



New species of *Elaphoidella* Chappuis, 1929 and *Schizopera* Sars, 1905 (Copepoda: Harpacticoida) from two caves in northeastern and southern Thailand

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Abstract

Two new copepod species from two caves in northeastern and southern Thailand are described. *Elaphoidella isana* sp. nov. and *Schizopera paktaii* sp. nov. were collected from the unsaturated zone of freshwater pools fed only by dripping water. They are closely related to *E. intermedia* Chappuis, 1931 and *S. validior* Sars, 1909, respectively. *Elaphoidella isana* sp. nov. can be distinguished from its closest relative by the armature of P4 and P5, and by the ornamentation of caudal rami. *Schizopera paktaii* sp. nov. differs from its relative *S. validior* in the armature of P1, P5 and caudal rami.

Key words: biodiversity, epikarst, freshwater, new species, stygobites

Introduction

Elaphoidella Chappuis, 1929 is one of the largest genera of freshwater Harpacticoida; it is well represented worldwide and is a common element of the cave-dwelling fauna of Thailand (Watiroyram *et al.* 2017). Currently, there are 28 *Elaphoidella* species in Southeast Asia (SEA), 11 of which are found only in Thailand (Brancelj *et al.* 2013; Watiroyram *et al.* 2017). The genus *Schizopera* Sars, 1905 is also a diverse group comprising 103 known species (Wells 2007; Walter & Boxshall 2019), which are predominantly found in the marine environment (Karanovic & Cho 2016), and only 11 species are recorded from freshwater habitats (Walter & Boxshall 2019). So far, four *Schizopera* species are known in SEA: *S. longirostris* (Daday, 1900), *S. subterranea* Lang, 1948, *S. clandestina* (Klie, 1923) and *S. tobac* Chappuis, 1931. The first two species were discovered in a marine environment in Thailand (Chertoprud *et al.* 2009; Defaye & Dussart 2011).

Intensive research on the subterranean fauna of Thailand during the last two decades has revealed approximately 470 terrestrial and aquatic cave-dwelling species (*i.e.* troglobitic and stygobitic species, respectively), 209 of them having been described as new to science (Martin Ellis, Shepton Mellet Caving Club, personal communication). About 10 % of the newly described subterranean fauna belong to the subclass Copepoda: six species were originally discovered from the northern part of Thailand (*Elaphoidella namnaoensis* Brancelj, Watiroyram & Sanoamuang, 2010; *E. jaesornensis* Watiroyram, Brancelj & Sanoamuang, 2015a; *E. thailandensis* Watiroyram, Brancelj & Sanoamuang, 2015a; *Bryocyclops maewaensis* Watiroyram, Brancelj & Sanoamuang, 2012; *Thermocyclops parahastatus* Karanovic, Koomput & Sanoamuang, 2017 and *T. thailandensis* Karanovic, Koomput & Sanoamuang, 2017). Four species were discovered in the western part (*Fierscyclops tanoasriensis* Boonyanusith, Brancelj & Sanoamuang, 2013; *F. solaris* Boonyanusith, Brancelj & Sanoamuang, 2013; *Metacyclops thailandicus* Boonyanusith, Sanoamuang & Brancelj, 2018b and *Siamcyclops cavernicolus* Boonyanusith, Sanoamuang & Brancelj, 2018b) and the remaining species were discovered in the southern and northeastern parts of the country (Brancelj *et al.* 2010, 2013; Watiroyram *et al.* 2012, 2015a, 2015b, 2017; Boonyanusith *et al.* 2013, 2018b; Karanovic *et al.* 2017).

The southern part of Thailand (from the northernmost to the southernmost: Chumphon Province to Yala Province) extends for approximately 70,000 km² and is predominantly characterized by hills and mountains. Seven stygobitic copepods belonging to the orders Cyclopoida and Harpacticoida were discovered from caves in the area, and those copepods are thus endemic to Thailand. The group Harpacticoida is represented by *Elaphoidella sanoamuangae* Watiroyram & Brancelj, 2016; *E. paraaffinis* Watiroyram, Sanoamuang & Brancelj, 2017; *E. ligorae* Watiroyram, Sanoamuang & Brancelj, 2017 and *Onychocamptus satunensis* Boonyanusith, Saetang, Wongkamheng & Maiphae, 2018a. The group Cyclopoida is represented by *Bryocyclops muscicoloides* Watiroyram, 2018a; *B. trangensis* Watiroyram, 2018a and *B. aetus* Watiroyram, 2018b (Watiroyram & Brancelj 2016; Watiroyram *et al.* 2017; Boonyanusith *et al.* 2018a; Watiroyram 2018a, 2018b).

The northeastern part of Thailand (from the westernmost Loei Province to the easternmost Ubon Ratchathani Province) extends for approximately 160,000 km². It is composed by a plateau with an elevation ranging from 500 m above sea level in the south to 1,000 m above sea level in the north and is covered with low hills on the northern-most rim. Although the northeastern part represents the majority of the country, our knowledge of the stygobiont copepods in the caves in that area remains limited; only one endemic cyclopoid species, namely, *Bryocyclops maholarnensis* Watiroyram, Sanoamuang & Brancelj, 2015b and one harpacticoid species, *Elaphoidella namnaoensis*, are known so far from there (Watiroyram *et al.* 2015b, 2017).

During a field expedition to Thai caves in both the southern and northeastern areas, two unknown species of Harpacticoida were found (one species in each area) and are described in this paper.

Material and methods

Samples were collected from the vadose zone in the Pha Dam Cave (Udon Thani Province, northeastern Thailand; indicated with a triangle) and in the Khao Chang Hai Cave (Trang Province, southern Thailand; indicated with a square) (Fig. 1).

The Pha Dam Cave is a small cave located in the temple area of the Charoen Suk village. It is approximately 30 m long, 5 m deep, and with an approximately 10 m thick ceiling. The entrance is found in the ground, and the gallery has a slight downward slope. The cave floor is tiled, which is kept wet by dripping water; there is not connection with any running water from outside. Samples were collected from three small and shallow pools in the dark zone of the cave. Approximately 200 mL of total water was filtered during sampling.

The Khao Chang Hai Cave is a large cave located in a conservation area surrounded by a rice field. The entrance is approximately 10 m above the valley. The cave is approximately 400 m long, with a 2–10 m high gallery and more than 10 m thick ceiling. In the gallery, there is a concrete path lit by electric lights. There is no running water in the cave, although many stalactites and pools ranging in volume from 1 L to more than 100 L are present; the water in the pools comes from dripping water only. Approximately 1 L of water was filtered from a small pool in the dark zone located in front of the Chang Hai bridge (the concrete bridge connected with the innermost part of cave).

Samples from the pools were filtered using a special sampling device with a mesh size of 60 µm (Brancelj 2004) and then immediately preserved in 70% ethanol.

In the laboratory, adult specimens were sorted under an Olympus SZ51 stereomicroscope at 40x magnification. The specimens were dissected under a stereomicroscope at 40–100x magnification. The dissected animals were mounted in pure glycerin on a glass slide, covered with a glass coverslip and sealed with transparent nail varnish. The rest of the specimens were stored in 70% ethanol.

All body parts and ornamentation were examined at 1,000x magnification under an Olympus CX31 compound microscope. The drawings were made using an Olympus U-DA drawing tube mounted on a compound microscope. The final versions of the drawings were made using the CORELDRAW® 12.0 graphic program.

Specimens for scanning electron microscopy (SEM) were dehydrated in a graded ethanol series consisting of concentrations of 50%, 70%, 80%, 90%, 95% and 100%, with individuals being kept for 15 min in each concentration. Specimens were dried in a critical point dryer, mounted on stubs and coated with gold in a sputter-coater. The SEM photographs were taken using a scanning electron microscope (FEI Helios NanoLab G3 CX).

Abbreviations used within the text are as follows: *Enp*, endopod; *Exp*, exopod; *Exp(Enp)-1(2, 3)*, proximal (middle, distal) segment of exopod (endopod); *P1–P5*, swimming legs 1–5; *s*, spine; *a*, aesthetasc; *NHMUK*, The Natural History Museum (United Kingdom); *NPU*, Faculty of Science, Nakhon Phanom University (Thailand). The descriptive terminology follows Huys & Boxshall (1991).

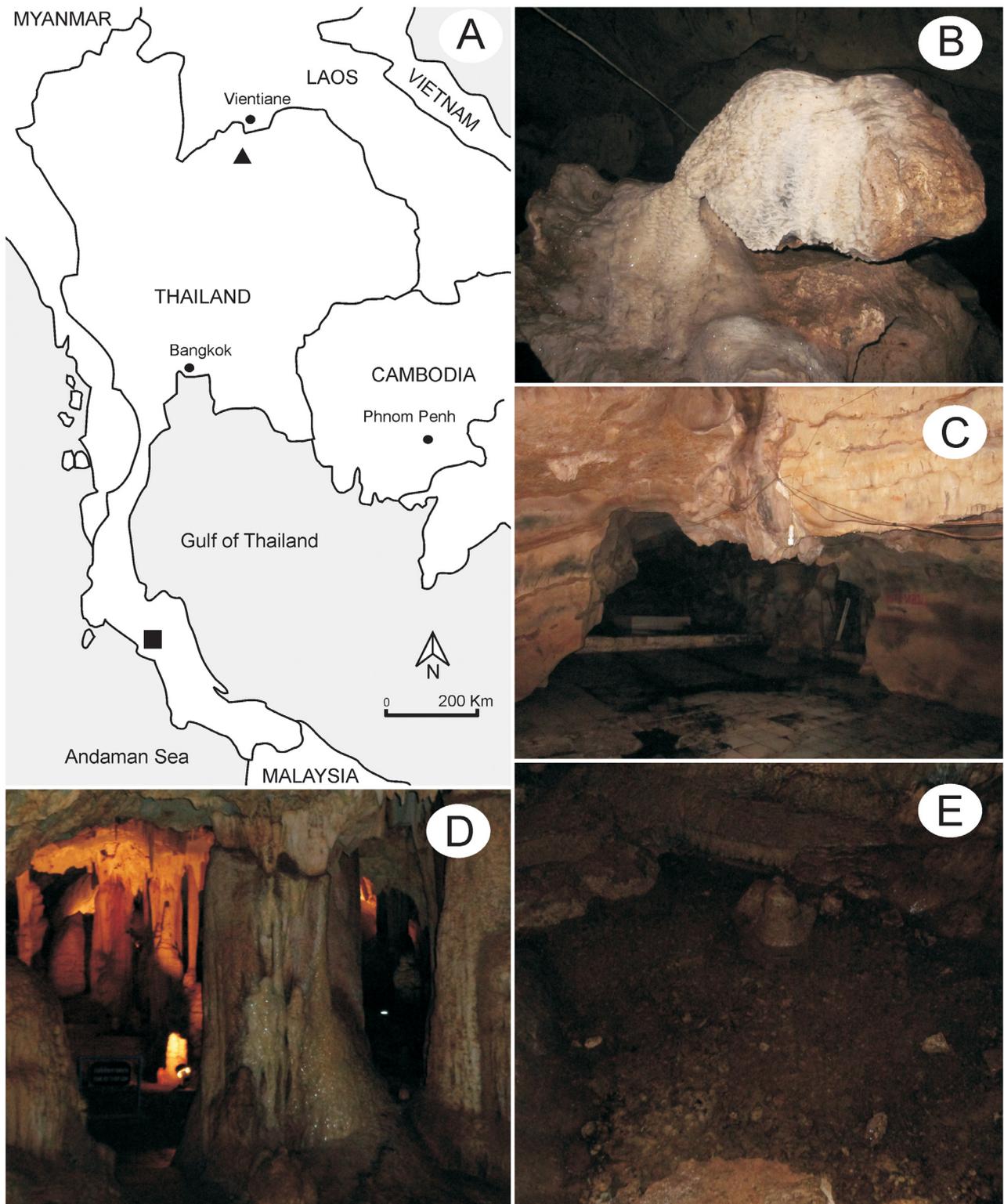


FIGURE 1. Sampling locations of the two new species from Thailand: (A) black circles: capital cities, black triangle: type locality of *Elaphoidella isana* **sp. nov.**; black square: type locality of *Schizopera paktaii* **sp. nov.**; (B–C), (D–E), images of sampling sites of *Elaphoidella isana* **sp. nov.**, and *Schizopera paktaii* **sp. nov.**, respectively.

Taxonomy

Order Harpacticoida Sars, 1903

Family Canthocamptidae Sars, 1906

Genus *Elaphoidella* Chappuis, 1929

Elaphoidella isana sp. nov.

(Figs. 2–6)

“(http://zoobank.org/urn:lsid:zoobank.org:act:7A63FD88-5292-4B23-8E84-3B5557EEC9F8)”

Type locality. Pha Dam Cave, Na Ngua Subdistrict, Nam Som District, Udon Thani Province, northeastern Thailand; coordinates of the cave entrance: 17°46'14.38"N, 102°12'36.72"E; altitude: 223 m a.s.l. (Fig. 1A–C).

Material examined. Holotype: adult female, length 420 µm (access no: NHMUK 2019.1001), completely dissected and mounted on one slide. Paratypes: five adult females, stored in 70% ethanol (access nos: NHMUK 2019.1002–1006, NPU 2019-1). All specimens were collected from the type locality on October 23, 2016 by Santi Watirogram.

Etymology. *Elaphoidella isana* sp. nov. is named after the Isan region (Thai name for northeastern part of Thailand) from where the specimens were collected. The species epithet is a feminine singular adjective.

Distribution. Known only from the pools fed by dripping water from the type locality.

Description of female. Body length measured from anterior margin of rostrum to posterior margin of caudal rami: 420–540 µm (mean = 450 µm, $n = 5$). Habitus elongate, subcylindrical, width evenly decreasing from cephalothorax to last urosomite; preserved specimens colourless (Fig. 2A–B). Naupliar eye not discernible. Cephalothorax with well discernible integumental saddle-shaped window; prosomites and urosomites with serrated posterior margins (Figs. 2C; 3A; 4A–C). Genital double-somite completely fused (Figs. 2A–C; 3A), about 0.9 times as long as wide, with row of strong spinules on distal dorso-lateral margin; two short rows of small spinules ventrally near insertion of P6. Genital complex (Fig. 3A) with large, bell-shaped median copulatory pore. Urosomites 3 and 4 with row of robust spinules dorso-laterally, laterally and ventro-laterally; urosomite 4 with row of small spinules ventrally located in middle of row. Anal somite (Figs. 2C–D; 3A–C; 4B–E) with one pair of sensilla dorsally at base of insertion of anal operculum; two strong spinules laterally and one strong spinule ventrally positioned at inner corner of base of each caudal ramus.

Anal operculum (Figs. 2C–D; 3C; 4D) well developed, slightly extending beyond anal somite; with 25 (range: 24–26) strong spinules on free margin.

Caudal ramus (Figs. 2C–D; 3A–C; 4D–E) asymmetrically conical, about 1.5 times as long as wide, with well developed dorsal keel; with oblique dorso-lateral row of spinules and row of spinules along distal inner margin; with prominent plate extending over base of caudal setae. Setae I–III and VI–VII bare and thin. Anterolateral accessory seta (I) slightly shorter than caudal ramus, inserted at about 1/4 of caudal ramus length. Anterolateral seta (II) short, inserted just below of seta I. Posterolateral seta (III) inserted at about middle of caudal ramus length, as long as seta I, with two strong spinules at its base. Outer apical seta (IV) about as long as caudal ramus, unipinnate, without breaking plane. Inner apical seta (V) longest, without breaking plane. Inner accessory seta (VI) slightly longer than seta III. Dorsal seta (VII) articulated, as long as seta III, inserted on keel at half length of caudal ramus.

Antennule (Fig. 5A) eight-segmented, not reaching to middle of cephalothorax. Both aesthetascs fused with seta at its base (forming acrothek on apical segment), proximal one larger and longer than distal one. Setal formula: 1, 9, 5, 2 + a, 1, 3, 2, 7 + a.

Antenna (Fig. 5B) comprising coxa, allobasis, and one-segmented Exp and Enp. Coxa slightly shorter than wide, unornamented. Allobasis about three times as long as wide, with four thin spinules on median margin. One-segmented Exp with two unipinnate setae subapically and two unipinnate setae apically, similar in length. Enp about five times as long as wide, with two strong spines laterally and several strong spinules along margin; apically with five elements: one strong unipinnate spine, one normal bare seta, three geniculate setae; external surface of Enp with two transverse rows of tiny spinules on distal part and thin seta inserted sub-apically.

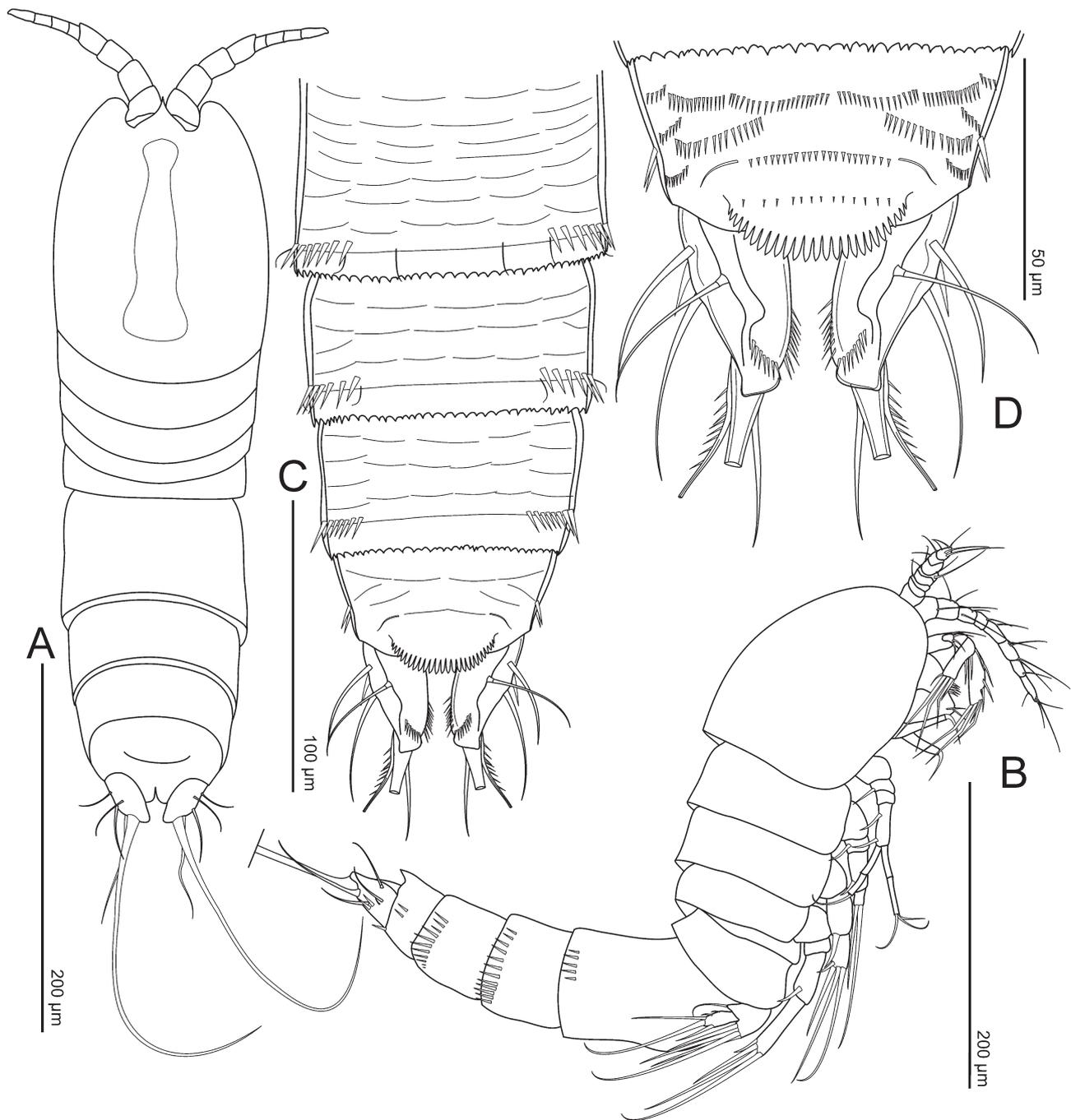


FIGURE 2. *Elaphoidella isana* sp. nov., female: (A) habitus, dorsal view; (B) habitus, lateral view; (C) urosome (without urosomite 1), dorsal view; (D) anal somite and caudal rami, dorsal view.

Mandible (Fig. 5C) robust, with six strong chitinized teeth and one unipinnate seta on gnathobase. Mandibular palp two-segmented; proximal segment with one bare seta on distal corner; distal segment with one seta laterally and four setae apically, all setae bare.

Maxillule (Fig. 5D) robust. Praecoxal arthrite with seven robust unipinnate spines; bare, slender seta on anterior surface. Coxal endite with one bipinnate seta. Basis with two bare, slender setae, one strong bipinnate seta apically. Enp and Exp represented by two bare, slender setae each.

Maxilla (Fig. 5E) short, robust. Syncoxa with two endites, each with one bare and two unipinnate setae inserted apically; row of long spinules inserted on outer margin of syncoxa. Basal endite drawn out into strong, claw-like apophysis, with few spinules distally, two bare setae laterally; Enp represented by one bare seta.

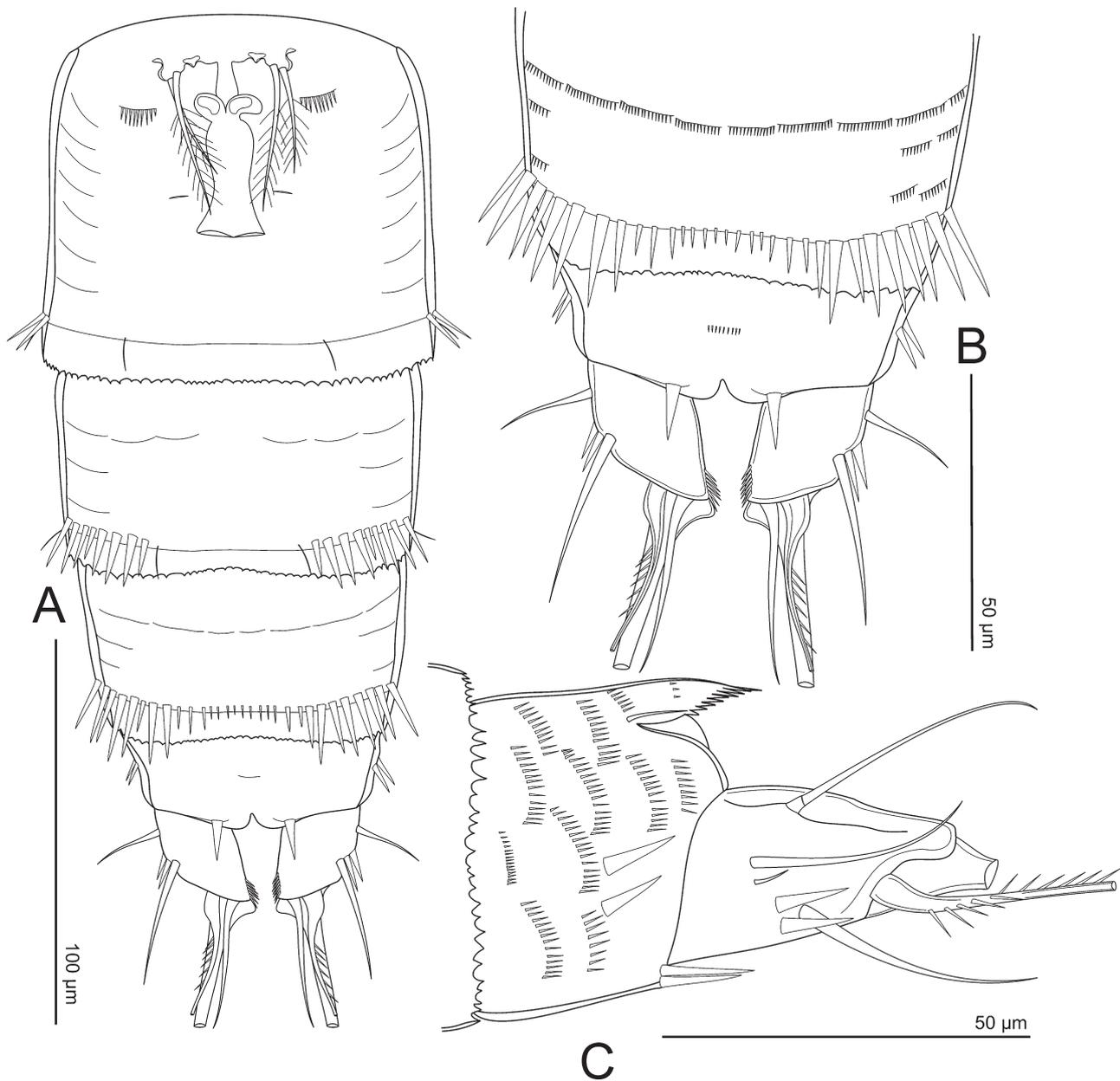


FIGURE 3. *Elaphoidella isana* sp. nov., female: (A) urosome, ventral view; (B) urosomite 4, anal somite and caudal rami, ventral view; (C) anal somite and caudal ramus, lateral view.

Maxilliped (Figs. 4F; 5F) prehensile. Syncoxa with spinules proximally and distally. Basis three times as long as wide, with 18–20 spinules on inner margin, additional two rows of small spinules on outer margin proximally and distally. Enp drawn into unipinnate claw, curved inwards; with bare thin seta at its base.

P1 with three-segmented Exp and Enp, P2–P4 with three-segmented Exp and two-segmented Enp. P1–P4 intercoxal sclerites with concave free margin without ornamentation. Distribution of spinules as indicated on Fig. 6A–D. Armature formula of P1–P4 as follows (legend: inner-outer seta/spine; inner-apical-outer; Arabic numerals represent setae, Roman numerals represent spines):

	Basis	Exp			Enp		
		1	2	3	1	2	3
P1	1-I	0-I	1-I	1-1+I-I	1-0	1-0	0-3-0
P2	0-I	0-I	1-I	1-2+I-I	1-0	2-2+I-0	-
P3	0-1	0-1	1-I	2-2+I-I	1-0	3-2+I-0	-
P4	0-1	0-I	1-I	2-2-II	1-0	2-1+I-0	-

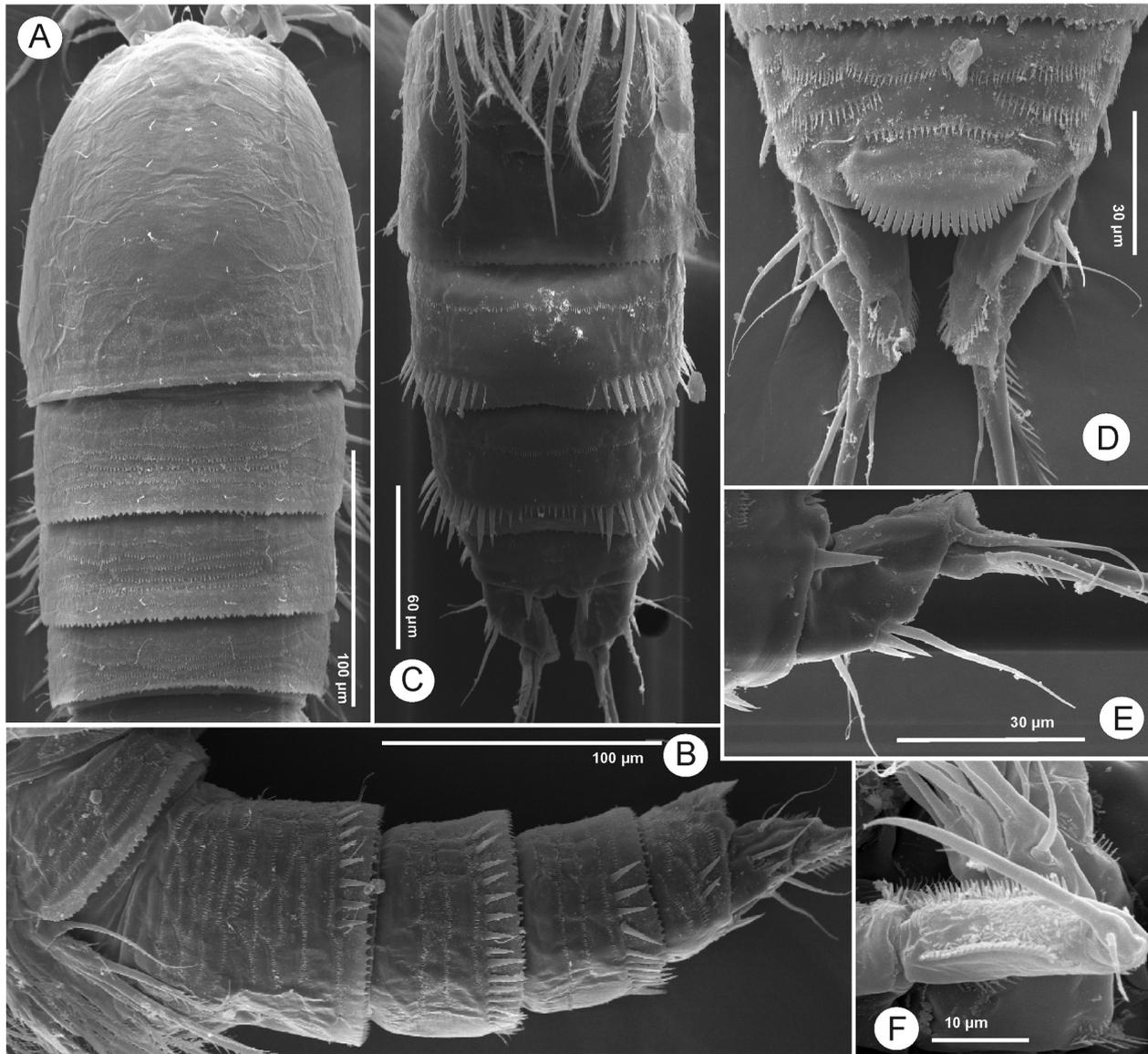


FIGURE 4. *Elaphoidella isana* sp. nov., SEM photographs of female: (A) prosome, dorsal view; (B) urosome, lateral view; (C) urosome (without urosomite 1), ventral view; (D) anal somite and caudal rami, dorsal view; (E) caudal ramus, ventral view; (F) maxilliped.

P1 (Fig. 6A) Enp slightly longer than Exp; Enp-1 about 3.2 times as long as wide, with unipinnate seta on inner margin distally. Enp-2 three times as long as wide, with one bare seta at inner corner distally. Enp-3 four times as long as wide, with one bare seta laterally, one geniculate and one unipinnate seta apically. Exp-1 about twice as long as wide, with one unipinnate spine on outer margin distally. Exp-2 as long as Exp-1 with one bare seta on inner margin distally and one unipinnate spine on outer margin distally. Exp-3 about three times as long as wide, with one geniculate seta on inner margin subapically, one geniculate seta and one unipinnate spine apically, and one unipinnate spine on outer margin distally.

P2 (Fig. 6B) Enp about half length of Exp-2. Enp-1 shorter than wide, with bare seta on inner margin. Enp-2 oval, about 2.5 times as long as wide; with two bare setae on inner margin, shorter than segment; two bipinnate setae, equal in length apically, about three times as long as segment; one spiniform seta apically, shorter than segment. Exp-1 and Exp-2 about 1.5 times as long as wide. Exp-1 and Exp-2 with one bipinnate spine on outer margin distally, Exp-2 with one bipinnate seta on inner margin distally. Exp-3 four times as long as wide; with one bipinnate seta on inner margin inserted in middle of segment, two bipinnate setae and one bipinnate spine on apical margin, apical setae unequal in length, longest one about twice as long as segment; outer margin with one bipinnate spine inserted at about 3/4 of margin.

P3 (Fig. 6C) Enp as in P2 but additional unipinnate seta on inner margin of Enp-2; apical setae longer than in P2 Enp, about four times as long as segment. Exp as in P2 but inner setae of Exp-2 and Exp-3 with unipinnate tips on inner margin (normal in P2) and long, robust spines with rounded tips on Exp-1 and Exp-2 (in contrast pointed in P2).

P4 (Fig. 6D) Enp shorter than Exp-1. Enp-1 small, with one bare seta on inner margin. Enp-2 rectangular, four times as long as wide, with two unipinnate setae on inner margin, longer than segment; apical margin with one seta, about four times as long as segment, and one spiniform seta slightly shorter than segment. Exp relatively long. Exp-1 about 2.5 times as long as wide; Exp-2 about four times as long as wide, Exp-3 about five times as long as wide. Setae on inner margin of Exp-2-3 as in P3. Exp-3 seta of apical margin about 1.5 as long as segment. Spines on Exp-1-2 with pointed tips, spines of outer margin of Exp-3 bare, spine of apical margin unipinnate.

P5 (Fig. 6E) seta on outer margin of baseoendopod long, thin, bare. Exp and baseoendopod well separated. Tip of baseoendopod reaching half of Exp length. Baseoendopod with four long, strong spiniform setae; three inner setae equal in length; outermost seta about half as long as longest one. Exp oval, with five elements: inner seta (I) as long as segment, spiniform; apical seta (II) longest, about four times as long as segment; outer seta (III) robust, spiniform, slightly longer than segment; two outermost setae (IV–V) thin, bare, very short.

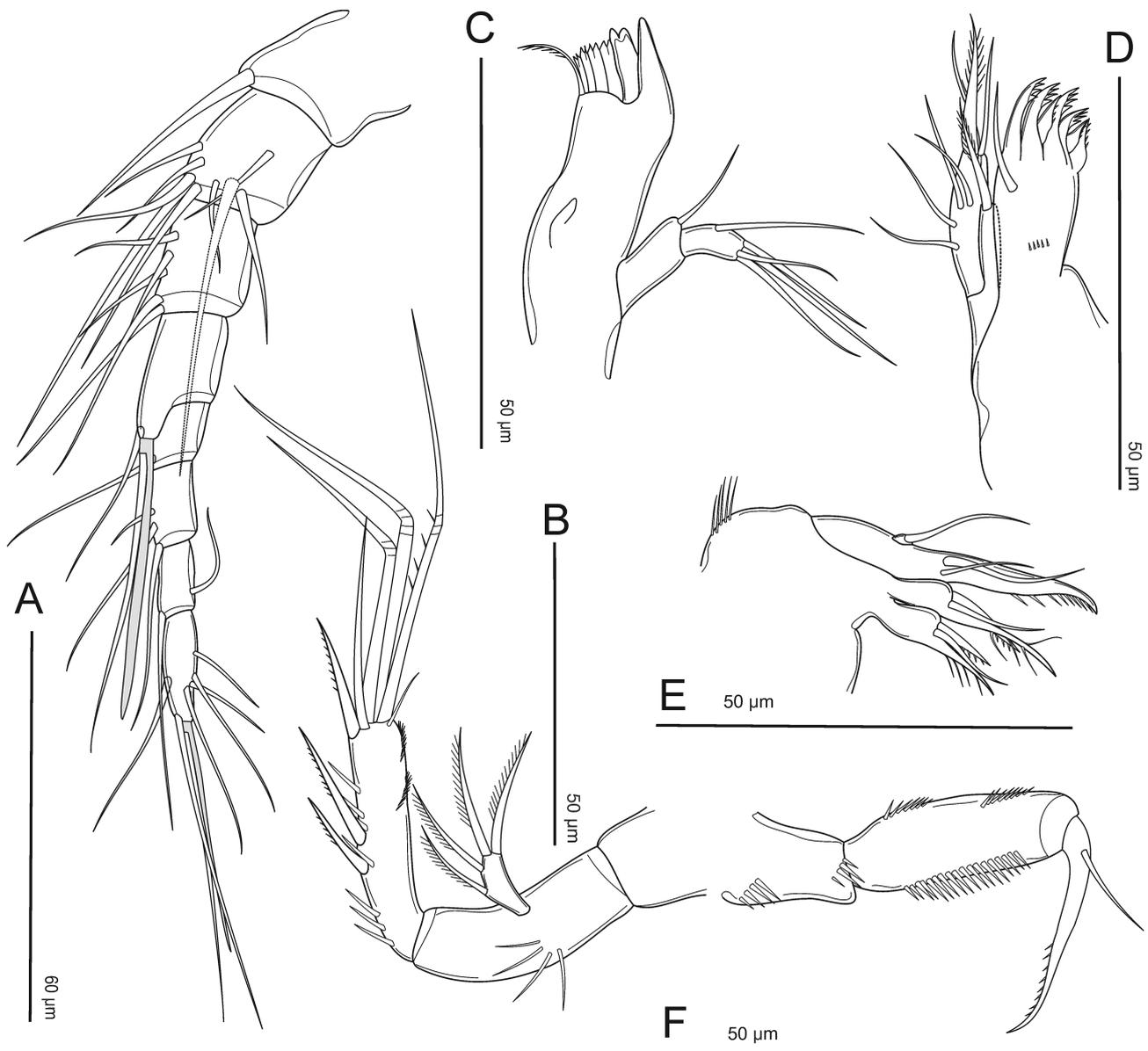


FIGURE 5. *Elaphoidella isana* sp. nov., female: (A) antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped.

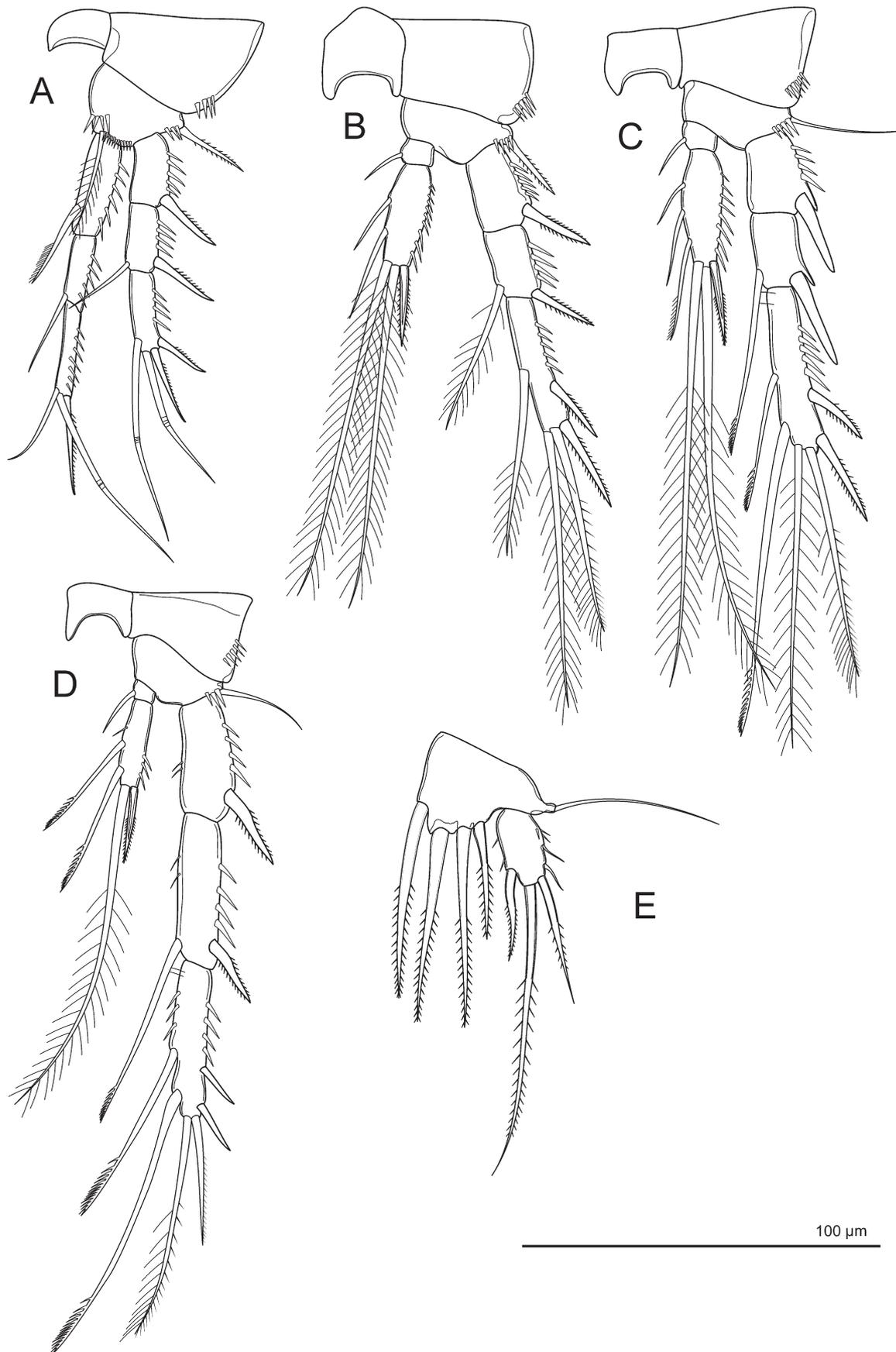


FIGURE 6. *Elaphoidella isana* sp. nov., female: (A) P1; (B) P2; (C) P3; (D) P4; (E) P5. All anterior view.

P6 (Fig. 3A) fused, forming reduced small simple plate located near base of copulatory tube; with two setae on each side, inner seta longer than outer one.

Variability. The only morphological variability was observed in the body size, varying from 420 to 540 μm ($n = 5$).

Male. Unknown

Family Miraciidae Dana, 1846

Genus *Schizopera* Sars, 1905

Schizopera paktaii sp. nov.

(Figs. 7–11)

(<http://zoobank.org/urn:lsid:zoobank.org:act:ABD44820-0ECE-4DA0-9516-CFCCB58B8E7F>)

Type locality. Khao Chang Hai Cave, Na Muen Si Subdistrict, Na Yong District, Trang Province, southern Thailand; coordinates of the cave entrance: 07°35'24.65"N, 099°34'08.62"E; altitude: 45 m a.s.l. (Fig. 1A, D–E).

Material examined. Holotype: adult female, length 510 μm (access no: NHMUK 2019.1007), completely dissected and mounted on one slide. Allotype: adult male, length 500 μm (access no: NHMUK 2019.1008), completely dissected on one slide. Paratypes: three adult females and three adult males, stored in 70% ethanol (access nos: NHMUK 2019.1009–1014, NPU 2019-02). All specimens collected from the type locality on December 1, 2017 by Santi Watiroyram.

Etymology. *Schizopera paktaii* sp. nov. is named after the Paktai region (Thai name for the southern part of Thailand), where the species was collected. The species epithet is a feminine singular adjective.

Distribution. Known only from the pools fed by dripping water at the type locality.

Description of female. Body length measured from anterior margin of rostrum to posterior margin of caudal rami: 460–540 μm (mean = 520 μm , $n = 5$). Habitus elongate, cylindrical, slightly tapering posteriorly; preserved specimens colourless (Figs. 7A; 8A). Cephalothorax rectangular, about 1.5 times as long as wide. Rostrum triangular, more than 2.0 times as long as wide, with pair of sensilla halfway rostrum length (Fig. 7B). Naupliar eye not discernible. Prosomites and urosomites dorsally with tiny spinules on posterior margins, continued by serrated hyaline frill dorso-laterally and ventrally on urosomites. Genital double-somite (Figs. 7C–D; 8B, D), completely fused, as long as wide. Genital complex (Fig. 7E) with single copulatory pore and two small seminal receptacles. Anal somite (Figs. 7F; 8C, E) with row of robust spinules dorso-laterally and ventrally; with oblique row of long hairs along inner margin, just below anal operculum.

Anal operculum (Figs. 7F; 8C) well developed, broadly rounded; not reaching to end of anal somite; free margin with fine, short hairs.

Caudal rami parallel (Figs. 7A, C, F; 8A–B). Caudal ramus subcylindrical, slightly tapering dorso-ventrally, about twice as long as wide; row of strong spinules dorsally at distal part of ramus, just above insertion of terminal caudal setae; three oblique rows of tiny spinules on dorsal surface; row of long hairs at distal 3/4 of inner margin. Caudal setae represented with six elements. Anterolateral accessory seta (I) absent. Anterolateral seta (II) strong, spiniform, about 0.3 times as long as ramus, located at 3/4 of ramus length. Posterolateral seta (III) slender, bare, about 0.5 times as long as ramus, inserted next to seta II. Outer apical seta (IV) slender, unipinnate, about twice as long as ramus, without breaking plane. Inner apical seta (V) longest, bipinnate, with breaking plane just posterior to swollen region, about 3.5 times as long as ramus. Inner accessory seta (VI) slender, bare, shorter than caudal width. Dorsal seta (VII) biarticulated, slender, as long as caudal ramus; positioned near-inner margin at about 1/3 of caudal ramus length.

Antennule (Figs. 8A, F; 9A) eight-segmented, short. Segments 1 and 2 swollen, oriented forward; other segments oriented laterally. Aesthetasc on segments 4 and 8 fused with seta at its base (forming acrothek on apical segment); aesthetasc on segment 4 larger and longer than distal one, reaching beyond tip of antennule; aesthetasc on segment 8 slim, about half length of former one. Setal formula: 1, 8, 6, 3 + a, 2, 4, 4, 6 + a.

Antenna (Figs. 8G; 9B) comprising coxa, allobasis, one-segmented Enp and two-segmented Exp. Coxa unornamented. Allobasis about 2.5 times as long as wide, not completely fused; with unipinnate seta on median

margin. Exp-1 with one unipinnate seta at inner corner distally. Exp-2 with one robust bipinnate seta and one slender, bare seta apically. Enp as long as allobasis, with several spinules and two strong spines along outer distal margin; apical margin with seven elements: three bare and four geniculate setae; additionally, Enp bearing two thin setae inserted sub-apically.

Mandible (Fig. 9C) robust, with seven strong chitinized teeth, one unipinnate seta on gnathobase. Mandibular palp two-segmented; proximal segment with three setae unequal in length, inserted distally, additional short seta at base of distal segment; distal segment with two lateral setae and five apical setae, unequal in length. All mandibular palp setae thin and bare.

Maxillule (Fig. 9D) comprising robust praecoxa, coxa, basis, Enp and Exp. Praecoxal arthrite with seven strong spines (one unipinnate, remaining spines bare) and one bare, slender seta; two additional setae positioned laterally on praecoxal surface. Coxal endite with one bare and one pinnate seta. Basis with one unipinnate, claw-like seta, one bipinnate and five bare apical setae, unequal in length. Enp about 1.5 times as long as wide, with three bare setae apically, unequal in length. Exp small, with two bare setae apically.

Maxilla (Fig. 9E) two-segmented; syncoxa with three endites, two proximal endites with one unipinnate and one bare seta; distal endite with two unipinnate setae. Basis drawn into strong, claw-like expansion, unipinnate. Exp and Enp reduced to two bare setae each.

Maxilliped (Figs. 8I; 9F) prehensile. Coxobasis with three unipinnate setae on median margin, with few strong spinules on anterior surface. Two-segmented Enp; Enp-1 about 2.4 times as long as wide, with two bare setae and row of strong spinules along inner margin, row of setules on outer margin proximally. Enp-2 smaller than Enp-1, about twice as long as wide; with claw-like unipinnate spine and three bare setae apically.

P1–P4 with three-segmented Exp and Enp; P2–P4 intercoxal sclerites with acute projections on distal margin. Armature formula of P1–P4 as follows (legend: inner-outer seta/spine; inner-apical-outer; Arabic numerals represent setae, Roman numerals represent spines); distribution of spinules and hairs as shown in Fig. 10A–D:

	Basis	Exp			Enp		
		1	2	3	1	2	3
P1	I-I	0-I	0-I	0-2+I-I	1-0	0-0	1-2-0
P2	0-I	0-I	1-I	0-2+I-I	0-0	1-0	1-2+I-0
P3	0-1	0-I	1-I	0-2+I-I	1-0	1-0	1-2+I-0
P4	0-1	0-I	1-I	0-2+I-I	1-0	1-0	0-2+I-0

P1 (Fig. 10A) Enp longer than Exp; Enp-1 slightly shorter than Exp, about 5.5 times as long as wide, with one slender, bare seta inserted on 3/4 length of inner margin; Enp-2 as long as wide; Enp-3 about twice as long as wide, with short bare seta on inner margin inserted subapically, one geniculate and one unipinnate seta on apical margin. Exp-1-2 with one spine on outer margin distally. Exp-3 with one spine on outer margin inserted subapically, two geniculate and one spiniform seta on apical margin.

P2 (Fig. 10B) Enp as long as Exp. Enp-2 with unipinnate seta in distal half on inner margin. Enp-3 with unipinnate seta in distal half on inner margin, two normal setae apically, subequal in length, longest one slightly longer than Enp. Exp-1-2 each with one spine on outer margin distally, as long as segment. Exp-3 with two setae and one spine apically; both setae as long as Exp; outer margin with spine inserted subapically.

P3 (Fig. 10C) Enp slightly shorter than Exp. Exp with armature similar to P2. Enp-1-3 each with one long plumose seta on inner margin inserted distally. Enp-3 with two plumose setae and one unipinnate spine apically, both setae subequal in length, longest seta longer than Enp.

P4 (Fig. 10D) with armature similar to P3 except Enp-3 without plumose seta on inner margin.

P5 (Fig. 10E) Exp and baseoendopod well separated. Seta on outer margin of baseoendopod long, thin, bare. Baseoendopod slightly shorter than Exp, with four long, strong spiniform setae; second outer seta (III) the longest, followed by second inner one (II), innermost seta (I) and outermost seta (IV); middle margin of baseoendopod with row of spinules. Exp small, subquadrangular, with five elements: second inner seta (II) the longest, about four times as long as segment, robust, bipinnate; innermost seta (I) spiniform, slightly longer than segment. Setae on outer margin bare, unequal in length.

P6 (Fig. 7C, E) reduced to simple plate, located near the base of copulatory tube, with one small bipinnate seta on outer side and one long bare seta on inner side. Outer seta about three times shorter than inner one.

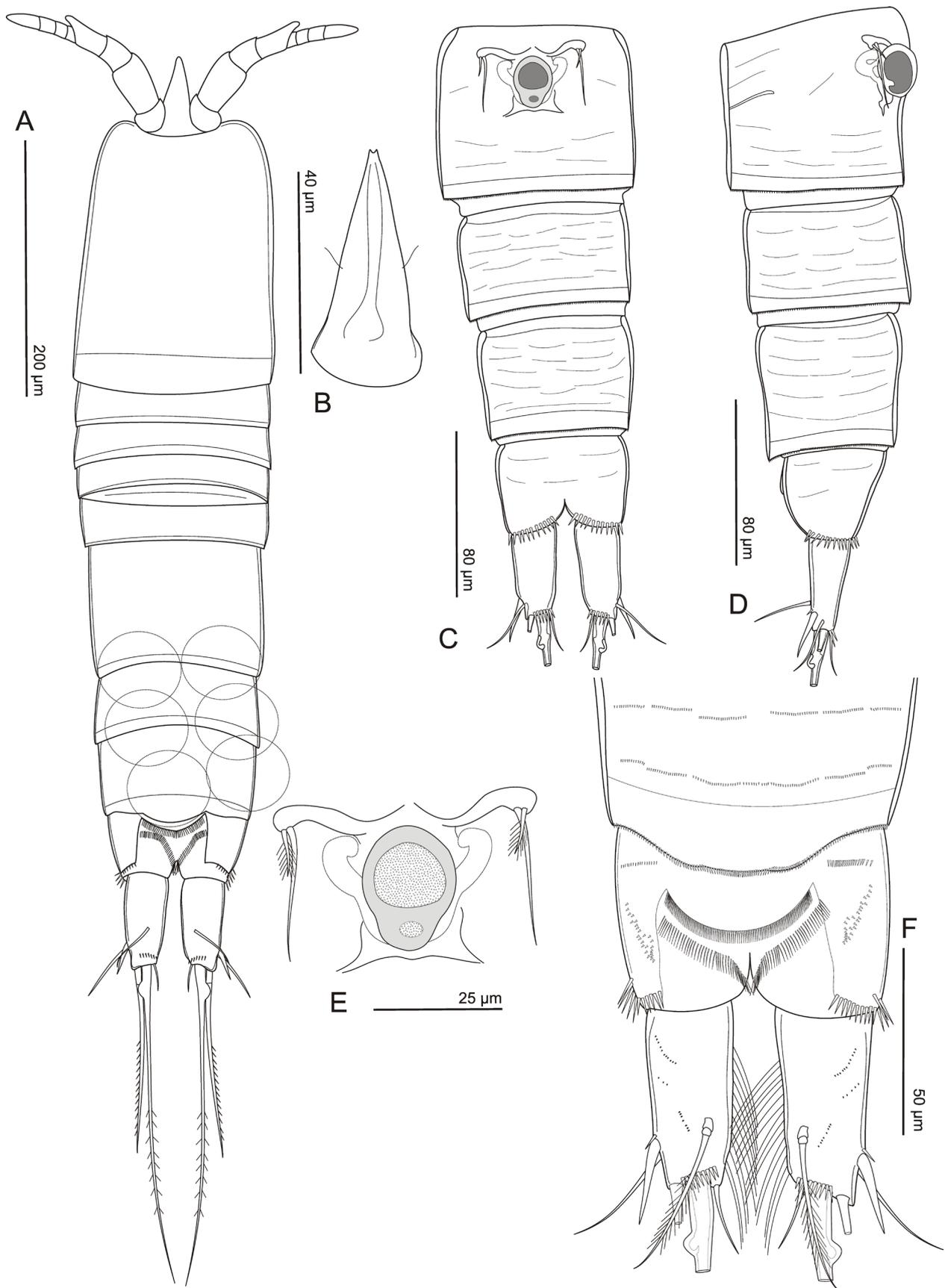


FIGURE 7. *Schizopera paktaii* sp. nov., female: (A) habitus, dorsal view; (B) rostrum; (C) urosome, ventral view; (D) urosome, lateral view; (E) genital complex; (F) urosomite 4, anal somite and caudal rami, dorsal view.

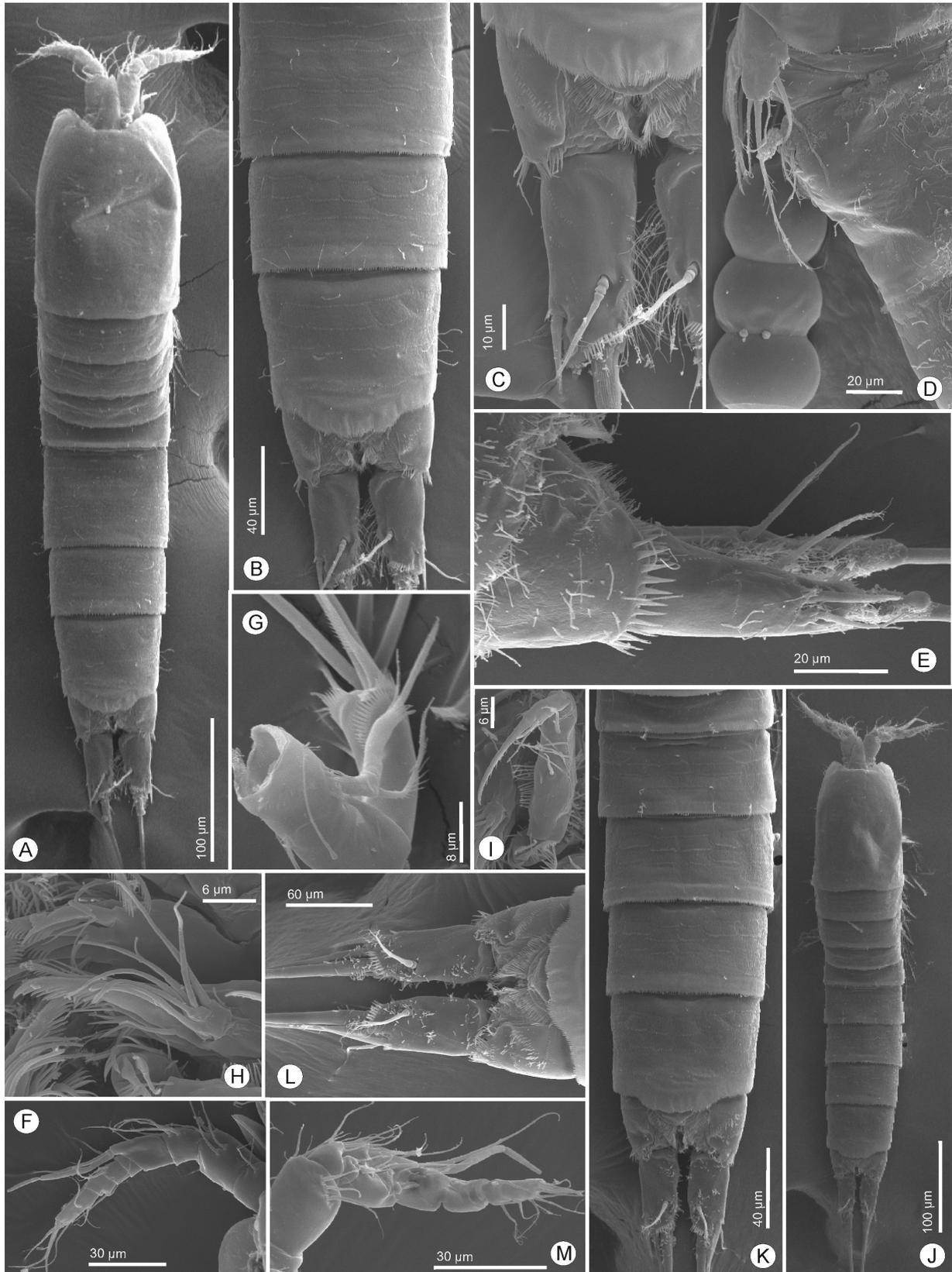


FIGURE 8. *Schizopera paktaii* sp. nov., SEM photographs of female (A–I) and male (J–M): Female: (A) habitus, dorsal view; (B) urosome, dorsal view; (C) anal somite and caudal rami, dorsal view; (D) pediger 5 (with P5) and genital double-somite (with eggs), lateral view; (E) anal somite and caudal ramus, lateral view; (F) antennules; (G) antenna; (H) maxillule and maxilla; (I) maxilliped. Male: (J) habitus, dorsal view; (K) urosome, dorsal view; (L) anal somite and caudal rami, dorsal view; (M) antennule.

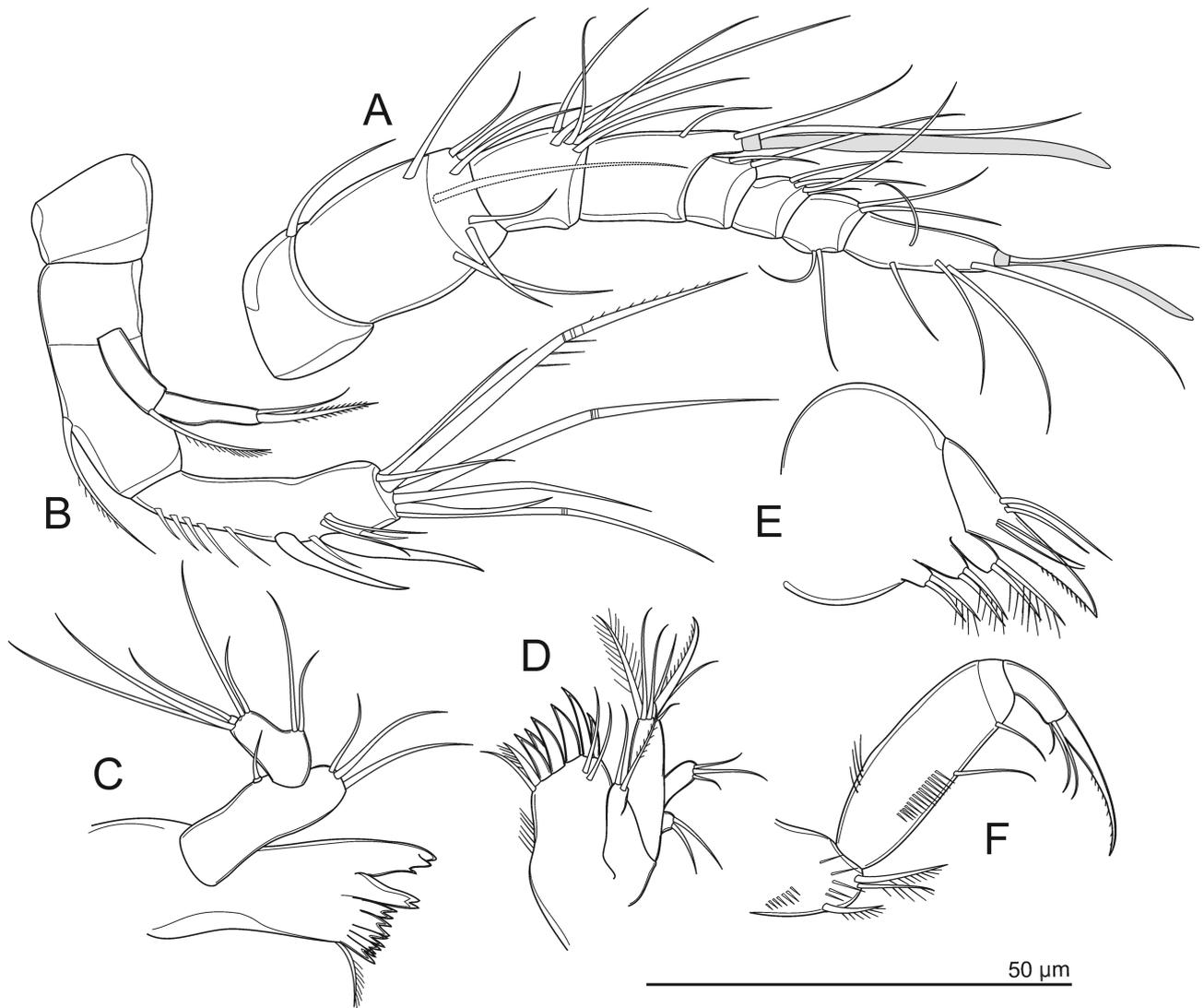


FIGURE 9. *Schizopera paktaii* sp. nov., female: (A) antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped.

Females (Figs. 7A; 8D) with two egg sacs, each containing three large eggs ($n = 5$).

Description of male (Figs. 8J; 11A). Slightly smaller than female; body length measured from anterior margin of rostrum to posterior margin of caudal rami: 470–530 μm (mean = 510 μm , $n = 5$). Habitus and ornamentation similar to female except number of urosomites (six compared with five in female), sexual dimorphism expressed in antennules, and caudal rami without long hairs on inner margin and lacking swollen region on inner apical seta (V) (Figs. 8L; 11C).

Antennule (Figs. 8M; 11D) eight-segmented, with minor geniculation between fifth and sixth segments. Aesthetascs on segments four and eight as in female. Setal formula: 1, 7, 8, 6 + a, 1 + 3s, 1, 4, 6 + a.

P1 (Fig. 10F) as in female, except basis with spine on inner margin transformed into finger-like process.

P2 (Fig. 10G) as in female except morphology and armature of Enp-2-3: Enp-2 with inner margin shaped into rounded lobe, with bare seta distally; outer distal part of segment produced into long apophysis. Enp-3 very small, slightly longer than wide, with two thin, bare equally long setae apically, accompanied by long unipinnate seta, twice as long as bare setae; unipinnate seta inserted subapically.

P3 (Fig. 10H) as in female except armature of inner margin of Exp-3: seta transformed into acute spine inserted on posterior surface of the segment near the inner margin, closely adpressed to segment, not reaching distal margin of Exp-3.

P4 (Fig. 10I) as in female.

P5 (Fig. 10J) Exp and baseoendopod well separated. Seta on outer margin of baseoendopod long, thin, bare. Baseoendopod slightly shorter than Exp, with two subequal spiniform setae, secondary setae limited to distal section of the armature. Exp as in female.

P6 (Fig. 11B, E) represented by simple unarmed bilobate plate.

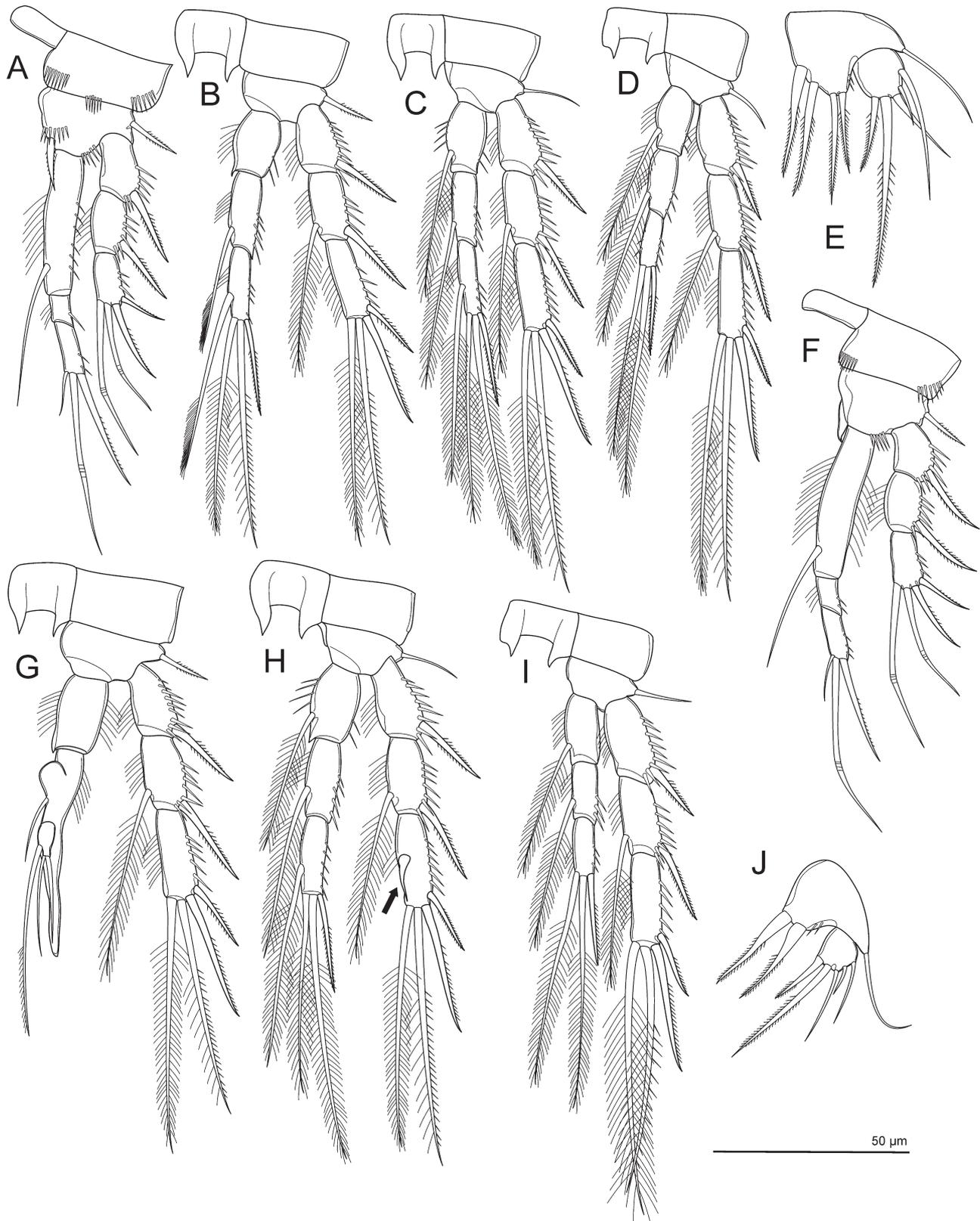


FIGURE 10. *Schizopera paktaii* sp. nov., female (A–E) and male (F–J): (A, F) P1; (B, G) P2; (C, H) P3, black arrow indicates a hyaline spine; (D, I) P4; (E, J) P5. All anterior view.

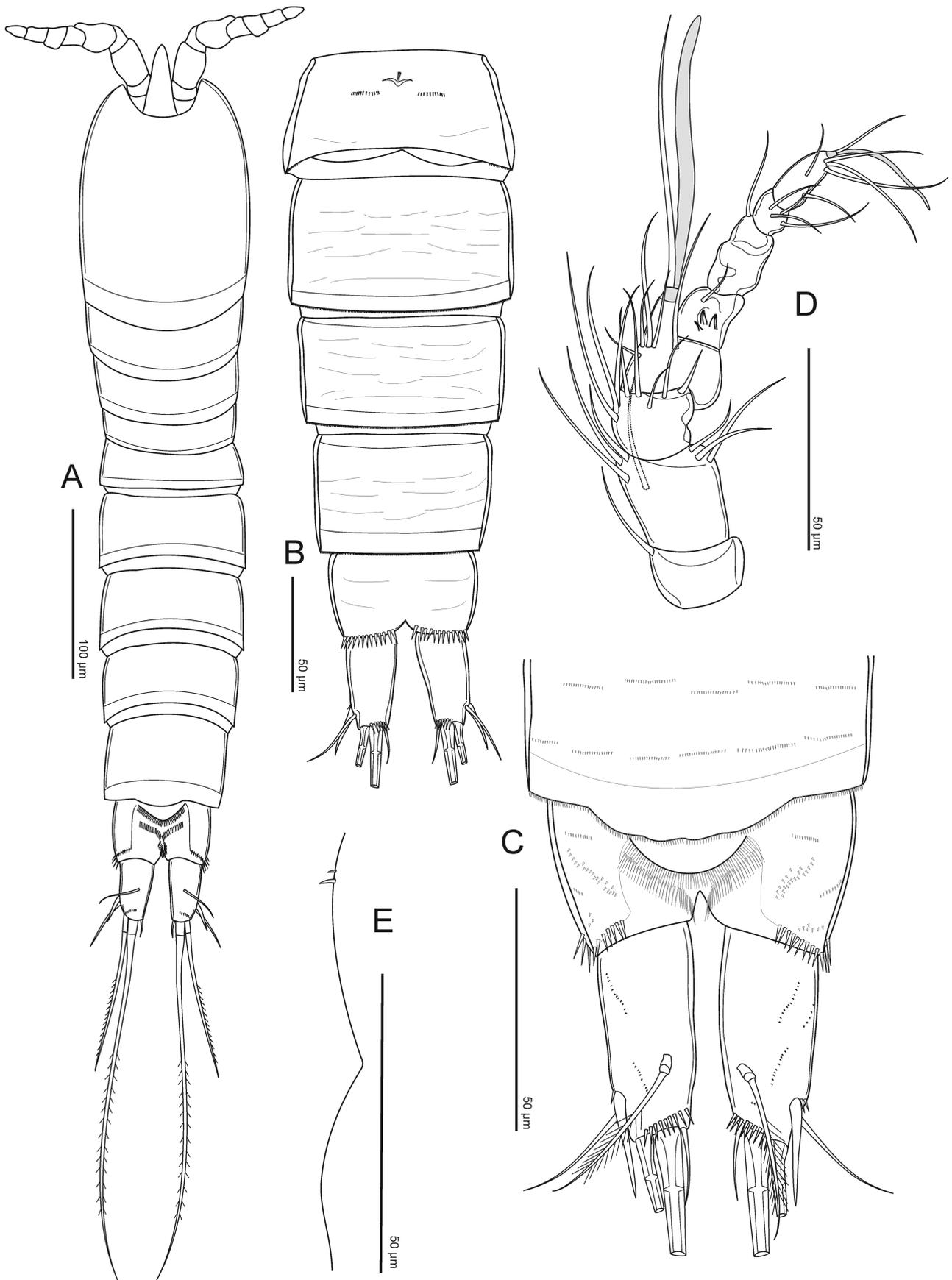


FIGURE 11. *Schizopera paktaii* sp. nov., male: (A) habitus, dorsal view; (B) urosomites 2 to 5, ventral view; (C) urosomite 6, anal somite and caudal rami, dorsal view; (D) antennule; (E) P6 plate.

Variability. Besides the differences in length among females and males, the only morphological variability was observed in one of the five examined male specimens showing a P6 which bears two tiny spinules on one side of the plate (Fig. 11E).

Discussion

Elaphoidella isana **sp. nov.** belongs to group II or gracilis-group *sensu* Lang (1948). Currently, this group comprises nine species and subspecies found in SEA (for a complete list of species see Watiroyram *et al.* 2017). The new species shares affinities with members of group II of Lang (1948) based on the female P5, including the presence of four long setae on the baseoendopod, the latter not extending to halfway the Exp length, and the Exp bearing 3–5 setae on Exp. Two more *Elaphoidella* species have been recorded from northeastern Thailand by Boonyanusith & Athibai (2014). One of them, identified as “*Elaphoidella* sp.1”, shares several characters with *E. isana* **sp. nov.** and is awaiting formal description.

Elaphoidella isana **sp. nov.** is closely related to *E. intermedia* Chappuis, 1931. Following the keys proposed by Wells (2007) and Watiroyram *et al.* (2017), the new species share the following characters with *E. intermedia*: (1) caudal ramus about twice as long as wide; (2) P1 with two-segmented Enp; (3) P2–P4 Enp-1 with seta on inner margin; (4) P2–P4 Enp-2 with five, six and four spines/setae, respectively, and (5) P5 Exp with five setae. Females of *Elaphoidella isana* **sp. nov.** differ from *E. intermedia* in (1) in the new species the sub-apicalmost seta of Enp-2 of P2 and P3 is as long as the segment bearing it, whereas *E. intermedia* the corresponding segments bear a clearly shorter inner seta apically; (2) in *E. isana* **sp. nov.** the P5 Exp displays two thin setae on the outer margin which are longer in *E. intermedia*; (3) the apical inner seta (II) on the caudal ramus in the new species is more than 2.0 times as long as the apical outer seta (III), but it is approximately only 1.5 times as long as the apical outer seta in *E. intermedia*; (4) the inner seta of the P5 baseoendopod is as long as the second outer one in the new species, whereas these setae are clearly unequal in *E. intermedia*; (5) the new species bears approximately 25 strong spinules on the free margin of the anal operculum, whereas in *E. intermedia* there are approximately 30 fine spinules; (6) the new species bears an outgrowth at the tip of the caudal ramus, whereas it is absent in *E. intermedia*; and (7) the new species has a row of spinules on the distal dorsal-inner margin of the caudal ramus, which is apparently absent in *E. intermedia*.

Twelve *Elaphoidella* species have been reported from Thailand from different freshwater habitats, mainly from the caves. One of the species, *E. namnaoensis*, was presumed to reproduce parthenogenetically (for more details see Watiroyram *et al.* 2017). In *E. isana* **sp. nov.**, adult females were abundant during the three-year sampling period (more than 200 individuals were found on each sampling date), but males could not be obtained. The new *Elaphoidella* species described herein, together with *E. namnaoensis*, have shown reproductive success in the subterranean environment. Thus, we presume that parthenogenetic reproduction is probably a common phenomenon among some subterranean species in the tropical region.

Schizopera paktaii **sp. nov.** displays the most significant diagnostic character that defines the genus *Schizopera*, *i.e.* the presence of a hyaline spine on the inner margin of the male P3 Exp-3 (Fig. 10H). Following the keys proposed by Chappuis (1931) and Wells (2007), the new species is closely related to *S. validior* Sars, 1909, which was discovered in Lake Tanganyika (Africa), because they share the common armature and ornamentation of P1–P4 and the caudal rami. The new species differs from *S. validior* based on the following characters: (1) the caudal ramus of the new species is subcylindrical and more than 2.0 times as long as wide, whereas that of *S. validior* is conical and approximately 1.5 times as long as wide; (2) the inner apical seta (V) on the caudal ramus of the new species has a swollen proximal part, which is absent in *S. validior*; (3) the P5 Exp of the new species bears five setae only, whereas that of *S. validior* bears six setae; and (4) the length/width ratio of P1 Enp-1 of the new species is more than 5.0 times whereas it is 3.0–4.0 times in *S. validior*.

The new species can be differentiated from its two congeners currently known from Thailand, *S. longirostris* and *S. subterranea*, by the combination of the characters presented in Table 1. The latter two species are inhabitants of marine environments. *Schizopera longirostris* is known from the Chao Prai River delta and *S. subterranea* from the coastal region of the inner gulf of Thailand (Maiphae & Sa-artrit 2011; Chullasorn *et al.* 2016). *Schizopera paktaii* **sp. nov.** is the first freshwater species of the genus to be described from Thailand. The genus *Schizopera* is poorly known in SEA and the only other (sub)species recorded in the region outside Thailand are *S. tobae tobae* Chappuis, 1931 from Java and Sumatra (Lang 1948) and *S. clandestina clandestina* Klie, 1923 from China and

Korea (Defaye & Dussart 2011). The new species differs from *S. longirostris* and *S. subterranea* as follows: (1) in *S. paktaii* **sp. nov.** the P5 Exp has five setae but there are six setae in the other two species; (2) the new species has long caudal ramus, being about twice as long as wide but only 1.5 times as long as wide in the other two species; (3) the P2 Enp-1 of *S. paktaii* **sp. nov.** has no inner seta whereas it is present in *S. longirostris*; and (4) the new species has hairs along the inner margin of the caudal rami which are absent in *S. subterranea*.

TABLE 1. Morphological comparison of Thai representatives of the genus *Schizopera* (females only).

	<i>S. longirostris</i>	<i>S. subterranea</i>	<i>S. validior</i> *	<i>S. paktaii</i> sp. nov.
Relative length of segments				
P1 Enp-1 : Exp-1-3	Enp-1 > Exp	Enp-1 < Exp	Enp-1 ≤ Exp	Enp-1 ≤ Exp
P1 Enp-1 : Enp-2-3	2.0 times	1.0 times	1.5 times	1.5 times
P1 Enp-1 length : width	3.0–4.0 times	≤ 2.0 times	3.0–4.0 times	> 5.0 times
Caudal ramus length : width	1.5 times	1.5 times	1.5 times	2.0 times
Number of setae and spines				
P2–P4 Exp-3	4.?.?	4.4.4	4.4.4	4.4.4
P2–P4 Exp-2	2.?.?	2.2.2	2.2.2	2.2.2
P3–P4 Enp-3	?.?	4.3	4.3	4.3
P2–P4 Enp-1	1.?.?	0.1.1	0.1.1	0.1.1
P5 baseoendopod / Exp	4 / 6	4 / 6	4 / 6	4 / 5
Ornamentation on inner margin of caudal rami	hairy	naked	hairy	hairy

* closely related to *S. paktaii* **sp. nov.**; originally described from Lake Tanganyika (Africa).

Schizopera species living in inland waters were mainly recorded from ancient lakes with slightly saline water, such as the Aydarkul Lake (with a salinity of 12 ppt) and Sudochie Lake (with a salinity of 4–6 ppt) in Uzbekistan (Mirabdullayev & Ginatullina 2007) and from groundwater in Western Australia and Israel (Karanovic 2004, 2006; Karaytuğ & Sak 2005). The species richness of the genus is much higher in saline water compared to freshwater, indicating its predominance in the former environment. Such distribution pattern suggests its marine origin and therefore that species inhabiting the freshwater environment are younger (Karanovic 2006). In fact, only two freshwater species flocks (*i.e.* the group of subterranean species) are currently recognized: one in Western Australia and another one in Lake Tanganyika in Africa (Karanovic & McRae 2013).

The new species reported herein is the second *Schizopera* species to be described from a cave, the first one being *S. tobae cubana* Petkovski, 1973, which was discovered in Cuba (Petkovski 1973). The existing flocks of stygobionts may have diversified from an ancestor with a wide distribution in surface waters or may have diversified from marine species (Karanovic & McRae 2013). The subterranean speciation was demonstrated by Karanovic & Cooper (2012) in partial phylogenetic analysis of the genus *Schizopera* based on cytochrome *c* oxidase subunit I (COI) sequence data. Their study revealed that explosive radiation and multiple colonization have probably affected regional diversity of Australia during independent invasions.

Schizopera paktaii **sp. nov.**, with a type locality near the Trang River basin and located approximately 20 km from the Andaman Sea (Thailand), is so far the only freshwater species other than the two species flocks indicated by Karanovic & McRae (2013). In addition, *Schizopera* – together with *Fierscyclops* Karanovic, 2004 – is one of the two freshwater genera from Thailand that indicates the Gondwana connection between SEA and Australia that dates back to before the Devonian (Metcalf 1998; Boonyanusith *et al.* 2013).

The two new species described in this article are new representatives of the epikarstic fauna of Thailand. Many studies revealed that the epikarstic zone or the uppermost of the vadose zone are an important environment for copepods (Brancelj *et al.* 2010; Watiroyam *et al.* 2012, 2015a, 2015b, 2017; Boonyanusith *et al.* 2013, 2018b; Watiroyam & Brancelj 2016; Watiroyam 2018a, 2018b). They are constantly washed out from the ceiling as drift by means of epikarstic drips. Frequently only one species per pool can be found—with two copepod species co-inhabiting the same pool being quite rare in subtropical/tropical zone. Epikarst drips are not connected to any surface running or standing water and are fed exclusively by precipitation. Copepod communities originating from the epikarst could be quite abundant in the pools, fed by percolating water because they lack predators and/or competitors (Brancelj 2006).

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References

- Boonyanusith, C. & Athibai, S. (2014) Harpacticoid copepods in Sakaerat Environmental Research Station. *NU Science Journal*, 11, 23–34.
- Boonyanusith, C., Brancelj, A. & Sanoamuang, L. (2013) First representatives of the genus *Fierscyclops* Karanovic, 2004 (Copepoda, Cyclopidae) from South East Asia. *Journal of Limnology*, 72 (2s), 275–289.
<https://doi.org/10.4081/jlimnol.2013.s2.e13>
- Boonyanusith, C., Saetang, T., Wongkamheng, K. & Maiphae, S. (2018a) *Onychocamptus* Daday, 1903 from Thailand, with descriptions of two new species and two new records (Crustacea, Copepoda, Harpacticoida, Laophontidae). *ZooKeys*, 810, 45–89.
<https://doi.org/10.3897/zookeys.810.29253>
- Boonyanusith, C., Sanoamuang, L. & Brancelj, A. (2018b) A new genus and two new species of cave-dwelling cyclopoids (Crustacea, Copepoda) from the epikarst zone of Thailand and up-to-date keys to genera and subgenera of the *Bryocyclops* and *Microcyclops* groups. *European Journal of Taxonomy*, 431, 1–30.
<https://doi.org/10.5852/ejt.2018.431>
- Brancelj, A. (2004) Biological sampling methods for epikarst water. In: Jones, W.K., Culver, D.C. & Hernan, J.S. (Eds.), *Epikarst: Proceedings of the Symposium. Shepherdstown, West Virginia, U.S.A. 1–4 October 2003. Special Publication 9*. Karst Waters Institute, Charles Town, West Virginia, pp. 99–103.
- Brancelj, A. (2006) The epikarst habitat in Slovenia and the description of a new species. *Journal of Natural History*, 40, 403–413.
<https://doi.org/10.1080/00222930600646608>
- Brancelj, A., Boonyanusith, C., Watiroyram, S. & Sanoamuang, L. (2013) The groundwater-dwelling fauna of South East Asia. *Journal of Limnology*, 72 (s2), 327–344.
<https://doi.org/10.4081/jlimnol.2013.s2.e16>
- Brancelj, A., Watiroyram, S. & Sanoamuang, L. (2010) The first record of cave-dwelling Copepoda from Thailand and description of a new species: *Elaphoidella namnaoensis*, sp. nov. (Copepoda, Harpacticoida). *Crustaceana*, 83, 779–793.
<https://doi.org/10.1163/001121610X502894>
- Chappuis, P.A. (1929) Révision du genre *Canthocamptus* Westwood (Note préliminaire). *Buletinul Societății de Științe din Cluj*, 4, 41–50.
- Chappuis, P.A. (1931) Copepoda Harpacticoida der Deutschen Limnologischen Sunda-Expedition. *Archiv für Hydrobiologie, Supplementband 8, Tropische Binnengewässer*, 1, 512–584.
- Chertoprud, E.S., Gómez, S. & Gheerardyn, H. (2009) Harpacticoida (Copepoda) fauna and the taxocene diversity of the South China Sea. *Oceanology*, 49, 488–498.
<https://doi.org/10.1134/S0001437009040079>
- Chullasorn, S., Kangtia, P. & Song, S.J. (2016) A new species of the genus *Parathalestris* (Copepoda: Harpacticoida: Thalestridae) from dead staghorn corals on Tao Island, southern Thailand. *Raffles Bulletin of Zoology*, 64, 343–350.
- Daday, E. von (1900) Mikroskopische Süßwasserthiere aus Deutsch-Neu-Guinea. *Természetrzaji füzetek kiadja a Magyar Nemzeti Múzeum*, 24, 1–56, pls. I–III.
- Dana, J.D. (1846) Notice of some genera of Cyclopacea. *American Journal of Science and Arts*, Series 2, 1, 225–230.
- Defaye, D. & Dussart, B.H. (2011) *World Directory of the Crustacea Copepoda of Inland Waters. III–Harpacticoida. IV–Gelyelloida*. Backhuys Publishers, Margraf Publishers GmbH, Weikersheim, 450 pp.
- Huys, R. & Boxshall, G.A. (1991) *Copepod Evolution*. The Ray Society, London, 468 pp.
- Karanovic, T. (2004) Subterranean Copepoda from arid Western Australia. *Crustaceana Monographs*, 3, 1–366.
- Karanovic, T. (2006) Subterranean copepods (Crustacea, Copepoda) from the Pilbara region in Western Australia. *Records of the Western Australian Museum*, Supplement 70, 1–239.
<https://doi.org/10.18195/issn.0313-122x.70.2006.001-239>
- Karanovic, T. & Cho, J.L. (2016) Four new *Schizopera* (Copepoda, Harpacticoida) from marine interstitial habitats in Korea. *Zootaxa*, 4114 (1), 1–32.
<https://doi.org/10.11646/zootaxa.4114.1.1>
- Karanovic, T. & Cooper, S.J.B. (2012) Explosive radiation of the genus *Schizopera* on a small subterranean island in Western Australia (Copepoda: Harpacticoida): Unravelling the cases of cryptic speciation, size differentiation and multiple invasions. *Invertebrate Systematics*, 26, 115–192.
<https://doi.org/10.1071/IS11027>

- Karanovic, T., Kim, K. & Grygier, M.J. (2015) A new species of *Schizopera* (Copepoda: Harpacticoida) from Japan, its phylogeny based on the *mtCOI* gene and comments on the genus *Schizoperopsis*. *Journal of Natural History*, 49, 2493–2526. <https://doi.org/10.1080/00222933.2015.1028112>
- Karanovic, T., Koomput, K. & Sanoamuang, L. (2017) Two new *Thermocyclops* species (Copepoda, Cyclopoida) from Thailand, with notes on the genus phylogeny inferred from *18S* and *ITS* sequences. *Zoologischer Anzeiger*, 269, 26–47. <https://doi.org/10.1016/j.jcz.2017.07.003>
- Karanovic, T. & McRae, J. (2013) The genus *Schizopera* (Copepoda, Harpacticoida) in the Pilbara region of Western Australia, with description of a new species and its molecular and morphological affinities. *Records of the Western Australian Museum*, 28, 119–140. [https://doi.org/10.18195/issn.0312-3162.28\(2\).2013.119-140](https://doi.org/10.18195/issn.0312-3162.28(2).2013.119-140)
- Karaytuğ, S. & Sak, S. (2005) A new species of *Schizopera* Sars, 1906 (Copepoda: Harpacticoida) from Israel. *Zoology in the Middle East*, 36, 33–42. <https://doi.org/10.1080/09397140.2005.10638125>
- Klie, W. (1923) Über eine neue Brackwasserart der Harpacticoiden-gattung *Amphiascus*. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 14, 335–339.
- Lang, K. (1948) *Monographie der Harpacticiden*. Håkan Ohlsson, Lund, 1682 pp.
- Maiphae, S. & Sa-arudit, P. (2011) Marine copepods at Mo Ko Thale Tai, Gulf of Thailand. *Songklanakar Journal of Science and Technology*, 33, 641–651.
- Metcalf, I. (1998) Palaeozoic and Mesozoic geological evolution of the SE Asian region: multidisciplinary constraints and implications for biogeography. In: Hall, R. & Holloway, J.D. (Eds.), *Biogeography and Geological Evolution of SE Asia*. Backhuys Publishers, Amsterdam, pp. 25–41.
- Mirabdullayev, I.M. & Ginatullina, E.N. (2007) The genus *Schizopera* (Copepoda, Harpacticoida) in Uzbekistan (Central Asia). *Vestnik Zoologii*, 41, 305–313.
- Petkovski, T.K. (1973) Subterrane Süßwasser-Harpacticoida von Kuba (Vorläufige Mitteilung). *Résultats des Expéditions biospéologiques cubano-roumaines à Cuba*, 1, 125–141.
- Sars, G.O. (1903) Copepoda Harpacticoida. Parts I & II, Misophriidae, Longipediidae, Cerviniidae, Ectinosomidae (part). *An account of the Crustacea of Norway, with short Descriptions and Figures of all the Species*, 5, 1–28, pls. I–XVI.
- Sars, G.O. (1905) Pacifische Plankton-Crustaceen. (Ergebnisse einer Reise nach dem Pacific. Schauinsland 1896–1897). II. Brackwasser-Crustaceen von den Chatham-Inseln. *Zoologische Jahrbücher für Systematik*, 21 (4), 371–414.
- Sars, G.O. (1906) Copepoda Harpacticoida. Parts XV & XVI. Diosaccidae (concluded), Canthocamptidae (part). *An Account of the Crustacea of Norway, with short Descriptions and Figures of all the Species*, 5, 173–196, pls. CXIII–CXXVIII.
- Sars, G.O. (1909) Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W.A. Cunnington, F.Z.S., 1904–1905.—Report on the Copepoda. *Proceedings of the Zoological Society of London*, 1909, 31–77, pls. VI–XXIII. <https://doi.org/10.1111/j.1096-3642.1909.tb01855.x>
- Walter, T.C. & Boxshall, G. (2019) World of Copepods database. *Schizopera* Sars G.O., 1905. Available from: <http://www.marinespecies.org/aphia.php?p=taxdetails&id=115325> (accessed 20 May 2019)
- Watiroyram, S. (2018a) Two new species of the genus *Bryocyclops* Kiefer, 1927 (Copepoda: Cyclopoida: Cyclopidae) from southern Thailand. *Raffles Bulletin of Zoology*, 66, 149–169.
- Watiroyram, S. (2018b) *Bryocyclops asetis* sp. n. and the presence of *Bryocyclops muscicola* (Menzel, 1926) from Thailand (Crustacea, Copepoda, Cyclopoida, Cyclopidae). *Zookeys*, 793, 29–51. <https://doi.org/10.3897/zookeys.793.25005>
- Watiroyram, S. & Brancelj, A. (2016) A new species of the genus *Elaphoidella* Chappuis (Copepoda, Harpacticoida) from a cave in the south of Thailand. *Crustaceana*, 89, 459–476. <https://doi.org/10.1163/15685403-00003536>
- Watiroyram, S., Brancelj, A. & Sanoamuang, L. (2012) A new *Bryocyclops* Kiefer (Crustacea: Copepoda: Cyclopoida) from karstic caves in Thailand. *Raffles Bulletin of Zoology*, 60, 11–21.
- Watiroyram, S., Brancelj, A. & Sanoamuang, L. (2015a) Two new species of *Elaphoidella* (Crustacea: Copepoda: Harpacticoida) with comments on geographical distribution and ecology of harpacticoids from caves in Thailand. *Zootaxa*, 3919 (1), 81–99. <https://doi.org/10.11646/zootaxa.3919.1.4>
- Watiroyram, S., Brancelj, A. & Sanoamuang, L. (2015b) A new cave-dwelling copepod from northeastern Thailand (Cyclopoida: Cyclopidae). *Raffles Bulletin of Zoology*, 63, 426–437.
- Watiroyram, S., Sanoamuang, L. & Brancelj, A. (2017) Two new species of *Elaphoidella* (Copepoda, Harpacticoida) from caves in southern Thailand and a key to the species of Southeast Asia. *Zootaxa*, 4282 (3), 501–525. <https://doi.org/10.11646/zootaxa.4282.3.5>
- Wells, J.B.J. (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). *Zootaxa*, 1568 (1), 1–872. <https://doi.org/10.11646/zootaxa.1568.1.1>