



Elaphoidella longiramus sp. nov. (Copepoda: Harpacticoida, Canthocamptidae), a new species of cave-dwelling copepod from central Thailand

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Abstract

A new species of harpacticoid copepod belonging to the genus *Elaphoidella* is described, based on materials collected from Thae Wa Phithak Cave, Lopburi Province, central Thailand. Specimens of *Elaphoidella longiramus* sp. nov. were found in a water bucket that was fully filled by dripping water from the cave ceiling. Of the 32 *Elaphoidella* species recorded from Southeast Asia, *E. longiramus* sp. nov. is the 14th member of this genus reported from Thailand. The new species is most similar to *E. thailandensis* by having four well-developed setae on the exopod of the female fifth leg. The endopod of the fourth leg is lacking, and the first leg has a two-segmented endopod in both sexes. However, it is distinguished from *E. thailandensis* by having elongated caudal rami, the exopod with a seta-like spinule on the inner margin of the female fifth leg, a different setal formula on the third exopod of the second to fourth legs, a different number of teeth on the anal operculum, and a different number of ventral spinules on the anal somite.

Key words: biodiversity, epikarst, limestone cave, Southeast Asia, subterranean habitats, taxonomy

Introduction

Copepods are a group of micro-crustaceans that inhabit marine and freshwater habitats. Among the free-living copepods, members of the order Harpacticoida are benthic, and many of them live in caves. From inland ground-water, approximately 900 copepod species are known (Galassi 2001). In the genus *Elaphoidella* Chappuis, 1929, a diversified member of the family Canthocamptidae Brady, 1880 (Wells 2007), and is a common inhabitant of the cave-dwelling fauna of Thailand (Watiroyram *et al.* 2017). Currently, over 250 species of this genus are known in various types of freshwater and subterranean habitats, both in unsaturated and saturated zones of karstic aquifers (Wells 2007; Brancelj *et al.* 2010). In Southeast Asia (SE Asia), 28 species of *Elaphoidella* were recently documented by Watiroyram *et al.* (2017). Subsequently, three more new species (*E. fatimae* Fefilova & Alekseev, 2018 from Malaysia; *E. isana* Watiroyram, Sanoamuang & Brancelj, 2021; and *E. brancelji* Sanoamuang & Watiroyram, 2021 from Thailand) have been described recently. Thus, a total of 31 species of *Elaphoidella* have been recorded to date. Among these, 15 and 13 species are reported from Indonesia and Thailand, while six, six, and three species are found in Vietnam, Malaysia, and the Philippines, respectively (Boonyanusith & Athibai 2014; Watiroyram *et al.* 2017, 2021; Fefilova & Alekseev 2018; Sanoamuang & Watiroyram 2021).

In Thailand, records of the genus *Elaphoidella* have been documented from different aquatic habitats. In 1985, the first stygobiotic copepod and endemic species, *E. margaritae* Pesce & Apostolov, 1985, was first described from the freshwater interstitial habitat in Phuket's southern region (Pesce & Apostolov 1985). After that, some epigean species commonly found in wet mosses, wet soils, and phytotelmata were also reported from caves in Thailand, including *E. bidens decorata* (Daday, 1901), *E. bromeliaecola* (Chappuis, 1928), and *E. intermedia* Chappuis, 1931. *Elaphoidella bidens decorata* is a cosmopolitan species, whereas *E. bromeliaecola* and *E. intermedia* seem to be en-

demio to SE Asia. *Elaphoidella grandidieri* (Guerne & Richard, 1893), usually found in shallow ponds worldwide, was also reported in Thailand. However, the habitat and location are currently unknown in the country (Brancelj *et al.* 2010, 2013; Gutierrez-Aguirre *et al.* 2011; Watiroyram *et al.* 2015, 2017). During the past 12 years, several intensive expeditions into the caves resulted in the discovery of eight newly described species. All of which appear to be endemic to Thailand, namely (1) *E. namnaoensis* Brancelj, Watiroyram & Sanoamuang, 2010, (2) *E. jaesornensis* Watiroyram, Brancelj & Sanoamuang, 2015, (3) *E. thailandensis* Watiroyram, Brancelj & Sanoamuang, 2015, (4) *E. sanoamuangae* Watiroyram & Brancelj, 2016, (5) *E. ligorae* Watiroyram, Sanoamuang & Brancelj, 2017, (6) *E. paraaffinis* Watiroyram, Sanoamuang & Brancelj, 2017, (7) *E. isana* Watiroyram, Sanoamuang & Brancelj, 2021, and (8) *E. brancelji* Sanoamuang & Watiroyram, 2021. Most of these harpacticoids were collected in the northern, northeastern, western, and southern regions of Thailand, whereas the central area has so far been poorly investigated. During the ongoing investigations of cave-dwelling copepods in the central region of Thailand, we found a hitherto unknown species of *Elaphoidella*. Thus, in this study, a description of *E. longiramus* **nov. sp.**, species affinities, and morphological adaptation of stygobiotic taxa are provided and discussed.

Materials and methods

Specimens of *Elaphoidella* were collected from Thae Wa Phithak Cave, Chong Sarika Subdistrict, Patthana Nikhom District, Lopburi Province, Central region of Thailand (Fig. 1). The cave is a limestone cave and is decorated with stalagmites and stalactites. The cave consists of a narrow horizontal entrance of about five m, connected to a wide, long vertical gallery. Inside the cave, natural light penetrates the cave from a circular opening on the cave ceiling. There is epikarstic water that drips directly from the cave ceiling to the floor, and another that runs along the walls to form a limestone pools. Water originating from the saturated zone and emerging on the cave floor is absent.

Samples were collected in a 5-liter bucket filled exclusively with dripping water from the cave ceiling. Samples were filtered through a filtering bottle with a 60 µm mesh size, transferred into 120 mL plastic bottles, and immediately fixed with a 4% formaldehyde solution. In the laboratory, specimens were sorted under a stereomicroscope at 40x magnification and transferred into a mixture of 1:10 (v/v) glycerol and 70% ethanol. The specimens were placed in a drop of pure glycerol before dissection for one hour. Specimens were dissected under an Olympus SZ3060 stereomicroscope at 40-100x magnification. Dissected specimens on a glass slide were sealed with transparent nail polish, and whole specimens were preserved in 70% ethanol for collections. Specimens were deposited at the Thailand Natural History Museum and Natural Science Museum, Thailand (THNHM).

Illustrations of all appendages and body ornamentation were drawn at 1000x magnification using a drawing tube attached to an Olympus CH30 compound microscope. The final drawings were digitally processed using the CorelDraw® Graphics Suite X7 program.

The following abbreviations are used throughout the text and figures: Enp, endopod; Exp, exopod; Exp/Enp-1, proximal segment; Exp/Enp-2, middle segment; Exp/Enp-3, distal segment; P1-P6, swimming leg 1-6; A, aesthetasc. The nomenclature and descriptive terminology follow Huys & Boxshall (1991).

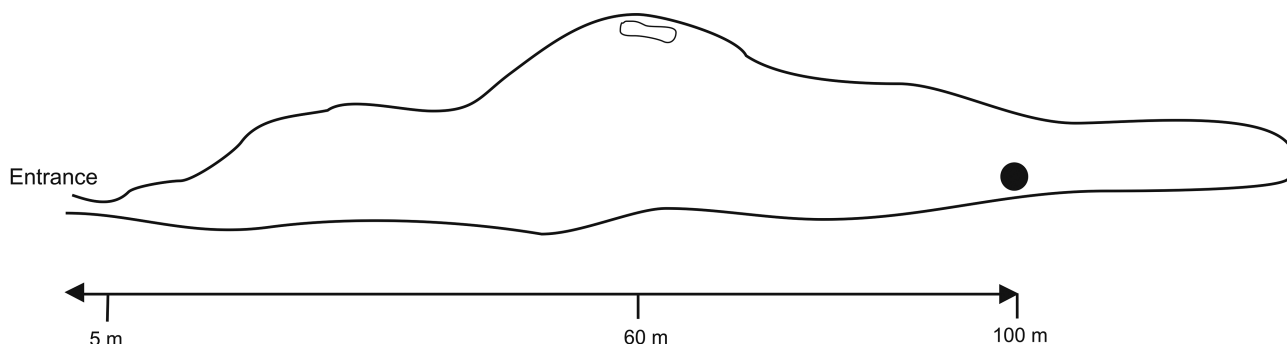


FIGURE 1. A planimetry of cave showing the sampling site (black circle) of *Elaphoidella longiramus* **sp. nov.**

Results

Taxonomy

Order Harpacticoida Sars, 1903

Family Canthocamptidae Brady, 1880

Genus *Elaphoidella* Chappuis, 1929

Elaphoidella longiramus sp. nov.

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(Figs. 2-6)

Type locality. Thae Wa Phithak Cave, Chong Sarika Subdistrict, Patthana Nikhom District, Lopburi Province, central Thailand. Cave entrance coordinates: 14° 47' 39.2" N, 100° 52' 35.0" E, elevation 267 m a.s.l.

Species diagnosis.— *Elaphoidella longiramus* sp. nov. has the following characteristics: 1) urosomites with deeply serrated-free posterior margins; 2) anal somite with seven ventral spinules at the base of the caudal ramus; 3) anal operculum with 6-7 teeth on the free margin; 4) caudal ramus long, 2.0 times as long as wide; 5) P1 has a two-segmented Enp; 6) P4 has a highly reduced Enp, which is represented by a segmental vestige; 7) P2–P4 Exp-3 with armature formula 5.6.6. Female with armature formula on P2–P4 Enp-2 as 2.3.0, P5 with four setae on Exp and baseopod, and P6 with a single seta. Male with only single seta on P2 Enp-2, with transformed P3–P4 (P3 with three-segmented Enp, Enp-3 with two long setae; P4 Exp-3 with one transformed spine), P5 with three exopodal setae, and P6 with two tiny spines.

Material examined. Holotype: one adult female, dissected and mounted on a slide (THNHM-Iv-18769). Allotype: one adult male, dissected and mounted on a slide (THNHM-Iv-18770). Paratypes: three adult females (THNHM-Iv-18771) and three adult males (THNHM-Iv-18772), stored in 70% ethanol. The material was collected from the type locality by W. Janpong on December 10, 2019.

Etymology. The new species name "*longiramus*" is an adjective, referring to the two elongated caudal rami, the longest caudal rami in the genus *Elaphoidella* recorded from Thailand.

Description of adult female. Body length, measured from anterior edge of rostrum to posterior edge of caudal rami, 460-600 µm (mean = 550 µm, n = 5). Habitus (Fig. 2A) elongated, cylindrical, preserved specimens colorless. Naupliar eye not discernible. Rostrum small. Cephalothorax with dorsally deeply-serrated posterior margin, with numerous pairs of sensilla, integumental window oval-shaped. Prosomites 2-4 and urosomites have several rows of longitudinal small spinules, and a deeply and irregularly serrated posterior margin dorsally (Fig. 2A). Genital double-somite about 0.8 times longer than wide, with two pairs of sensilla and several rows of tiny spinules dorsally (Fig. 2C), with a discontinuous row of spinules on posterior margin ventrally (Fig. 2B). Genital complex with a single large median copulatory pore and a bell-shaped copulatory duct, seminal receptacles symmetrically, well-developed (Fig. 2B). Urosomite 3 has one pair of dorsal sensilla and a discontinuous row of spinules ventrally. Urosomite 4 with a latero-ventral row of distal spinules. Anal somite with seven ventral strong spinules at base of each caudal ramus (Fig. 2B), and 6–7 transverse rows of strong spinules laterally (Fig. 2D). Anal operculum with a row of tiny spinules basally, six large triangular teeth on free distal margin, slightly overreaching posterior end of anal somite, and one pair of sensilla dorsally near anal operculum basally (Fig. 2C).

Caudal rami (Fig. 2A-D) relatively conical, flattened dorsoventrally, about 2.0 times as long as wide, with a dorsal keel well-developed and with an acute distal tip, with several strong ventral spinules on distal margin and a few strong lateral spinules at insertion of setae II-III. Each ramus armed with seven setae (setae I, II, III, VI and VII bare). Anterolateral accessory seta (I) small and thin, inserted below seta II. Anterolateral seta (II) inserted at about one-third of ramus length with an oblique line of 4-5 spinules near its insertion. Posterolateral seta (III) slightly shorter than seta II, inserted laterally at about two-third of ramus length, with four strong spinules close to its insertion. Outer terminal seta (IV) about 1.5 times as long as caudal ramus, spiniform-shaped, without breaking plane. Inner terminal seta (V) longest, pinnate, and about two-third of its length, with no visible breaking plane. Inner accessory seta (VI) about as long as caudal ramus. Dorsal seta (VII) as long as seta II, inserted dorsally at about two-third of caudal ramus length.

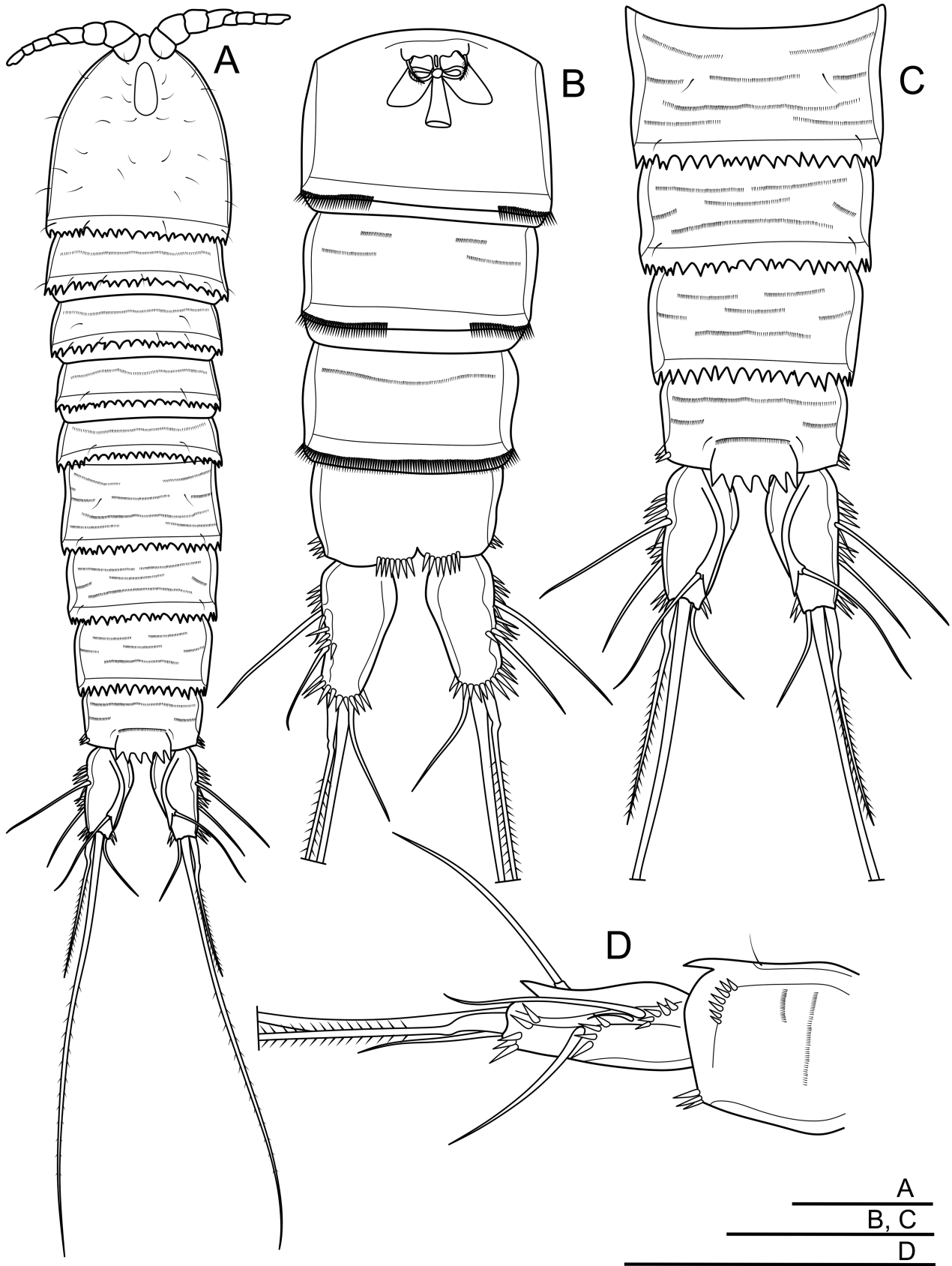


FIGURE 2. *Elaphoidella longiramus* sp. nov., female: A, habitus, dorsal view; B, urosome (without urosomite 1), ventral view; C, urosome (without urosomite 1), dorsal view; D, anal somite with caudal ramus, lateral view. Scale bar = 100 μ m.

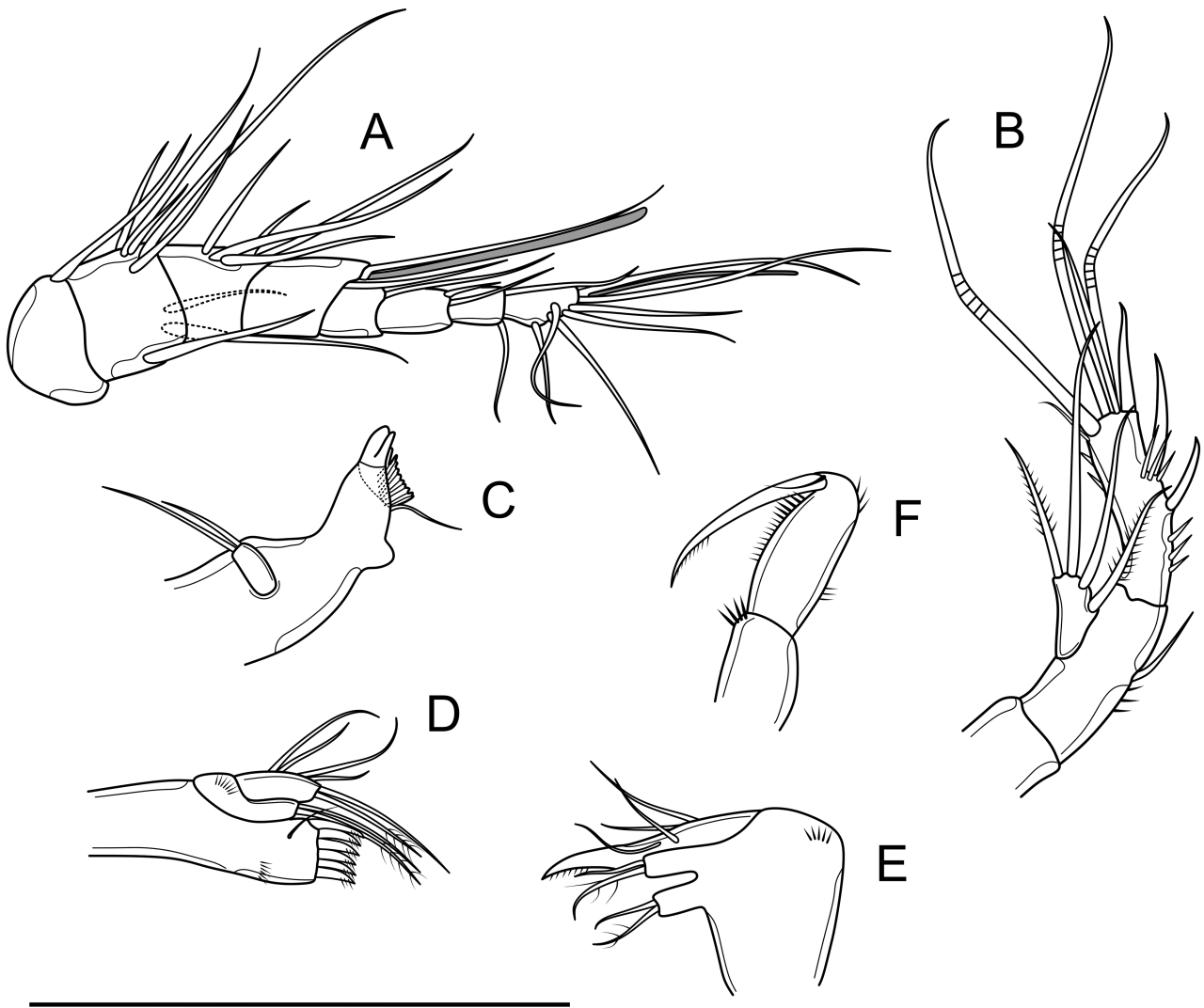


FIGURE 3. *Elaphoidella longiramus* sp. nov., female: A, antennule; B, antenna; C, mandible; D, maxillule; E, maxilla; F, maxilliped. Scale bar = 100 μ m.

Antennule (Fig. 3A) relatively short, eight-segmented, not reaching posterior margin of cephalothorax. Aesthetasc on segment 4, cylindrical, with a rounded tip surpassing distal segment. Second aesthetasc on segment 8, long and thin. Each aesthetasc fused with one seta at its base. Setal formula: 1, 8, 5, 1+(1+A), 1, 2, 2, 6+(1+A).

Antenna (Fig. 3B) comprised of coxa, allobasis, one-segmented Exp and Enp. Coxa shorter than wide, unarmed. Allobasis with one seta and three tiny spinules on abexopodal margin. Exp with two apical setae and two subapical setae. Enp with two strong inner spines and several spinules of various lengths. Distal margin of Enp with one strong spine, normal seta, and three geniculate setae. Outer margin of Enp with two spinules and one short seta on distal corner.

Mandible (Fig. 3C) with one short seta at the corner dorsally and two strongly chitinized teeth on gnathobase. One-segmented mandibular palp, with two smooth setae on distal margin.

Maxillule (Fig. 3D) comprised of praecoxa, coxa and basis. Praecoxal arthrite with six strong spines, a bare seta and tiny spinules on anterior part. Coxa and basis, each with one bare seta and one pinnate seta on endite distally. Exp and Enp reduced to four bare setae.

Maxilla (Fig. 3E) with a row of outer spinules. Syncoxa with two endites, each with one normal and one pinnate setae distally. Allobasis drawn out into a slightly curved claw distally, with one seta on median margin. Enp reduced to three smooth setae.

Maxilliped (Fig. 3F) composed of syncoxa, basis and one-segmented Enp. Syncoxa with four spinules on distal margin. Basis about twice as long as wide, with one group of spinules at about one-third, and one distal on outer

margin, and row of several spinules along inner margin. Enp as long as basis, drawn out into a unipinnate claw, with one small seta on its base.

P1-P4 Exp three-segmented, Enp two-segmented (except P4 without Enp). Armature formula of legs 1-4 as follows (inner-outer seta/spine; inner-apical-outer seta/spine; Arabic numerals represent setae, Roman numerals represent spines):

Leg	Coxa	Basis	Exp			Enp	
			1	2	3	1	2
1	0-0	1-I	0-I	0-I	1-2-I	1-0	0-3-0
2	0-0	0-I	0-I	1-I	1-2-II	0-0	0-1+I-0
3	0-0	0-1	0-I	1-I	2-2-II	0-0	1-1+I-0
4	0-0	0-1	0-I	1-I	2-2-II	-	-

P1 (Fig. 4A) intercoxal sclerite smooth. Coxa with a few strong spinules at outer distal margin. Basis with one robust outer spine and one slender inner seta. Two-segmented Enp, with several spinules on outer margin. Enp-1 long, reaching to end of corresponding Exp-2, with a robust inner spiniform seta. Enp-2 shorter than Enp-1, reaching slightly below end of corresponding Exp-3, with three apical setae; outermost seta unipinnate, middle seta geniculate, about 1.5-2.3 times as long as outermost seta, innermost seta bare and shortest. Three-segmented Exp, each segment with one robust outer unipinnate spine and several lateral spinules. Exp-3 with one inner subapical geniculate seta, two apical geniculate setae, and one outer unipinnate spine.

P2 (Fig. 4B) intercoxal sclerite with a coupler of two strong spinules on anterior surface. Coxa with a few strong spinules at outer distal margin. Basis with a robust outer spine. Enp two-segmented. Enp-1 small and short, unarmed. Enp-2 with 2-3 spinules on inner margin and one slender spine apically and a pinnate seta about 3.0 times as long as outer spine. Exp-1 as long as Exp-2, each segment with outer robust spine. Exp-2 with an additional inner feather-like seta. Exp-3 about 2.5 times as long as wide, with one inner feather-like seta. Exp-3 has two strong outer spinules and two outer unipinnate spines sub-distally, two pinnate setae apically, and one inner feather-like seta.

P3 (Fig. 4C) intercoxal sclerite and coxa similar to P2. Basis with a long outer seta. Enp-1 bare, shorter than wide. Enp-2 twice as long as wide, with a short inner spiniform seta, two outer spinules, one pinnate seta and one spiniform seta apically (spine slender, about 1.5 times as long as Enp-2; seta about 6.0 times as long as Enp-2). Exp-1 as long as Exp-2, with a robust outer spine. Exp-2 with one short inner feather-like seta and one robust outer spine. Exp-3 with two inner apically feather-like setae, two outer unipinnate spines, and two apical pinnate setae.

P4 (Fig. 4D) intercoxal sclerite similar to P2, coxa unornamented. Basis with a long outer seta. Enp reduced, represented by a segmental vestige. Three-segmented Exp, Exp-1 with a robust outer spine, Exp-2 with a robust outer spine and one additional inner feather-like seta. Exp-3 with spinules and two spiniform spines on outer margin; two unipinnate and pinnate setae apically; and two inner feather-like setae.

P5 (Fig. 4E) intercoxal sclerite small and unornamented. Basis and Exp separated. Basis well-developed, overreaching one half of Exp, with four long setae: innermost seta pinnate, remaining setae bare; second outermost longest. Exp small, oval-shaped, with four bare setae of unequal lengths: second innermost seta shortest, about 2.2-2.5 times as long as Exp length; with one seta-like spinule on inner margin of Exp.

P6 (Fig. 2B) fused into a small single plate, with a short pinnate seta on each side of copulatory pore.

Egg sac: not found.

Description of adult male. Body length slightly shorter than in female, 470-560 μm (mean = 510 μm , $n = 5$), measured from anterior edge of rostrum to posterior edge of caudal rami. Body colorless, naupliar eye not discernible. Cephalothorax and prosomites 2-4 similar to female (Fig. 5A). Genital somite with serrate posterior margin laterally. Urosomites 3-5 have smooth posterior margins ventrally; with each having a row of continuous spinules on disto-ventral margin (Fig. 5C). Anal somite (Fig. 5D), caudal rami (Fig. 5C, D, E), antenna, mouthparts and P1 (Fig. 6A), P2 and P3 intercoxal sclerite, coxa, basis and Exp similar to female. Anal operculum with 7-8 triangular teeth, slightly surpassing posterior margin of somite bearing it.

Antennule (Fig. 5B) 7-segmented. Geniculation between segments 4 and 5. First aesthetasc long and cylindrical, surpassing posterior margin of distal segment. Second aesthetasc cylindrical and smaller than first one. Both aesthetascs fused into a seta at their bases. Setal formula as 1, 9, 11+(1+A), 1, 0, 0, 7+(1+A).

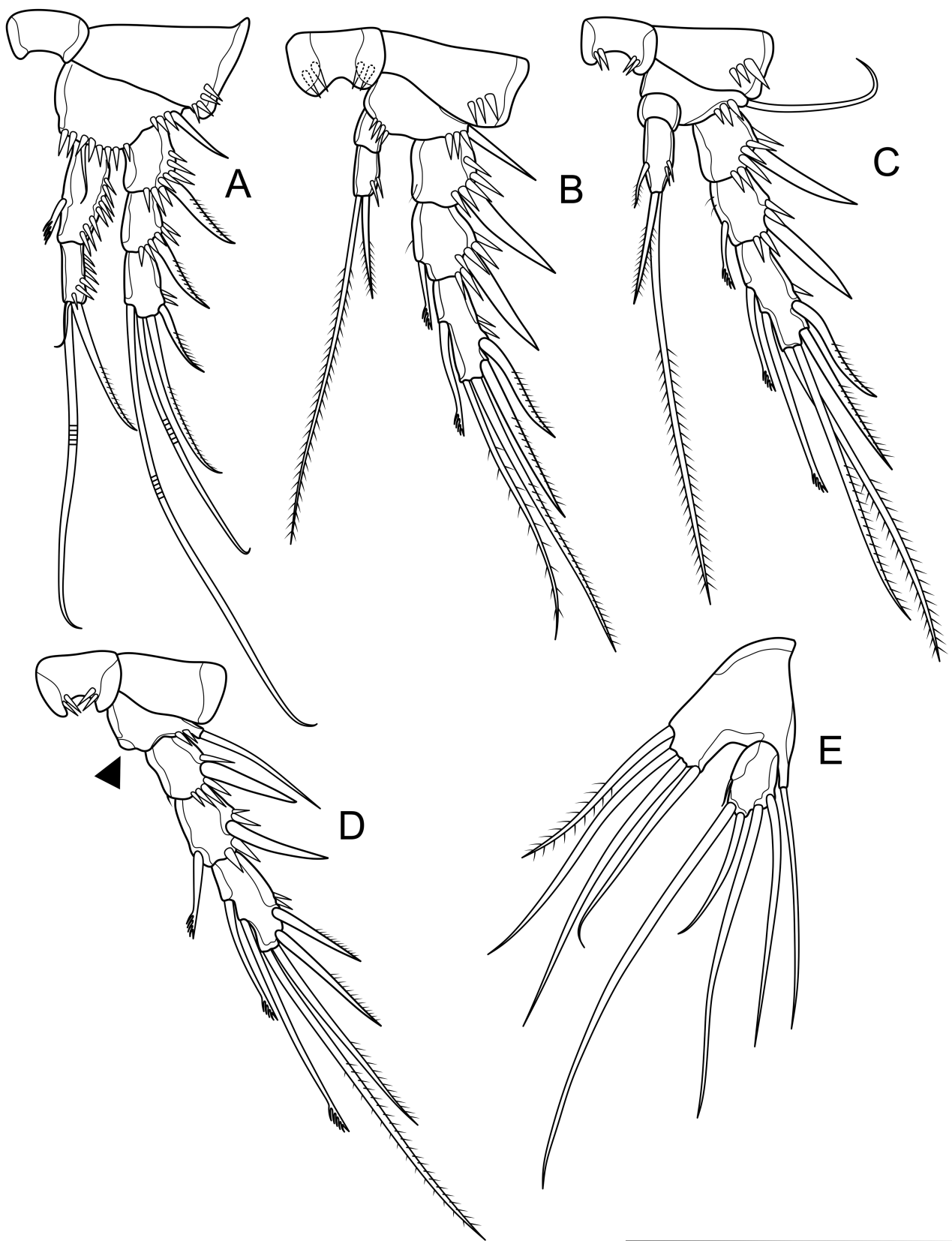


FIGURE 4. *Elaphoidella longiramus* sp. nov., female: A, P1; B, P2; C, P3; D, P4, a black arrow indicates the vestigial Enp; E, P5. Scale bar = 100 μ m.

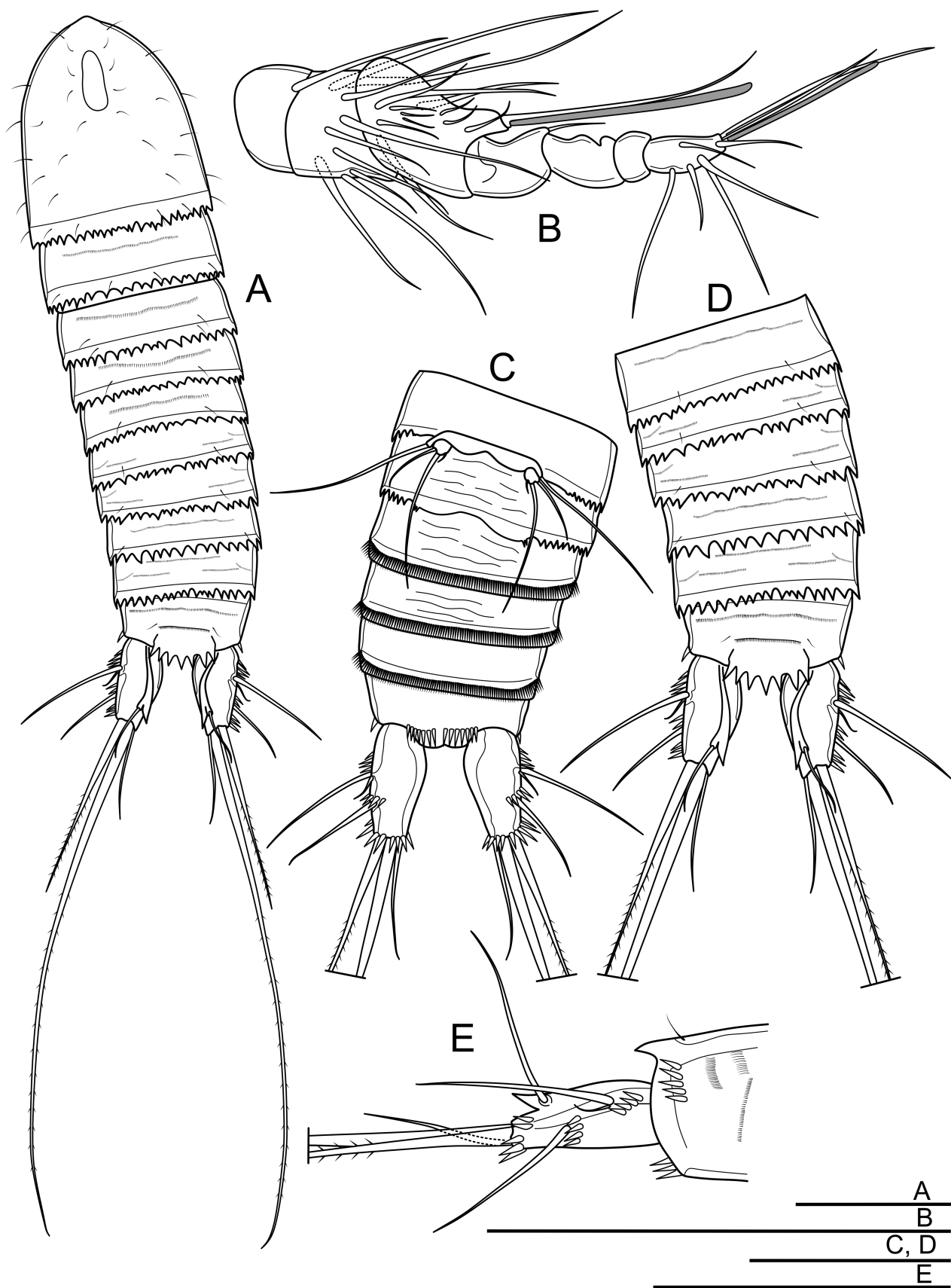


FIGURE 5. *Elaphoidella longiramus* sp. nov., male: A, habitus, dorsal view; B, antennule; C, urosome, ventral view; D, urosome, dorsal view; E, anal somite with caudal ramus, lateral view. Scale bar = 100 μ m.

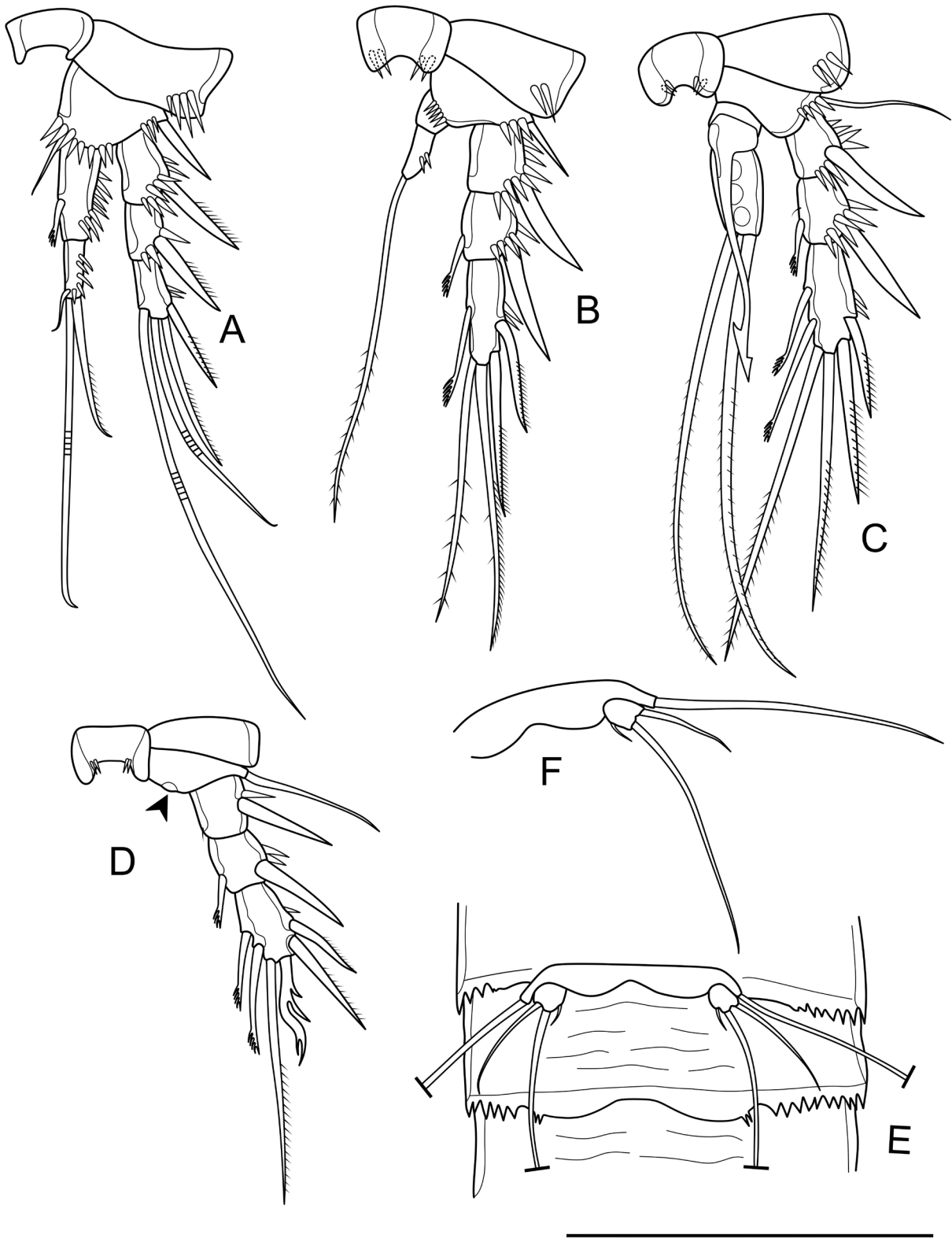


FIGURE 6. *Elaphoidella longiramus* sp. nov., male: A, P1; B, P2; C, P3; D, P4, a black arrow indicates the vestigial Enp; E, urosomite 1-2 with P5 and P6 respectively, ventral view; F, P5. Scale bar = 100 μ m.

P2 (Fig. 6B) with two-segmented Enp. Enp-1 without inner seta, unornamented. Enp-2 with two spinules on outer margin and one apical pinnate seta, as long as segment bearing it.

P3 (Fig. 6C) with three-segmented Enp, Enp-1 shortest and bare. Enp-2 with inner apophysis with a harpoon-like tip, slightly surpassing end of Exp-3. Enp-3 about 2.0 times as long as wide, with two sub-equally long pinnate setae apically.

P4 (Fig. 6D) basis with a long, bare outer seta. Enp absent, represented only by a segmental vestige. Three-segmented Exp, Exp-1 as long as Exp-2, each with one outer robust spine. Exp-2 with a short, feather-like seta at distal inner margin. Exp-3 twice as long as wide, with shorter setae than in female: two inner feather-like setae, two outer unipinnate spines, one apical unipinnate seta and one apical transformed spine, antler-like shaped.

P5 (Fig. 6E, F) with Exp and baseoendopod completely separated. Baseoendopod with a long and bare outer seta. Exp small, with three bare setae; inner seta very short, inner apical seta about 2.5 times as long as outer apical seta.

P6 (Fig. 6E) reduced to a round and shallow plate, with two tiny spines fused to somite.

Variability. The number of teeth on the anal operculum ranged from 5-8 in males (n = 17) and 6-8 in females (n = 12). Ventral spinules on the anal somite ranged from 7-8 in males (n = 17) and 7-9 in females (n = 12).

Differential diagnosis. *Elaphoidella longiramus* **sp. nov.** clearly fits into the genus *Elaphoidella* for the armature of P5 and the segmentation of P1-P4 and the armature of P2-P4 Exp-3. The new species belongs to group VIII (i.e., the *sewelli* group Lang, 1948) based on the presence of a transformed spine on the male P4 Exp-3, and the armature formula and shape of the female P5. The new species is most similar to *E. thailandensis* due to the lack of P4 Enp and the presence of a two-segmented Enp of P1, in both sexes. However, the new species can be distinguished from *E. thailandensis* by several characteristics: (1) *E. longiramus* **sp. nov.** has a slender spinule at the inner margin of the female P5 Exp, whereas *E. thailandensis* lacks such a spinule; (2) the setal formula of the Exp-3 of P2-P4 in both sexes of the new species is 5, 6, 6, whereas it is 4, 5, 6 in both sexes of *E. thailandensis*; (3) in both sexes of *E. longiramus* **sp. nov.**, the caudal ramus is about 2.0 times as long as wide, with a smooth inner margin, whereas in *E. thailandensis*, it is about 1.5 times as long as wide, with spinules along the inner margin; (4) the anal operculum of *E. longiramus* **sp. nov.** has six teeth in the female and 7-8 teeth in the male, whereas *E. thailandensis* has 10-11 teeth in both sexes; and (5) the anal somite of *E. longiramus* **sp. nov.** frequently has seven ventral spinules in both sexes, whereas that of *E. thailandensis* has four ventral spinules in both sexes.

Key to the species of *Elaphoidella* from Thailand caves

[Modified from Sanoamuang & Watirogram (2021)]

Female:

1.	Urosomites with smooth free posterior margins dorsally	2
—	Urosomites with serrated free posterior margins dorsally	3
2.	P5 Exp with four setae	<i>E. sanoamuangae</i>
—	P5 Exp with five setae	<i>E. jaesornensis</i>
3.	P5 Exp with four setae	4
—	P5 Exp with five setae	10
4.	P4 Enp completely absent or with segmental vestige	5
—	P4 Enp present	6
5.	P3 Enp-2 with one spine and one seta	<i>E. thailandensis</i>
—	P3 Enp-2 with three setae	<i>E. longiramus</i> sp. nov.
6.	P3 Enp-1 with inner seta	7
—	P3 Enp-1 without inner seta	8
7.	P3 Enp-2 with three spines and setae	<i>E. bromeliaecola</i>
—	P3 Enp-2 with six spines and setae	<i>E. namnaoensis</i>
8.	P2 Enp-1 with inner seta	<i>E. ligorae</i>
—	P2 Enp-1 without inner seta	9
9.	P4 Enp-2 with three spines and setae	<i>E. brancelji</i>
—	P4 Enp-2 with four spines and setae	<i>E. paraaffinis</i>
10.	Posterior margin of urosomites finely serrated	11
—	Posterior margin of urosomites coarsely serrated	<i>E. bidens decorata</i>
11.	Caudal ramus without spinules at distal inner margin	<i>E. intermedia</i>
—	Caudal ramus with spinules at distal inner margin	<i>E. isana</i>

Male (unknown for *E. bidens decorata*, *E. isana*, *E. jaesornensis*, and *E. namnaoensis*):

1.	Urosomites with smooth free posterior margins dorsally	<i>E. sanoamuangae</i>	2
—	Urosomites with serrated free posterior margins dorsally		3
2.	P4 Enp completely absent or with segmental vestige		4
—	P4 Enp present	<i>E. thailandensis</i>	5
3.	P2 Enp-2 with two setae	<i>E. longiramus sp. nov.</i>	6
—	P2 Enp-2 with one seta		7
4.	P2 Enp-1 without inner seta	<i>E. brancelji</i>	8
—	P2 Enp-1 with inner seta	<i>E. paraaffinis</i>	9
5.	P2 Enp-2 with three spines and setae		10
—	P2 Enp-2 with four spines and setae	<i>E. ligorae</i>	11
6.	P4 Exp-3 with transformed spine	<i>E. intermedia</i>	12
—	P4 Exp-3 without transformed spine	<i>E. bromeliacola</i>	13
7.	Transformed spine of P4 Exp-3 presented with reduced spine		14
—	Transformed spine of P4 Exp-3 presented with antler-like spine		15

Discussion

The genus *Elaphoidella* has a widespread distribution across SE Asia. Thirty-two species were reported, most of which were collected from Indonesia (15 species), followed by Thailand (14 species, including the new species). From Vietnam, Malaysia, and the Philippines, six, six, and three species have been reported, respectively (Watiroyram *et al.* 2017, 2021; Sanoamuang & Watiroyram 2021). The distribution of the 14 *Elaphoidella* species currently known from Thailand is shown in Fig. 7.

In SE Asia, group VIII (*sewelli* group) comprises five species, i.e., *E. sewelli* (Chappuis, 1928), *E. malayica* (Chappuis, 1928), *E. vietnamica* Borutzky, 1967, *E. thailandensis* Watiroyram, Brancelj & Sanoamuang, 2015, and *E. longiramus sp. nov.* They were mostly recorded from karst areas, except for *E. sewelli* and *E. malayica*, which were reported from epigeal habitats. In the Philippines, *E. sewelli* has been reported from rivers, ditches, and ponds (Mamaril 2001). *Elaphoidella malayica* was found in Malaysia in phytotelmata of a bromeliad plant, *Billbergia pyramidalis* (Sims) Lindl (Jocque *et al.* 2013; Watiroyram *et al.* 2015). Even though the rest of the species that were mentioned above were similarly reported from caves, *E. vietnamica* was found in a phreatic aquifer of the saturated zone from Vietnam (i.e. a cave water reservoir) (Borutzky 1967; Brancelj *et al.* 2010; Tran & Chang 2012), while *E. thailandensis* and *E. longiramus sp. nov.* were found in pools fed by dripping water from a cave ceiling, an unsaturated zone (Watiroyram *et al.* 2015; this study).

Elaphoidella longiramus sp. nov. is most similar to *E. thailandensis*. Both species are originally from small fractures in the cave ceiling (=epikarst) which are frequently inhabited by "stylobionts" (Watiroyram *et al.* 2015). The space limitation of the unsaturated zone may be forced to adapt to cave life in epikarst fauna (Brancelj *et al.* 2010; Watiroyram *et al.* 2015, 2017; Watiroyram & Brancelj 2016). Trontelj *et al.* (2012) define epikarst as an extreme habitat with small pore size and high flow velocity as limiting factors for inhabitants. The setae and spines are usually shown in robust, strong and short form which enhancing animals to movement and grasp against water current, not be washed out from epikarst. Thus, the absence and/or reduction of endopodal segments and armatures on swimming legs are thus absent or reduced in epikarst copepods (Brancelj 2009; Galassi *et al.* 2009; Brancelj *et al.* 2010; Watiroyram *et al.* 2015; Culver *et al.* 2019). Even though *E. vietnamica* was found in subterranean habitats, it has similar characteristics to *E. sewelli* and *E. malayica*, which are found in surface waters, i.e., P1 with three-segmented Enp and the presence of P4 Enp. However, *E. vietnamica* has four setae on P3 Enp-2, which is less than those of *E. malayica*, which has five setae, including a lack of inner setae on P2-P4 Enp-1, which is different from *E. sewelli* and *E. malayica* (as shown in Table 1). The lack of P4 Enp in *E. thailandensis* and *E. longiramus sp. nov.* is a conspicuous feature that distinguishes them from the other species in the genus. The two-segmented Enp of P1 in both species is shorter than that of other species in the *sewelli* group, and P1 Enp-1 with an inner seta transformed into a spiniform seta in *E. thailandensis*. In addition, the number of setae and spines on the P2-P3 Enp-2 of the new species and of *E. thailandensis* are less than those in the other species of group VIII and the P2-P4 Exp-2 of *E. longiramus sp. nov.* with short, robust feather-like seta (see Table 1). The common characteristics of stylobionts are also present in the new species: lack of eyes, short antennules, and an elongated body (Brancelj *et al.* 2010; Watiroyram *et al.* 2015).

TABLE 1. Morphological features of five species of *Elaphoidella* belonging to group VIII (*sensu* Lang, 1948) in SE Asia.

Character (female only)	1	2	3	4	5
Dorsal hyaline frill on posterior margin of urosomites	smooth	smooth	smooth	serrate	serrate
No. of setae and spines on Enp and Exp of P5	4.4	4.4	4.4	4.4	4.4*
P4 Enp	present	present	present	absent	absent
No. of endopod segment of P1	3	3	3	2	2
No. of inner setae on Enp-1 of P2-P4	1.1.0	0.1.0	0.0.0	0.0.-	0.0.-
No. of setae and spines on Enp-2 of P2-P4	4.4.3	4.5.3	4.4.3	2.2.-	2.3.-
Ventral spinules on the base of caudal ramus	5	4-7	3	4-6	7-9
Shape of caudal ramus	Asymmetrically conical	Square	Sub-conical	Sub-conical	Sub-conical
Caudal ramus length/width	1.6 times	1.0 times	1.5 times	1.5 times	2.0 times
Inner margin of caudal ramus	smooth	smooth	smooth	with spinules	smooth
Teeth on anal operculum	ca. 25-30	Smooth	18-20	10-11	6-8

* a spinule present on inner margin

1 = *E. sewelli* s.str., 2 = *E. malayica*, 3 = *E. vietnamica*, 4 = *E. thailandensis*, 5 = *E. longiramus* **sp. nov.**

The feather-like seta on appendages can probably help stygobionts gather fine particles of food (Brancelj *et al.* 2010). It was observed on P1 Enp and P2-P4 Exp of *E. longiramus* **sp. nov.** in both sexes (Fig. 4A-D, Fig. 6A-D). Similarly, *E. jaesornensis*, *E. tarmani* Brancelj, 2009 and *E. millennii* Brancelj, 2009, collected from the unsaturated zone, also have setae adapted into feather-like setae (Brancelj 2009; Brancelj *et al.* 2010; Watiroyram *et al.* 2015). However, this feather was also noted in stygophilic species such as *E. intermedia* and *E. namnaoensis* (Brancelj *et al.* 2010; Watiroyram *et al.* 2017). Thus, this adaptation is probably one of the characteristics shared by stygobitic and stygophile copepods for living in caves.

Copepods have morphological diversity and adaptations in different subterranean habitats, indicating their degree of adaptation and habitat heterogeneity. The network of fractures in epikarst also provided different microhabitats, diversity, and morphological adaptation (Galassi *et al.* 2009). The morphological adaptation of *Elaphoidella* living exclusively in the unsaturated zone of karst (i.e., epikarst) is characterized by body elongation, reduction of segments and setae on swimming legs (Brancelj 2009; Brancelj *et al.* 2010), whereas eyelessness is a common characteristic of stygobionts in all groundwater habitats. The new species shows morphology similar to most stygobionts of *Elaphoidella* species from temperate zones as well as *E. thailandensis* by having (1) an elongate body, (2) relatively short antennules, and (3) short legs (P1 two-segmented Enp, P2-P4 Exp-3, which is or less than 2.5 times as long as it is wide, and additionally, the new species and *E. thailandensis* show the most reduction of P4 Enp among its congeners). In conclusion, the new species and *E. thailandensis* have unique characteristics of stygobionts from epikarst and it is presumed that they are inhabitants there because they have highly adapted to their home, which is not present in any stygobionts or stygophiles from other groundwater.

Elaphoidella longiramus **sp. nov.** was found together with *Bryocyclops maewaensis* Watiroyram, Brancelj & Sanoamuang, 2012 and *E. isana*, which are also stygobionts typical of the unsaturated zones (Watiroyram *et al.* 2012, 2021; Brancelj *et al.* 2013). Furthermore, both sexes of *E. longiramus* **sp. nov.** were collected in the same sample with almost the same abundance (17 males and 12 females). It is possible that *E. longiramus* **sp. nov.** can breed in the epikarst, but individuals with egg sacs or spermatophores and copepodites were not collected. The presence of copulas in the epikarst zone can also be used to identify a stygobiont or stygoxene, especially during high-discharge periods when epigeal species are more easily transported into epikarst (Watiroyram *et al.* 2015; Cicco *et al.* 2021). Therefore, future studies should include more observations over a longer period of time in order to corroborate its life cycles and originating habitats.

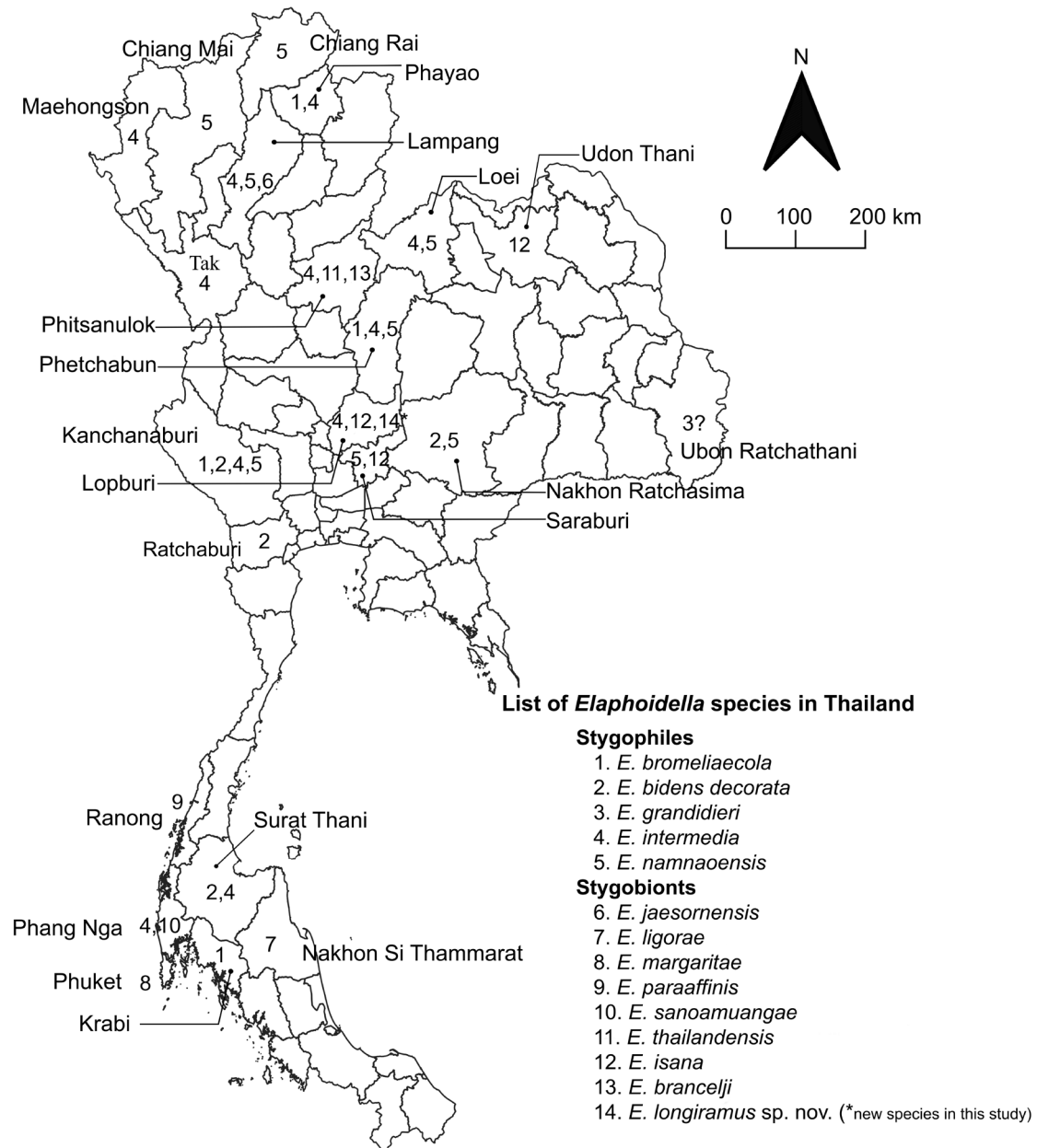


FIGURE 7. Geographical distribution of 14 species of *Elaphoidella* in Thailand.

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