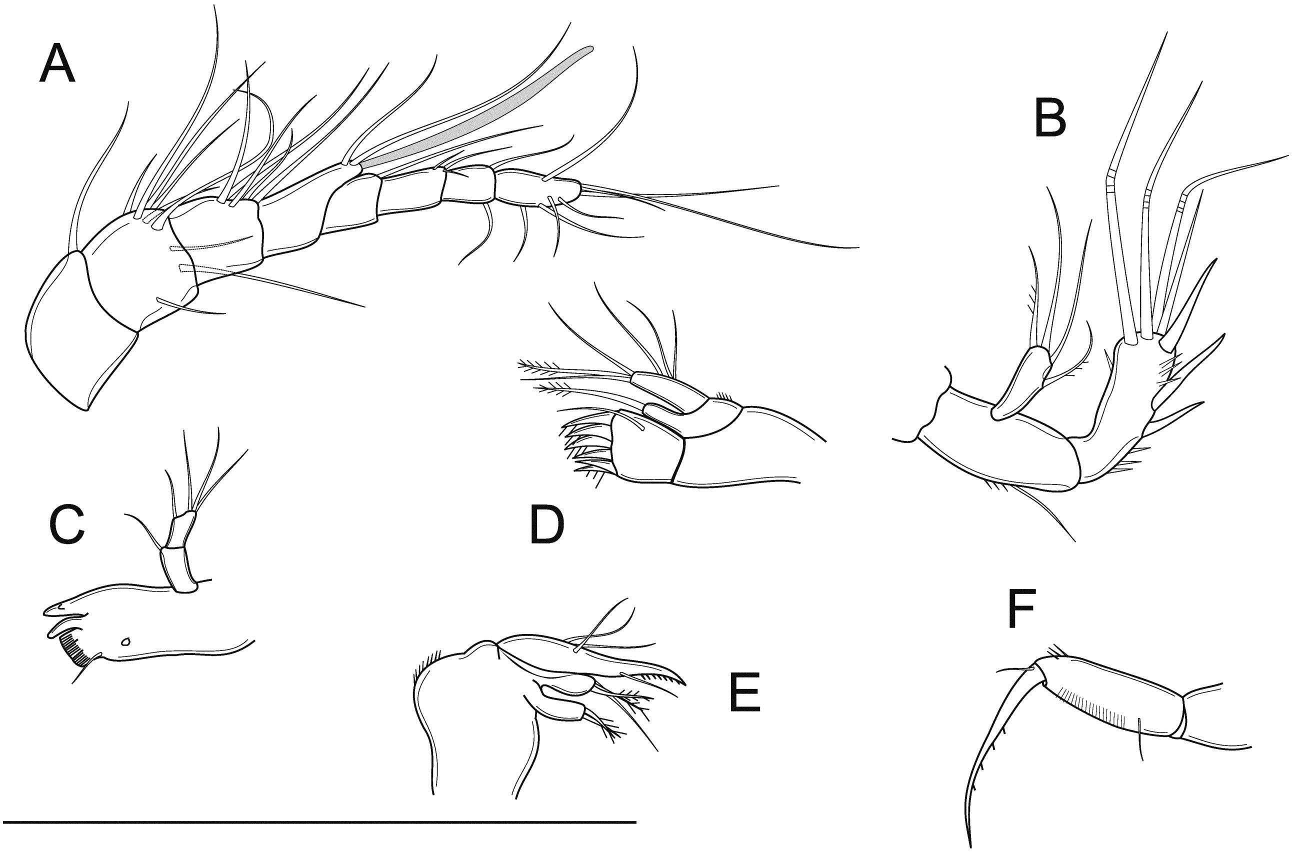

FIGURE 2. *Elaphoidella thailandensis* **sp. nov.**, female (holotype): A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped. Scale bar = 100 µm.

P1–P4 with bare intercoxal sclerite (Figs. 3B, C, D). P1–P3 with three-segmented Exp and two-segmented Endp.

P1 (Fig. 3A) basis with thin inner seta and robust outer spine. Endp and Exp segments with several strong outer spinules. Endp-1 with one strong spine-like inner seta. Endp-2 shorter than Endp-1, with three apical, bare setae; innermost very short, middle one geniculate and longest, outermost normal, the latter about 0.7 times as long as middle one. Exp-1, 2 and 3 with strong unipinnate outer spine. Exp-3 with strong unipinnate seta, and two long geniculate distal setae.

P2 (Fig. 3B) basis with robust outer spine. Endp-1 small, shorter than wide, without inner armature. Endp-2 twice as long as wide, with spiniform outer terminal seta, long pinnate inner terminal seta and inner-distal spinule. Exp-1 as long as Exp-2, with one strong, blunt spine at distal outer corner. Exp-2 with strong blunt outer spine and strong spiniform seta at distal inner margin. Exp-3 2.5 times as long as wide, shorter than Exp-1 and Exp-2 combined; with outer blunt sub-distal spine, one terminal spine and two terminal setae. Inner apical seta soft and pinnate, slightly shorter than outer terminal spine. Middle apical seta unipinnate, as long as Exp.

P3 (Fig. 3C) basis with long and thin outer seta. Endp-1 shorter than wide. Endp-2 twice as long as wide, with spiniform outer terminal seta, long pinnate inner terminal seta and inner-distal spinule. Exp-1 as long as Exp-2, with strong, blunt outer-distal spine. Exp-2 with strong blunt outer spine and strong inner-distal spiniform seta. Exp-3 2.5 times as long as wide; with outer blunt spine, one terminal spine and two terminal setae, and strong inner-subdistal seta.

P4 (Fig. 3D) basis with long and thin outer seta. Endp absent, only remains represented by small thickening. Three-segmented Exp, Exp-1 and Exp-2 similar to those of P3. Exp-3 with two strong outer lateral spines and two smooth setae on inner margin. Two terminal setae: outer unipinnate one about twice as long as Exp-3; inner pinnate seta 5 times as long as Exp-3.

Armature formula of P1–P4 as follows (Arabic numerals = setae; Roman numerals = spines):

	Exopod			Endopod	
	1	2	3	1	2
P1	0-I	0-I	0-2,I-I	1-0	0-3-0
P2	0-I	1-I	0-2,I-I	0-0	0-1,I-0
P3	0-I	1-I	1-2-II	0-0	0-1,I-0
P4	0-I	1-I	2-2-II	-	-

P5 (Fig. 3E) with separate Exp and baseoendopod, without surface ornamentation. Baseoendopod lobe relatively well developed, with four long, strong spiniform setae of unequal length; the second outermost longest; outermost longer than innermost, about 70% the length of second outer one. Baseoendopodal outer seta long and bare. Exp small, sub-oval, slightly longer than baseoendopodal lobe; with four setae of unequal length, decreasing in length from inner margin but the second inner one shortest, thin and bare; remaining setae long, robust and pinnate.

P6 (Fig. 1B) fused, small, forming single plate, with short, robust and pinnate seta on each side of copulatory pore.

Egg sac: slightly longer than genital double-somite, oval, with 9–11 eggs.

Male. Slightly longer than female; body length, measured from anterior margin of rostrum to posterior of caudal rami, 590–630 µm (mean = 610 µm, n = 5), colorless, naupliar eye not discernible, no integumental window on cephalothorax and somites. Body similar to that of female but slightly more tapered posteriorly (Fig. 4A). Ornamentation of cephalothorax, thoracic somites, first urosomite, 4th, 5th urosomite, anal somite, similar to those of female. Genital somite and second urosomite with smooth posterior margin ventrally, third urosomite with row of strong spinules along ventrodistal margin (Fig. 4C). Anal operculum, antenna, mouthparts, P1 (Fig. 5A) and P2–P3 exopods (Fig. 5B, 5C) similar to those of female; P3 Exp-3 (Fig. 5C) with shorter, inner seta than in female.

Antennule (Fig. 4B) seven-segmented, geniculation between fifth and sixth segment. Ancestral third and fourth segment fused to form third segment. Fifth segment with spinous process in median anterior margin and accompanied by one seta. Sixth segment enlarged, spoon-like. Aesthetasc on fused third and fourth segment cylindrical, with rounded tip, not reaching to distal end of antennules. Aesthetasc on terminal segment shorter than on segment 3, about 1.5 times as long as last segment. Setal formula: 1, 9, (12+A), 1, 1, 0, 8+A.

P2 (Fig. 5B) Endp two-segmented, as long as Exp-1. Endp-1 small, shorter than wide, without inner seta or spine. Endp-2 twice as long as wide, with two apical setae; outer one shorter than supporting segment, robust and bare; inner seta long, bipinnate, reaching the distal end of Exp.

P3 (Fig. 5C) Endp-1 shorter than wide, without inner seta or spine. Endp-2 with long inner apophysis with harpoon-like tip, reaching slightly beyond Exp-3. Endp-3 about 1.5 times as long as wide, with two long, bare setae equal in length; two latter elements about 5 times as long as supporting segment.

P4 (Fig. 5D) Endp absent, only remains represented by small thickening. Exp three-segmented. Exp-1 and Exp-2 similar to those of P3 but slightly shorter and more robust. Exp-3 shorter than in female, about 1.2 times as long as wide, with the same armature complement as in female, with inner two setae comparatively shorter in male; apical outer spine transformed and antler-like in shape.

Additional ornamentation of P1-P4 as in Fig. 5A–D.

P5 (Fig. 5E) with distinct Exp and baseoendopod. Baseoendopodal lobe small, without armature. Outer baseoendopodal seta long and bare. Exp small, with three setae; inner subapical seta very small and bare, outer apical seta bare, inner apical one bipinnate, 2.5 times as long as outer apical seta.

P6 (Fig. 5E) fused to genital somite, with 2 minute spines.

Variability. There are variations in the number of spinules at the base of each caudal ramus; the number of spinules varies between 4 and 6, but at least one side always with four spinules.

Differential diagnosis. *Elaphoidella thailandensis* **sp. nov.** has the diagnostic features of the genus *Elaphoidella* based on the armature of the P5, shape of the female genital complex, and on the presence of a transformed spine on the male P4 Exp-3. Based on the male P4 Exp-3 armature formula and on the presence of an antler-like modified apical seta, as well as on the armature formula of the male and female P5, *E. thailandensis* is

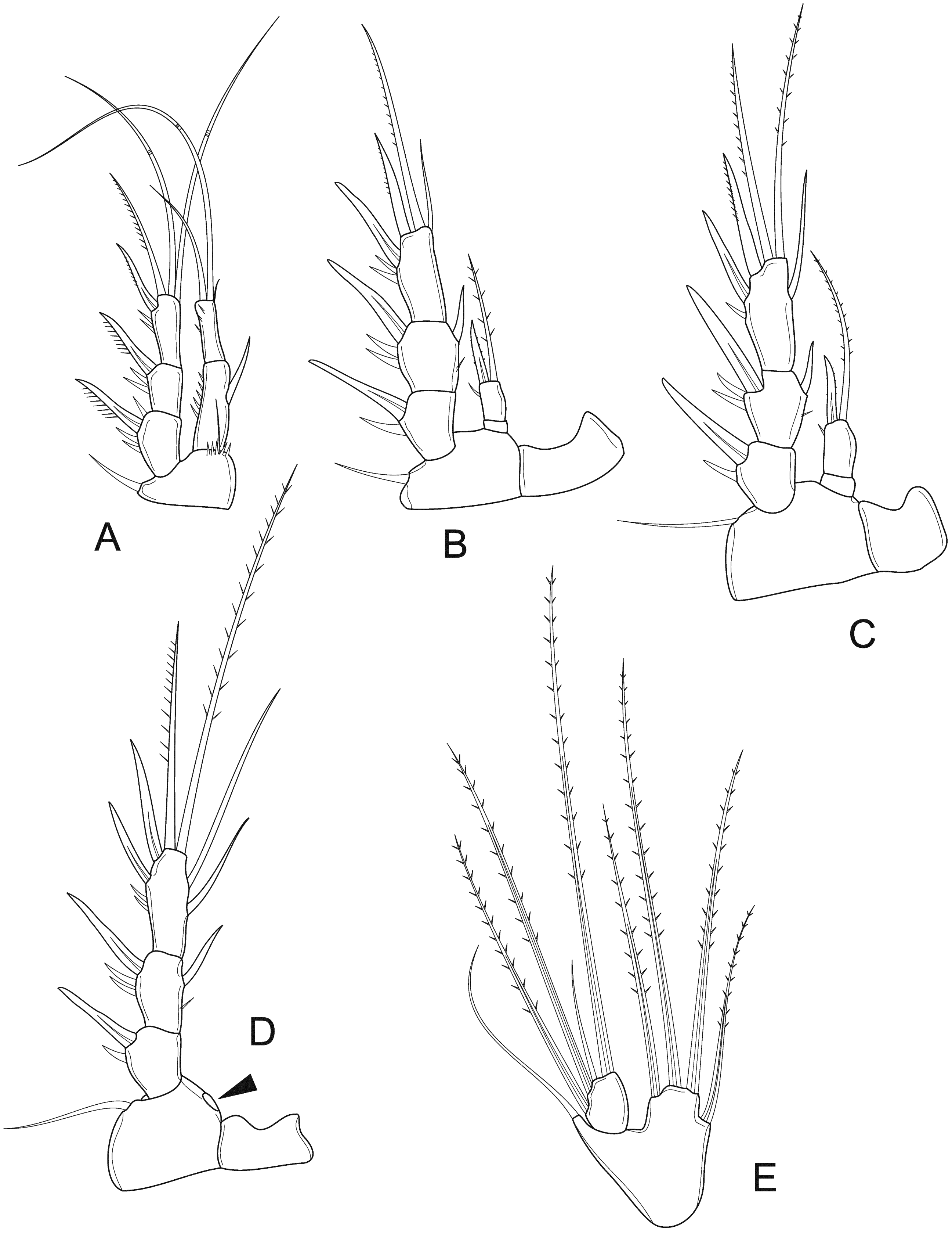

FIGURE 3. *Elaphoidella thailandensis* **sp. nov.**, female (holotype): A, P1; B, P2; C, P3; D, P4; E, P5. Scale bar = 100 µm.

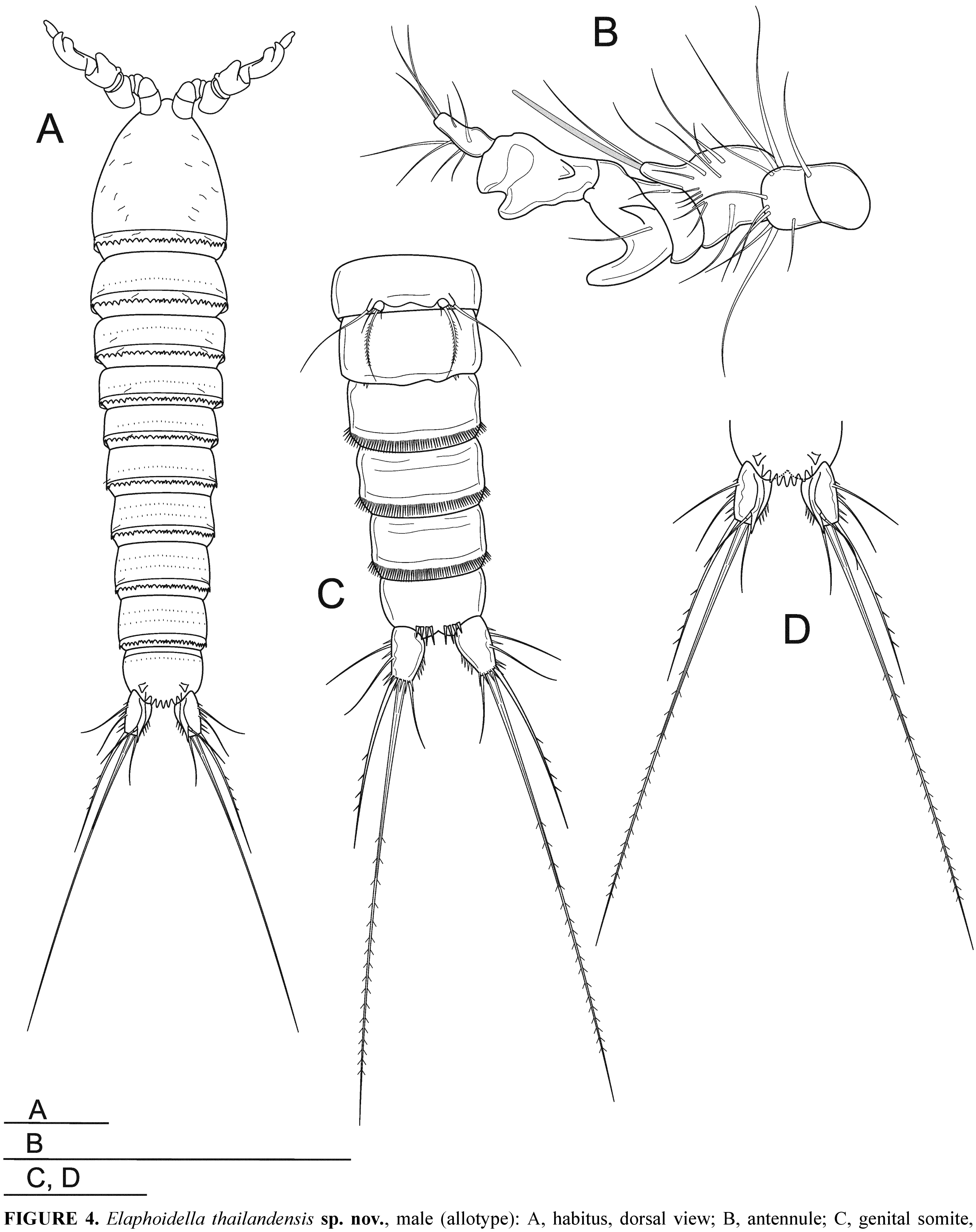

FIGURE 4. *Elaphoidella thailandensis* **sp. nov.**, male (allotype): A, habitus, dorsal view; B, antennule; C, genital somite, abdominal somites, and anal somite, ventral view; D, anal somite and caudal rami, dorsal view. Scale bars = 100 µm.

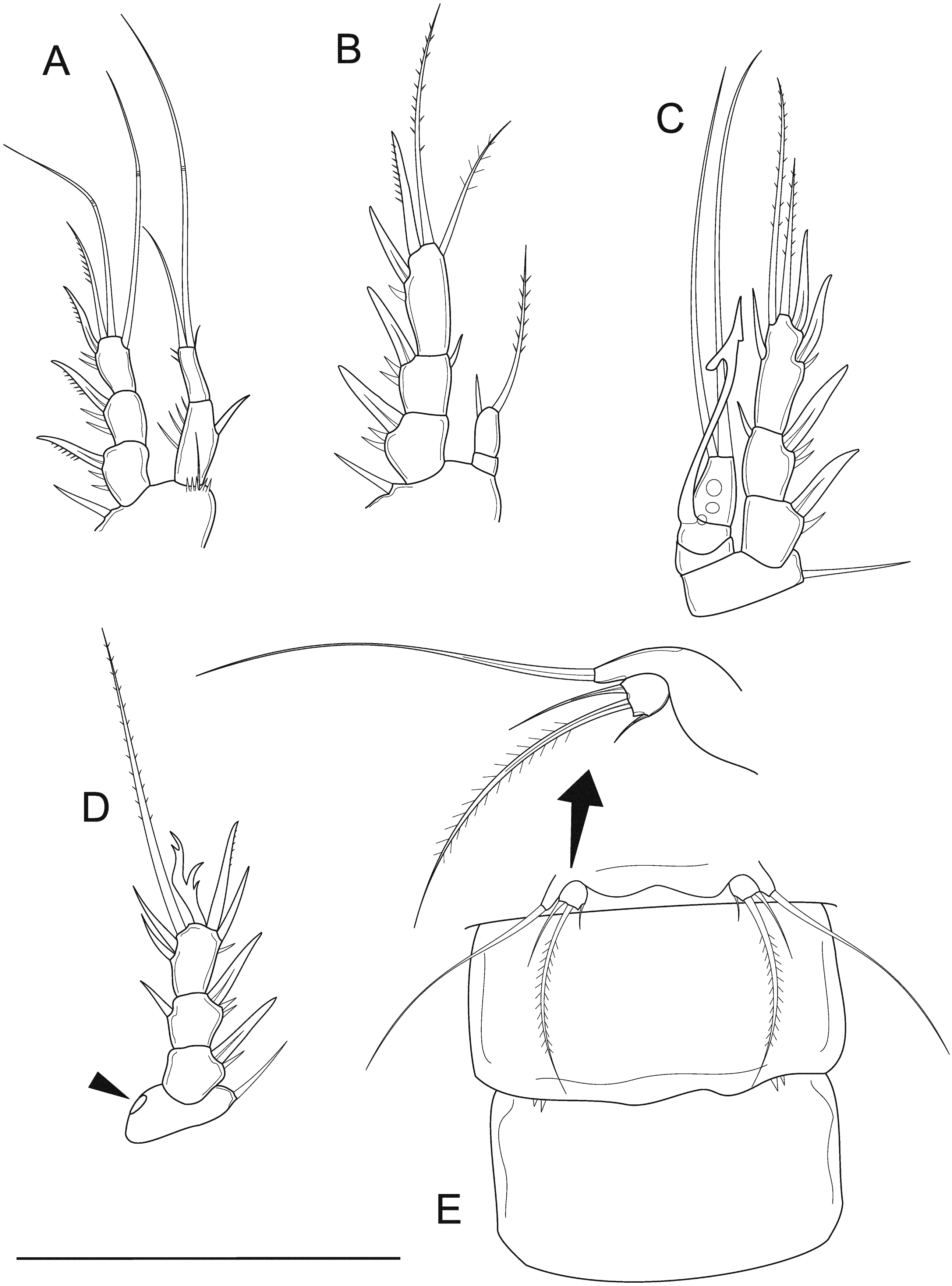

FIGURE 5. *Elaphoidella thailandensis* **sp. nov.**, male (allotype): A, P1; B, P2; C, P3; D, P4; E, P5 and P6. Scale bar = 100 µm.

suggested to belong to group VIII (i.e. *sewelli* group) *sensu* Lang (1948). The two-segmented P1 Endp and the lack of Endp in P4 would suggest affinities with the genus *Neoelaphoidella* as defined by Apostolov (1985), which was separated from group X *sensu* Lang (1948). However, the new species belongs to group VIII of the genus *Elaphoidella* by having a transformed spine on P4 Exp-3 in male, which do not fit with the proposal of Apostolov (1985). *Elaphoidella thilandensis* is easily distinguished from its congeners by a combination of morphological characters including P5 Exp and baseoendopod in females with four setae each; the absence of Endp of P4 in both sexes (which is the most obvious discernible character of the new species); the two-segmented Endp P1; the setal formula 4, 5, 6 for Exp-3 P2–P4 (see table above). The new species is similar to *E. coiffaiti* Chappuis and Kiefer 1952 and *E. reducta* Rouch 1964 (both described from groundwater in France) in the lack of Endp on P4. However, these two European species differ from *E. thailandensis* by a three-segmented Endp P1. Additionally, the armature of the distal segments of Exp P2–P4 is in *E. thailandensis,* 4, 5, 6, versus 5, 6, 5 in *E. coiffaiti* and 5, 5, 5 in *E. reducta*.

Elaphoidella jaesornensis **sp. nov.**
(Figs. 6–7)

Etymology. The new species is named after Jaesorn National Park, the place where it was found for the first time. The name is a noun composed from the name Jaesorn, and the Latin suffix –ensis, denoting a place (meaning: "from Jaesorn").

Type locality. Tham Phar Ngam cave is located in Jaesorn National Park (Lampang Province, Northern Thailand). The coordinates of the entrance are: 19° 06′ 39.6″ N, 99° 34′ 42.4″ E, 305 m above sea level. The cave is about 1 km long, represented by a horizontal gallery. For the fauna survey, several small pools filled with dripping water from the ceiling were sampled at about 100 m from the entrance. Some pools were on solid rock and others were on a muddy substrate. Their volume varied between less than 0.5 to 2 L. Specimens of the new species were found only in the drips forming the small pools on the muddy floor. On 5 October 2009, water temperature at the nearest pool to the entrance where specimens were selected as type specimens, was 22.7 °C, pH was 8.0, and conductivity was 255 μS cm^{-1}.

Material examined. Holotype: adult female, completely dissected and mounted on a slide: NHMUK 2012. 301. Paratypes: three females without egg sac (stored in 70% alcohol): NHMUK 2012. 302–304; two females without egg sac (stored in 70% alcohol): KKU-COP-2011-005. Additional material, nine females stored in 70% alcohol: KKU-COP-2011-006. All material collected by S. Watiroyram on 5th October 2009.

Description. Female. Body length, measured from anterior margin of rostrum to posterior end of caudal rami, 520–640 µm (mean = 550 µm, n = 5); elongated; cephalothorax wider than rest of body, colourless, naupliar eye absent. Rostrum small. Cephalothorax with three pairs of sensilla and with well-developed dorsal integumental window (Fig. 6A). Posterior margins of thoracic and abdominal somites smooth dorsally. Prosomites with one pair of sensilla each. Genital double-somite wider than long (Fig. 6B–C), without trace of former division between genital and third urosomites; division between genital and third urosomite evidenced only by row of spinules. All urosomites, including genital double-somite, with pair of sensilla and medially interrupted row of rather strong spinules dorsally, ventrally with row of tiny spinules. Genital complex (Fig. 6D) with a single large, bell-shaped copulatory pore; paired seminal receptacles well developed. Additional row of tiny spinules on ventro-distal side of 4th and 5th urosomite. Anal somite with paired dorsal sensilla at base of operculum (Fig. 6B, 6E), interconnected with transversal row of small spinules. Two-four ventral strong and robust spinules decreasing in length from innermost to outermost, inserted at base of each caudal ramus (Fig. 6C). Anal somite with rounded operculum flanked by one pair of dorsal sensilla (Fig. 6B), and ornamented with transverse row of small spinules. Anal operculum (Fig. 6B) large, rounded, with 20–25 spinules along free margin; not reaching beyond distal margin of anal somite.

Caudal rami (Fig. 6A–C, E) approximately conical, parallel, short, as long as wide, with dorsal keel along 2/3 of ramus length. Inner margin smooth. Each ramus with 7 setae; seta I very small. Setae II, III, VI and VII bare; anterolateral seta (II) inserted at about proximal third of caudal ramus; posterolateral seta (III) slightly longer than anterolateral (II), with few spinules along outer margin; outer terminal seta (IV) about two times as long as caudal ramus, without breaking plane; inner terminal seta (V) long, distal two-thirds bipinnate, fracture plane not visible;

inner terminal seta (VI) thin, slightly shorter than caudal ramus; dorsal seta (VII) thin and short, inserted at distal end of keel on middle point of each ramus.

Antennule (Fig. 6F) relatively short and stout, eight-segmented, not reaching posterior margin of cephalothorax (Fig. 6A). Aesthetasc on fourth segment cylindrical. Aesthetasc on terminal segment long and slim, overreaching tip of the first aesthetasc. Setal formula as follows: 1, 9, 5, 3+A, 1, 2, 2, 7+A. All setae thin and bare except for one bipinnate seta on first and second segment. No additional ornamentation.

Antenna (Fig. 6G) robust, with allobasis; one-segmented Exp and Endp. Allobasis with two thin setae midway on outer margin. Exp with two apical and two lateral setae, subequal in length; all setae unipinnate. Endp with two strong outer spines accompanied by several strong, short spinules; distally with three geniculate setae, one normal seta and one strong spine.

Mandible (Fig. 6H) short and robust, with two strongly chitinized teeth and one row of smaller teeth on gnathobase; with short seta at dorsal corner and knob. Mandibular palp two-segmented; proximal segment with one seta, distal segment with one subapical and three apical setae. All setae thin and bare.

Maxillule (Fig. 6I) consists of robust praecoxa, coxa, and basis. Praecoxal arthrite with five strong apical spines. Coxa with cylindrical endite bearing one pinnate and one smooth seta. Basal endite with one smooth and one pinnate seta. Exp and Endp represented by one and three thin, smooth setae, respectively.

Maxilla (Fig. 6J) two-segmented, composed of syncoxa and allobasis. Syncoxa with two endites; proximal endite with three setae, distal endite with two setae. Allobasis drawn out into strong serrate claw with one accompanying seta. Endp fused to basis, represented by two thin, smooth setae.

Maxilliped (Fig. 6K) three-segmented, composed of syncoxa, basis, and one-segmented Endp. Syncoxa small, without ornamentation. Basis 3.2 times as long as wide, with about 20 outer spinules. Endp represented by strong, acutely curved, unipinnate claw; accessory armature represented by short seta at base of Endp.

P1 (Fig. 7A) with three-segmented Exp and Endp. Basis with thin inner pinnate seta and robust outer spine. Endp longer than Exp. Endp-1 longer than Endp-2 and Endp-3, reaching middle of second exopodal segment, with robust and pinnate inner seta. Endp-2 as long as Endp-3, with long thin inner seta. Endp-3 with three terminal setae; innermost thin, as long as outer one, middle one geniculate and longest, outermost spiniform, about 0.5 times as long as middle one. Exp-2 with thin inner seta. Exp-3 with strong outer spine, and one spine and two long geniculate setae distally.

P2 (Fig. 7B) with three-segmented Exp and two-segmented Endp. Basis with robust outer spine. Endp-1 shorter than wide, without armature. Endp-2 about 2.5 times as long as wide, with two inner sub-equal setae (distalmost unilaterally feather-like, proximal one unipinnate); with two setae and one spine apically; setae long and pinnate, innermost shorter. Exp-1 as long as Exp-2. Exp-2 with one long seta with unilaterally feather-like tip. Exp-3 3 times as long as wide, with outer spine, one spine and two setae apically; one long unilaterally feather-like seta inserted at about midway of inner margin.

P3 (Fig. 7C) with robust outer basal spine. Endp 2-segmented, Endp-1 shorter than wide, without armature. Endp-2 about 2.5 times as long as wide, with two long, apical setae (innermost slightly shorter) and one outer distal spine; with three inner setae slightly decreasing in length from distalmost seta (apicalmost seta unipinnate, other two bare). Exp similar to that of P2 except for additional unilaterally feather-like seta on inner distal corner of Exp 3.

P4 (Fig. 7D) with long and thin outer basal seta. Two-segmented Endp, Endp-1 small, without inner seta. Endp-2 with inner unipinnate seta at midlength of segment, one inner pinnate seta and one outer pinnate spine apically; inner pinnate seta about 3.0 times as long as segment, outer spine as long as segment. Three-segmented Exp, Exp-1 and Exp-2 similar to those of P3. Exp-3 with strong outer lateral spine, two long, unilaterally feather-like setae on inner margin, and two terminal setae and spine.

Armature formula of P1– P4 as follows (Arabic numerals = setae; Roman numerals = spines):

	Exopod			Endopod		
	1	2	3	1	2	3
P1	0-I	1-I	0-2,I-I	1-0	1-0	1-2-0
P2	0-I	1-I	1-2,I-I	0-0	2-2,I-0	-
P3	0-I	1-I	2-2,I-I	0-0	3-2,I-0	-
P4	0-I	1-I	2-2,I-I	0-0	1-1,I-0	-

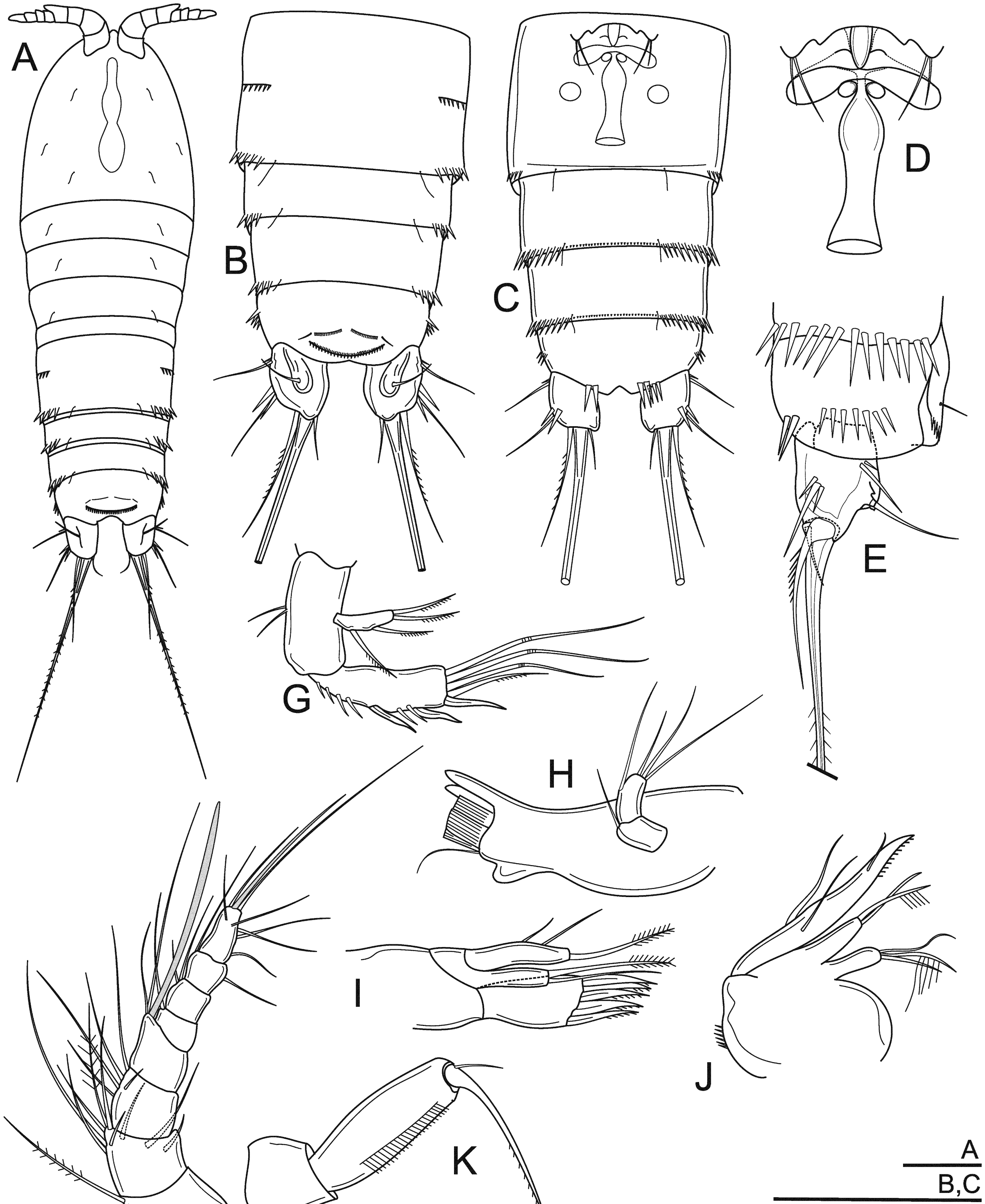

FIGURE 6. *Elaphoidella jaesornensis* **sp. nov.**, female (holotype): A, habitus, dorsal view; B, genital double-somite, abdominal somites, and anal somite, dorsal view; C, genital double-somite, abdominal somites, and anal somite, ventral view; D, genital complex; E, anal somite and caudal ramus, lateral view; F, antennule; G, antenna; H, mandible; I, maxillule; J, maxilla; K, maxilliped. Scale bars = 100 µm.

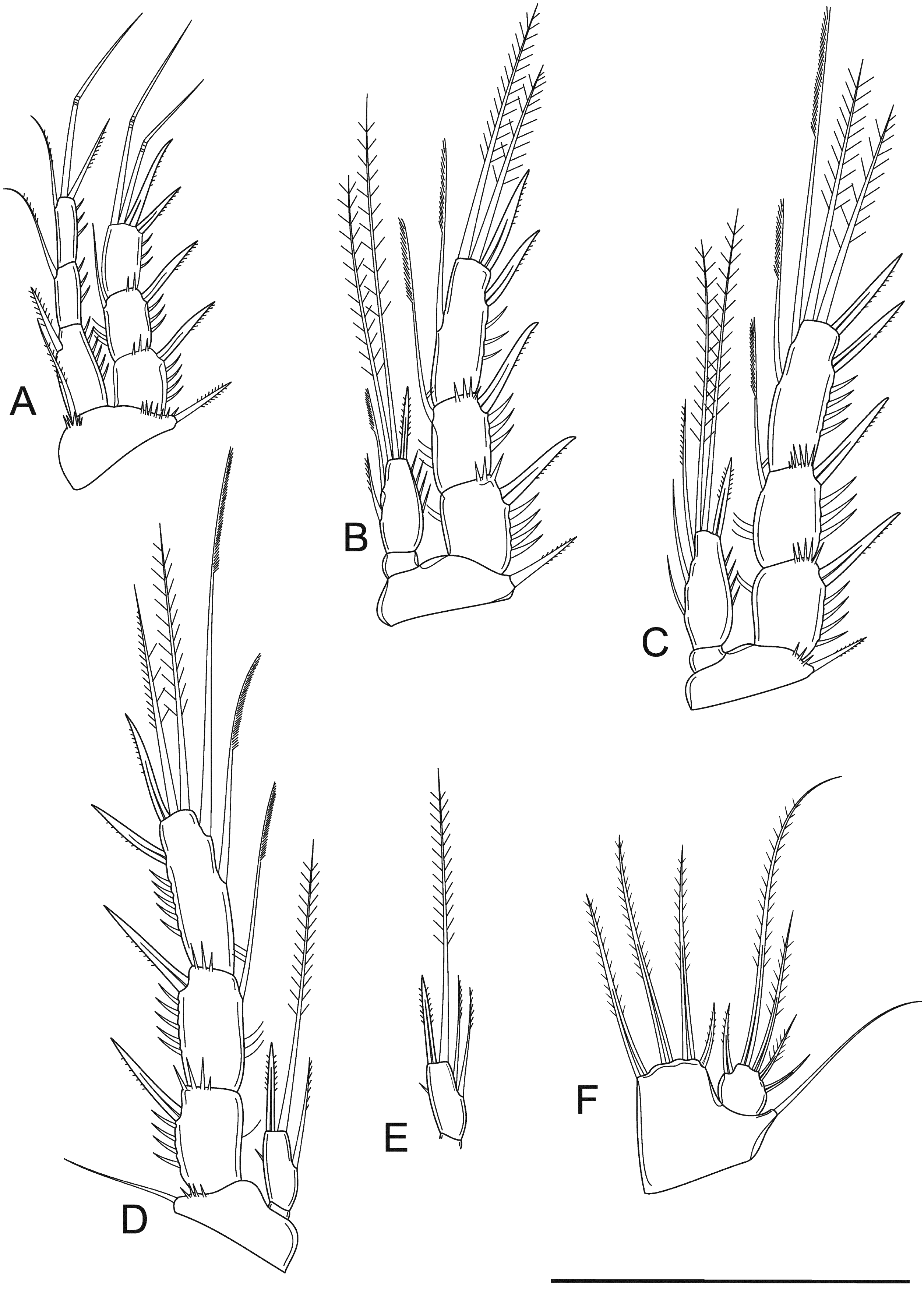

FIGURE 7. *Elaphoidella jaesornensis* **sp. nov.**, female (holotype): A, P1; B, P2; C, P3; D, P4; E, Enp-2 P4 (variability); F, P5. Scale bar = 100 μm.

Additional ornamentation of P1–P4 as in Fig. 7A–D.

P5 (Fig. 7F) with separate Exp and baseoendopod, without surface ornamentation. Baseoendopod well-developed, about 2.0 times as long as wide, with four strong spiniform setae of unequal length; the second innermost element longest, followed by the second outermost, and innermost seta; outermost seta shortest. Outer basal seta long and bare. Exp small, rounded; with five setae of unequal length, all setae spiniform except for outermost element. Second innermost longest, about 7.0 times as long as segment; middle seta about 0.5 times as long as second innermost element; other setae short, sub-equal in length.

P6 (Fig. 6D) fused, small, forming single plate; with two thin, smooth setae (innermost longest).

Egg sac: with 8–9 eggs.

Male unknown.

Variability. In two specimens the anal somite exhibits two rows of spinules ventrally at base of caudal rami, 2 upper spinules, and additional 3 lower spinules on ramus (Fig. 6C). In one specimen, the number of inner setae on Endp-2 P4, differed between the two legs, i.e., carrying one or two setae (Fig. 7E).

Differential diagnosis. The new species described herein was allocated into the genus *Elaphoidella* Chappuis, 1929, given the presences of a three-segmented Endp-P1, a two-segmented Endp of P2–P4, and four and five setae on the baseoendopod and exopod of P5, respectively (Fig. 7F). The armature formula of P5 of *E. jaesornensis* **sp. nov.** suggests it belongs to IV group *sensu* Lang (1948) (i.e. *elaphoides*). Other *Elaphoidella* species belonging to the same group collected in Thailand are *E. intermedia* Chappuis, 1931 and *E. namnaoensis* Brancelj, Watiroyram & Sanoamuang, 2010.

Elaphoidella jaesornensis is clearly distinguished from *E. intermedia* Chappuis, 1931 by several characters. Regarding the original description of *E. intermedia* given by Chappuis (1931), *E. jaesornensis* differs in the armature of P2–P4 Endp-1 and 2; in the new species this is 0, 0, 0 and 5, 6, 3 respectively, but 1, 1, 1 and 5, 6, 4 respectively in *E. intermedia*. The P5 of *E. jaesornensis* has a well-developed baseoendopod, which is about 2.0 times as long as wide, but less than 1.5 as long as wide in *E. intermedia*. The P5 Exp is oval, with short lateral spinules in *E. intermedia*, but it is round, small and without surface ornamentation in *E. jaesornensis***.** The posterior margin of the prosomites and urosomites is smooth in *E. jaesornensis*, but serrate in *E. intermedia*.

The new species is similar to *E. namnaoensis* described from a cave in North-western Thailand (Brancelj *et al.* 2010). However, a number of morphological differences between those species were observed. The anal operculum of *E. namnaoensis* is ornamented with well-developed spinules which reach beyond the distal margin of the anal somite, but these spinules are rather short in *E. jaesornensis* and not reach the distal end of the anal somite. P2–P3 Endp-1 lack inner seta in *E. jaesornensis*, but an inner seta is present in P2–P3 Endp1 of *E. namnaoensis*. *Elaphoidella jaesornensis* possesses 4, 6, and 3 setae/spines on the P2–P4 Endp-2, but there are 5, 6, 4 setae/spines in *E. namnaoensis*. There are also differences in the armature of P5. *Elaphoidella jaesornensis* possesses 5 setae on the P5 Exp, but there are 3 long setae, 1 spiniform element, and 2 outer spines in *E. namnaoensis* (for more details see Brancelj *et al.* 2010; Figs. 1B–D, 3B–E). There are also obvious differences in the shape of the P5 Exp of these two species. The P5 Exp of *E. namnaoensis* is about twice as long as wide, reaching beyond the baseoendopod, but it is rounded and does not reach beyond the distal margin of the baseoendopod in *E. jaesornensis***.** All segments of Exp and Endp P1–P4 in *E. namnaoensis* are more elongated, compared to those in *E. jaesornensis***.** However, some other features, especially the unique feather-like transformation of the setae on the inner margin of Exp and Endp P1–P4 as well as the similar shape of integumental window indicates close relationship between both taxa as a result of allopatric speciation. Relatively close localities of both taxa indicate that allopatric speciation is the most likely option especially as epikarst aquifers are highly fragmented even on short distance and prevailing water flow there is in vertical direction and thus lateral connections are weak or non-existing (Brancelj & Culver 2006).

The morphological comparisons among known species of the genus *Elaphoidella* from Thailand are presented in Table 1.

TABLE 1. Morphological features of *Elaphoidella* species from Thailand.

Character (female only)	*E. thailandensis*	*E. jaesornensis*	*E. margaritae*
Dorsal part of hyaline frill on urosome	Serrate	Smooth	Serrate?
No. of segments on Endp of P1–P4	2.2.2.0	3.2.2.2	3.2.2.2
Spinules on anal operculum	10–12	20–25	13–16
Inner spine on Endp-1 P4	-	Absent	Absent
Inner marginal seta on Endp-2 P4	-	Longer than Endp-2 P4	Very short
Spinules at the base of caudal ramus	4–6	2	5
Shape of caudal ramus	Sub-conical	Asymmetrically conical	Sub-conical
Length of Exp P5 vs. tip of baseoendopod lobe	Exceeding the tip	Shorter than the tip	Exceeding the tip
No. setae/spines on Exp: baseoendopod lobe of P5	4:4	5:4	2:4

continued.

Character (female only)	*E. namnaoensis*	*E. bromeliaecola*	*E. intermedia*
Dorsal part of hyaline frill on urosome	Smooth	Serrate	Serrate
No. of segments on Endp of P1–P4	3.2.2.2	3.2.2.2	3.2.2.2
Spinules on anal operculum	c.20	10–14	c.30
Inner spine on Endp-1 P4	Absent	Absent	Present
Inner marginal seta on Endp-2 P4	Longer than Endp-2 P4	Longer than Endp-2 P4	Longer than Endp-2 P4
Spinules at the base of caudal ramus	1	3–5	0
Shape of caudal ramus	Asymmetrically conical	Asymmetrically conical	Asymmetrically conical
Length of Exp P5 vs. tip of baseoendopod lobe	Exceeding the tip	Shorter than the tip	Exceeding the tip
No. setae/spines on Exp: baseoendopod lobe of P5	4:4	4:4	5:4

Discussion

Geographical distribution of Harpacticoida from Thai caves. One hundred and fifty four copepod samples were collected from 17 caves in Northern Thailand (Fig. 8) during years 2007–2011. In total, 905 specimens of 11 harpacticoid species, belonging to two families, were collected (Table 2). The family Laophontidae Scott, 1905 was represented by a single species: *Onychocamptus mohammed* (Blanchard & Richard, 1891). The Canthocamptidae Sars, 1903 were represented by five species of *Elaphoidella* Chappuis, 1929, two species of *Attheyella* Brady, 1880 and one species of the genera *Bryocamptus* Chappuis, 1928, *Epactophanes* Mrázek, 1893 and *Moraria* T. & A. Scott, 1893. Two of those taxa, *Attheyella* sp. and *Moraria* sp., are still undescribed and are considered as stygophilic when considered on their habitats. However, they were found in low numbers, thus their ecological affinities (i.e. either stygobionts or stygophiles) are not yet clear. *Epactophanes richardi* Mrázek, 1893 and *Onychocamptus mohammed* (Blanchard & Richard, 1891) are cosmopolitan. Some evidence indicates that further detailed analyses of microcharacters could eventually reveal them to be cryptic species (Schizas & Shirley 1994; Bruno & Cottarelli 1999). The ecology of the two species in Thai caves differs. *Epactophanes richardi* was collected from the pools in Tham Chiang Dao cave (Chiang Mai Province) and Tham Phar Ngam cave (Lampang Province) filled exclusively by dripping water and was mainly colonized by epikarstic species as a result of limitation of water bodies connection. On the other hand, *O. mohammed* was collected in a spring with many water bodies connection as well as species interactions, from Tham Yai Nam Nao cave, Phetchabun Province (see Fig. 8).

We collected *Bryocamptus* cf. *echinatus* (Mrázek, 1893) in several sites either in pools filled partly by swallow streams after heavy rain and partly by dripping water or in a spring. The species has been recorded in caves from two provinces: Phetchabun Province (Tham Yai Nam Nao cave (c. 500 m from the entrance) and Tham Bar Dahn cave (10 m from the entrance) of Nam Nao National Park) and Lampang Province (Tham Nam cave of Jaesorn National Park). The species was always collected in low numbers. Copulas were not observed but copepodites were present in some localities, suggesting that caves are also an alternative habitat for this taxon. Sometimes it co-occurs with *E. namnaoensis* and *E. intermedia*. *Bryocamptus echinatus* (Mrázek, 1893), which was initially described from Europe, has been so far reported from different habitats, mainly from the Palaearctic zooregion, including porous aquifers (=alluvium), caves, springs and lakes (Stoch *et al*. 2011).

TABLE 2. List of Harpacticoda collected from caves in the northern part of Thailand; (+ = present, - = absent).

	Females	Males	juveniles		Unsaturated zone	Saturated zone
Family Canthocamtidae Sars, 1906						
*Attheyella vietnamica**	3	-	-	stygobite	+	-
Attheyella sp.	2	1	-	stygophile	-	+
Bryocamptus cf. *echinatus**	26	-	16	stygophile	-	+
*Elaphoidella bromeliaecola**	223	60	25	stygophile	+	+
*Elaphoidella intermedia**	136	-	11	stygophile	+	+
Elaphoidella namnaoensis	248	-	66	stygobite	+	+
Elaphoidella thailandensis	24	9	-	stygobite	+	-
Elaphoidella jaesornensis	30	-	3	stygobite	+	-
*Epactophanes richardi **	19	-	-	stygophile	+	-
Moraria sp.**	2	-	-	stygobite(?)	+	-
Family Laophontidae Scott, 1905						
Onychocamptus mohammed	1	-	-	stygoxene	-	+

* = new record for Thailand; ** = species presumed to be new to science.

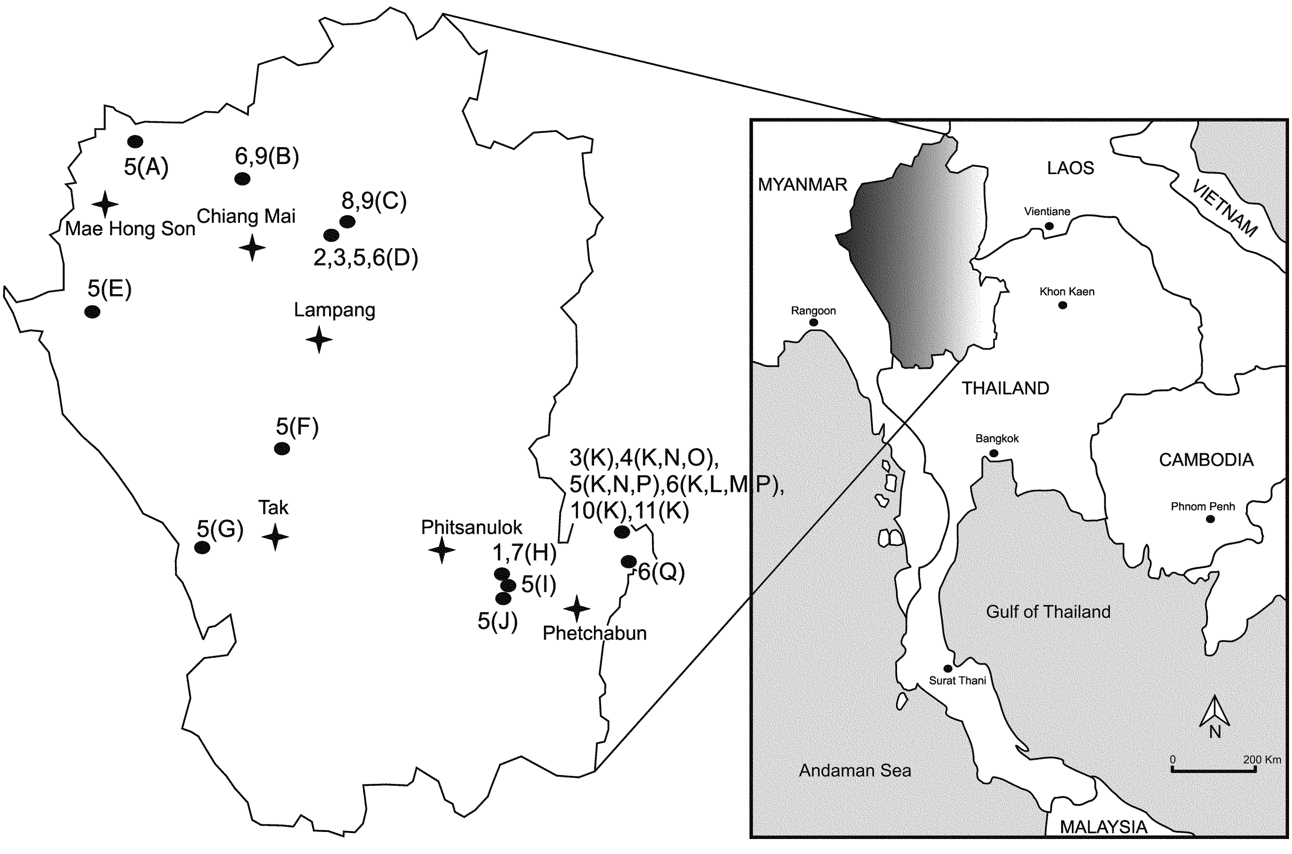

FIGURE 8. The geographical distribution of harpacticoids in caves from Northern Thailand: dots = sampling sites (sites K–O are represented by one common dot); stars = towns; numbers = species numbers as in Table 2; Sampled caves: A, Tham Lod cave; B, Tham Chiang Dao cave; C, Tham Phar Ngam cave; D, Tham Nam cave; E, Tham Keaw Komon cave; F, Tham Nam Phar Pha Ngam cave; G, Tham Mae Usa cave; H, Tham Khun cave; I, Tham Bot Wangna cave; J, Tham Duean Tham Dao cave; K, Tham Yai Nam Nao cave; L, Unnamed cave; M, Tham Song Hong cave; N, Tham Phar Pha Rai cave; O, Tham Payanaak cave; P, Tham Bar Dahn cave; Q, Tham Phar Hong cave.

Attheyella vietnamica Borutzky, 1967, which was originally described from a cave water reservoir in Vietnam, was also found in Thailand. They were collected only in pools filled by percolating water in Tham Bot Wangna cave (Phitsanulok Province).

Representatives of the genus *Elaphoidella* are, beyond any doubt, the most common inhabitants of karstic environments in Thailand. So far, representatives of six *Elaphoidella* species (including the two new species described here) have been recorded from groundwater habitats in Thailand. Five of them (*E. bromeliaecola* (Chappuis, 1928), *E. intermedia* Chappuis, 1931, *E. namnaoensis* Brancelj, Watiroyram & Sanoamuang, 2010, *E. thailandensis* **sp. nov.** and *E. jaesornensis* **sp. nov.**) inhabit the unsaturated zone in karstic caves**.** From porous aquifers in Thailand only *E. margaritae* Pesce & Apotolov, 1985 is known so far, which was found in a dug well in Phuket Province (southern Thailand). All these species still seem to be restricted to Southeast Asia.

Among the six *Elaphoidella* species recorded from Thailand, *E. thailandensis* and *E. jaesornensis* are rare. The former species has been so far found only in two caves located 1 km apart, Tham Bot Wangna cave and the type locality (Phitsanulok Province). The latter species seems to be restricted to a single cave in Lampang Province, Tham Phar Ngam cave. Three other species, *E. intermedia*, *E. namnaoensis* and *E. bromeliaecola* are more frequent and are discussed in detail below.

Ecology of Harpacticoida from Thai caves. Some preliminary conclusions on the ecology of cave-dwelling harpacticoids could be drawn only for the most common species, i.e., those which were collected on several occasions and in different locations.

Elaphoidella intermedia was the most frequently encountered species and widely distributed throughout the study areas, except in Chiang Mai Province. This is probably the result of the low number of samples taken from the latter locality (see Fig. 8). Also, it was found in a wide range of habitats: pools on muddy floor fed by percolating water or/and stream water, pools on solid rock and on the bottom of streams. Egg-carrying females (9–15 eggs per clutch) were abundant in dripping pools (on 8 January 2011) compared to those in samples from amphibious and saturated zones; actually no males were found in habitats connected with subterranean streams. *Elaphoidella intermedia* co-occurred with *E. namnaoensis*, *E. bromeliaecola* and *B.* cf. *echinatus*.

Elaphoidella bromeliaecola was found in both unsaturated and saturated zones in three caves of Nam Nao National Park. More than 200 individuals were collected in one single sample taken from a Buddha's pot filled exclusively with dripping water (on 27 January 2008). It was much less common in pools in a gallery filled with percolated water and/or stream water. In the case of the pot sample, the sex ratio was 2: 1 (female: male). Among all Harpacticoida, it was the only species with specimens found also in copula (found in pot only): 20 pairs in copula (with 8 females already with egg sacs (ranging from 9–24 eggs per clutch) and 12 females with spermatophores). In addition, there were 40 females with egg-sacs and 18 females with spermatophores. Presence of copulas, egg-sacs and spermatophores indicates that *E. bromeliaecola* can probably breed in small cracks in the ceiling (i.e. subterranean habitat) which are inhabited by true stygobionts. As mentioned in the introduction, *E. bromeliaecola* was originally described from phytothelmata (i.e. epigean habitat) which could somehow characterised it as a "stygophilic species". In fact, connection between phytothelmata and dripping water is not unlikely in karstic areas, as animals from phytothelmata can be easily washed into the epikarstic zone during heavy rain. A high population in a single pot suggests that the cave habitat is suitable for this species, but additional studies on its local distribution in epigean habitats (phytothelmata) are needed.

The two new species have been found only in pools filled with dripping water in small caves, with no connection to surface waters (for details on water characteristics see Table 3). This indicates that the original habitat of the species is the unsaturated karstic zone, inhabited by true stygobionts (Table 2). Additional support for their stygobiotic nature comes from the fact that specimens of both new species are eyeless, a common characteristic of stygobiotic species worldwide.

A comparison of the distribution of three stygobiotic species (*E. namnaoensis*, *E. thailandensis* and *E. jaesornensis*) revealed that *E. namnaoensis* is rather common, both in unsaturated as well as in saturated zones throughout the study areas (present in 75 % of samples), whereas *E. thailandensis* and *E. jaesornensis* are rare, each of them present in about 7 % of the samples. The two new species appear to be well specialized to epikarst and thus cannot survive for a longer time in the pools, filled with percolating water, whilst *E. namnaoensis* which is less specialized species is different. We suppose that due to different physical and chemical properties of water in the pools as competitors/predators were rare or absent.

TABLE 3. Range of values of some environmental parameters from localities where harpacticoid copepods were sampled.

Species	Altitude (m a.s.l.)	Water temperature (°C)	pH	Conductivity ($\mu S\ cm^{-1}$)
Attheyella vietnamica	202	25.8	8.0	320
Attheyella sp.	165	22.2	8.1	390
Bryocamptus cf. *echinatus*	167–740	20.0–22.2	7.2–8.1	410–558
Elaphoidella bromeliaecola	684	16.2–21.6	7.9–8.4	593–752
Elaphoidella intermedia	298–878	17.6–24.0	7.3–8.5	380–834
Elaphoidella namnaoensis	457–878	16.7–23.8	7.2–8.7	360–745
Elaphoidella thailandensis	159–202	25.2–26.3	8.0–8.2	320–445
Elaphoidella jaesornensis	167	22.0–22.8	8.0–8.1	210–348
Epactophanes richardi	457	23.1	7.9	531
Moraria sp.	684	not measured	not measured	not measured
Onychocamptus mohammed	650	18.4	7.8	698

In *E. thailandensis*, the inner seta on P1 Endp2 are reduced and very short, while P1 Endp1 and P2–P4 Exp2 and 3 are transformed into spine-like setae (see fig. 3A–D). Morphological adaptations, the feather-like transformed seate on P2–P4 Exp of *E. jaesornensis* resemble more those of *E. namnaoensis*, with which it may be closely related, especially if the hypothesis about allopatric speciation is correct. *Elaphoidella thailandensis* also shares some more pronounced morphological adaptations with stygobiotic species living in the epikarst in the temperate zone (i.e. *E. franci* Petkovski, 1983, *E. tarmani* Brancelj, 2009 or *E. millennii* Brancelj, 2009), than the other two *Elaphoidella* species, including the reduction in number of segments of swimming legs (Endp P4 completely absent in *E. thailandensis*), short antennules, an elongated body and reduction of the setae, which are frequently spine-like (Brancelj 2009). These morphological similarities are present also in species of *Morariopsis* and *Paramorariopsis* (Brancelj 2006, 2009; Brancelj *et al.* 2010).

Differences in species composition and abundance were observed between unsaturated and saturated zones. *Elaphoidella thailandensis*, *E. jaesornensis*, and *E. bromeliaecola* were relatively common in the unsaturated zone. This is especially evident for *E. bromeliaecola,* which was represented by numerous females with eggs (as mentioned before). *Elaphoidella namnaoensis* and *E. intermedia* were common to both zones, while *B.* cf. *echinatus* appeared to be restricted to the saturated zone. In samples originating directly from the epikarst, usually only one species was found, but it was represented by numerous specimens. This reflects the environment, where possibility for horizontal dispersion of aquatic fauna is rather limited, thus inhabitants (i.e. copepods) can have proportionally less predators or competitors than in larger water bodies (Brancelj 2006). The hypothesis, in which number of specimens and species depend on size, inter-connections, and predation within the drainage basin of each dripping point is supported by Brancelj (2002). In contrast, the species inhabiting amphibious and/or saturated zones were less abundant, but up to 4 harpacticoid species were found together (*E. intermedia*, *E. bromeliaecola*, *B.* cf. *echinatus*, and *Attheyella* sp.) along with cyclopoid copepods (*Eucyclops serrulatus* (Fischer, 1851) and *Paracyclops fimbriatus* (Fischer, 1853)). In saturated systems, there is a greater dispersion for animals in a horizontal distribution as a result of good interconnection between water bodies. Therefore, different species could be found together easier than those in epikarst, but their abundance is controlled by the co-occurring species.

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