



Two new species of *Waynokiops* Hill *et al.* 2010 (Ephemeroptera: Baetidae) from the Oriental Region

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Abstract

A new species found in northern Thailand and northern India, *Waynokiops pentacanthus* **sp. n.**, is described based on eggs, larvae, subimagines and imagines of both sexes associated by rearing. A new species from southern India, *Waynokiops palifer* **sp. n.** is described based on a mature larva with female subimago and eggs extracted from this larva. All larvae of both species were collected in rivers running in mountain areas. Formerly, the genus *Waynokiops* Hill *et al.* 2010 included a single species *W. dentatogriphus* Hill *et al.* 2010 known from a few larvae collected in lakes of North America and unknown before 2007. Based on the fact that two newly discovered species of *Waynokiops* have an Oriental distribution, an assumption is expressed, that *W. dentatogriphus* is also originally distributed somewhere in the Oriental Region, from where it was introduced into North America. Winged stages are described for *Waynokiops* for the first time, allowing a more complete generic diagnosis and a better understanding of its systematic position.

Key words: mayflies, systematics, Thailand, India

Introduction

The taxon with the rank-free hierarchical name Cloeon/fg1 *sensu* Kluge 2012, or tribe Cloeonini Newman 1853 (*sensu* Kluge 2012), corresponds to the branch «6» on the phylogenetic tree by Kluge & Novikova (1992: Fig. 11) and includes *Cloeon* Leach 1815, *Similicloeon* Kluge & Novikova 1992, *Pseudocentropilum* Bogoescu 1947 (*sensu* Kluge & Novikova 1992), *Procloeon* Bengtsson 1915, *Pseudocentropiloides* Jacob in Jacob & Glazaczow 1987, *Securiops* Jacobus, McCafferty & Gattolliat 2006, *Oculogaster* Kluge 2016 and *Monilistylus* Kluge 2020a, treated as genera or subgenera. Cloeon/fg1 does not include *Centropilum* Eaton 1869, which is often confused with four-winged representatives of *Procloeon*, *Pseudocentropilum* and *Pseudocentropiloides*, but differs from all Cloeon/fg1 by retention of free gonovectes and some other characters (Kluge 2012). According to this interpretation, *Centropilum* includes only *Centropilum luteolum* (Müller 1776) and closely related species.

The taxon Cloeon/fg1 is a member of the taxon Anteropatellata Kluge 1997, which comprises majority of Baetidae and is characterized by a secondary restoration of the patella-tibial suture on fore legs of larva and winged stages of female. In most cases, representatives of Anteropatellata are clearly distinguishable from representatives of the plesiomorphon Protopatellata Kluge & Novikova 2011. However, some taxa cause problems. Thus, *Anafroptilum* Kluge 2012 combines characters of Cloeon/fg1 and Protopatellata (Kluge 2012, Kluge & Novikova 2017).

Hill *et al.* (2010) described the genus *Waynokiops* Hill, Pfeiffer & Jacobus, 2010, based on larvae of the single species *W. dentatogriphus* Hill, Pfeiffer & Jacobus, 2010 from lakes and reservoirs in central and eastern areas of the United States of America. Those larvae have features of Cloeon/fg1 but differ from all other representatives of this taxon by unusual lateral and dorsal abdominal expansions. Besides the characters common for *Waynokiops* and the *Cloeon* complex of genera, Hill *et al.* (2010) reported a similarity between *Waynokiops* and *Securiops* in shape of labial palp.

Here are described two new species of *Waynokiops* from the Oriental Region, *W. pentacanthus* **sp. n.** and *W. palifer* **sp. n.** This new material allows for revision of the generic description of *Waynokiops*, taking into account its species variability and adding characters of winged stages and eggs.

Material and methods

Larvae, imagines and subimagines were associated by rearing. For this purpose subimagines were reared from larvae in cages placed in natural current water or in containers with stagnant water; imagines were reared from subimagines in wide glass tubes closed with wet cotton and protected from direct sun light. Slides are made in Canada balsam.

Material reported in this paper will be deposited in Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; now this material is temporarily located in the Department of Entomology of Saint Petersburg State University.

In the lists of material examined, the following arbitrary signs are used: **L**—larva; **S**—subimago; **I**—imago; **L-S-I♂**—male imago reared from larva, with larval and subimaginal exuviae; **L-S/I♂**—male subimago reared from larva and ready to molt to imago, with larval exuviae.

The term «microlepidés» is used according to Kluge (2022); the term «protopteron» according to Kluge (2005); other terms according to Kluge (2004).

Waynokiops Hill, Pfeiffer & Jacobus 2010

(Figs 1–63, 65–94)

Type species: *Waynokiops dentatogriphus* Hill, Pfeiffer & Jacobus 2010.

Diagnosis and comparison

Larva:

- (1) Head is narrowed, with frontal suture acute-angled (Fig. 15; Hill *et al.*, 2010: fig. 1).
- (2) Labrum is trapezoidal, i.e. widened distally, with lateral margins diverging and distal margin more straight than in other Baetidae; median emargination is widened and shallow (Figs 26–27, 65–67; Hill *et al.* 2010: fig. 2). At least in *W. pentacanthus* sp. n. and *W. palifer* sp. n., bottom of median emargination is straight; 4 sensilla form transverse row on ventral side of labrum proximad of the median emargination (Figs 27, 66) (in contrast with the majority of Baetidae, where the bottom of the median emargination forms a sclerotized projection). Stout setae, forming regular row on distal margin, are spaced (in contrast to most other Baetidae, in which sockets of these setae are contiguous). At least in *W. pentacanthus* sp. n. and *W. palifer* sp. n., dorsal surface of labrum bears only irregularly situated fine setae, without distinguishable submedian pair and without distinguishable pair of submarginal rows. Shape and setation of labrum are similar to that of *Securiops* (Jacobus *et al.* 2006: fig. 7).
- (3) Mandibles are of the «*Centroptilum*-type», i.e. with the kinetodontium separated from the incisor (but remains to be immovable) and rotated perpendicular to the plane of the mandible (Figs 21–22, 33–34; Hill *et al.* 2010: figs 3–4). The same in some other taxa (Kluge 2020b: 440).
- (4) Maxilla is of the «*Cloeon*-type», i.e. with all three canines and three dentisetae long, slender and bent in the same direction. Outer side laterad of canines lacks setae (Figs 23, 68; Hill *et al.* 2010: fig. 5). The same in other *Cloeon*/fg1.
- (5) Maxillary palp is long and 2-segmented (Figs 23, 68; Hill *et al.*, 2010: fig. 5).
- (6) Labium has glossae and paraglossae equally wide (Fig. 24; Hill *et al.* 2010: fig. 6), with setation of the «*Cloeon*-type» (Fig. 70).
- (7) Distal (3rd) segment of labial palp is widened distally and truncate (as in other *Cloeon*/fg1).
- (8) Distal (3rd) segment of labial palp is especially wide, with the inner-distal angle acute; the outer-distal angle is sharply stretched into a small, blunt projection (Figs 24, 71; Hill *et al.* 2010: fig. 7). This resembles *Securiops* Jacobus *et al.* 2006, which has pointed projection on the same place.
- (9) Femora have no any stout setae on outer side and apex (in contrast to other Baetidae); inner side of femur with row of stout setae (Figs 37, 79).
- (10) Tibiae also have no any stout setae on outer side and apex, with row of stout setae on inner side (Figs 35, 39–40, 79). Patella-tibial suture varies among species (see below).

- (11) Claw is long and slender, slightly arched, symmetric, with two equal rows of denticles (Figs 36, 79, 87; Hill *et al.*, 2010: fig. 11) (this structure is primitive for Baetidae).
- (12) Abdominal terga and other body parts without scales and scale sockets (at least in *W. pentacanthus* sp. n. and *W. palifer* sp. n.) (Figs 3–9, 88–91) (in contrast to majority of other Cloeon/fg1 and majority of Baetidae).
- (13) Each abdominal tergum II–VI bears unpaired dorsal protrusions hooked backward (Figs 3–4, 10, 72, 88–89; Hill *et al.*, 2010: fig. 9).
- (14) Posterior abdominal segments, at least segments 8–9, bear denticles on lateral margins (Figs 28, 72) (that is characteristic for Cloeon/fg1).
- (15) Tergalii of certain pairs with additional dorsal lamella; the dorsal lamella arises as an expansion of the anal margin of tergalium, is bent dorsally and overlaps the tergalium from dorsal side (Figs 28–32, 75–78, 94; Hill *et al.*, 2010: fig. 12) (this is characteristic for Cloeon/fg1). Tergalii are capable of rhythmic respiratory movements (as in other Cloeon/fg1).
- (16) All three caudalii (cerci and paracercus) are equally long, with rows of primary swimming setae on inner sides of the cerci and outer sides of the paracercus; there are no secondary swimming setae on lateral sides of cerci (Figs 11, 19) (that is primitive for Baetidae and Ephemeroptera in general).
- (17) Posterior margin of each 4th segment of cercus and paracercus darkened and bears enlarged denticles (Figs 11, 19) (that is characteristic for Cloeon/fg1).

Wings:

- (18) Hind wings are completely absent; larval metanotum lacks vestiges of hind proptera.

Male genitalia (known for *W. pentacanthus* sp. n. only):

- (19) Before molt to subimago, subimaginal gonostyli are bent under the larval cuticle in the «*Cloeon*-type» pose, i.e. with 2nd segments directed laterally (Fig. 56).
- (20) Sterno-styliger muscle is retained (Fig. 58).
- (21) Gonovectes are fused with penial bridge (Fig. 58) (as in other Cloeon/fg1).
- (22) Imaginal gonostyli are similar to that of other Cloeon/fg1: with 2nd segment widened at apex, 3rd segment small and petiolate (Figs 53, 58).

Among these characters, the following are apomorphies of *Waynokiops*:

- (2) median emargination of labrum widened, without projection, with transverse row of four sensilla on ventral side (the same in *Securiops*);
- (8) distal segment of labial palp with outer-distal angle stretched into peculiar narrow projection (similar to that of *Securiops*);
- (9) outer margin of the femur without stout setae;
- (12) abdominal terga without scales and scale sockets (the same in *Securiops*);
- (13) each abdominal segment II–VI with a medial dorsal hooked protrusion.

The following characters are autapomorphies of Cloeon/fg1:

- (7) distal (3rd) segment of labial palp is widened distally and truncate;
- (14) posterior abdominal segments with denticles on lateral margins;
- (15) tergalium with additional dorsal lamella;
- (17) posterior margin of each 4th segment of cercus and paracercus darkened and bears enlarged denticles;
- (21) gonovectes fused with penial bridge (the same in some other taxa);
- (22) gonostyli with 2nd segment widened at apex, 3rd segment small and petiolate.

The following characters are plesiomorphies present in all Cloeon/fg1 and some other taxa:

- (4) maxilla with all three canines and three dentisetae long, slender and bent in the same direction;
- (6) labium with glossae and paraglossae of equal width;
- (11) larval claw symmetric, with two equal rows of denticles;
- (16) cerci and paracercus equally long, with rows of primary swimming setae on inner sides of cerci and outer sides of paracercus, without secondary swimming setae on lateral sides of cerci;
- (19) subimaginal gonostyli bent under larval cuticle in the «*Cloeon*-type» pose;
- (20) sterno-styligeral muscle retained.

The following characters are found in some non-related taxa:

- (1) head narrowed, with frontal suture acute-angled;
- (3) mandibles of the «*Centroptilum*-type»;
- (5) maxillary palp 2-segmented (resulted by fusion of initial for Ephemeroptera muscle-less 2nd and 3rd palpomeres);
- (10) tibiae lacking stout setae on outer side and apex, with row of stout setae on inner side;
- (18) hind wings lost.

Comments: Structure of labrum, labial palp and abdominal terga (characters 2, 8, 12) and some other features suggest relationship between *Waynokiops* and *Securiops* (Hill *et al.* 2010: 66–67). However, *Securiops* is placed in Procloeon/g1 (a taxon subordinated to Cloeon/fg1) based on the presence of one greatly elongated spine on posterior margin of each segment of its larval cercus (Kluge 2020a: 577). Larval cerci of *Waynokiops* have no such spines (Fig. 19).

Species composition. Three species: *Waynokiops dentatogriphus* Hill, Pfeiffer & Jacobus, 2010 is known from Nearctic Region, probably introduced; 2 species are described here from Oriental Region: *Waynokiops pentacanthus* sp.n. and *Waynokiops palifer* sp. n.

Key to larvae of *Waynokiops*

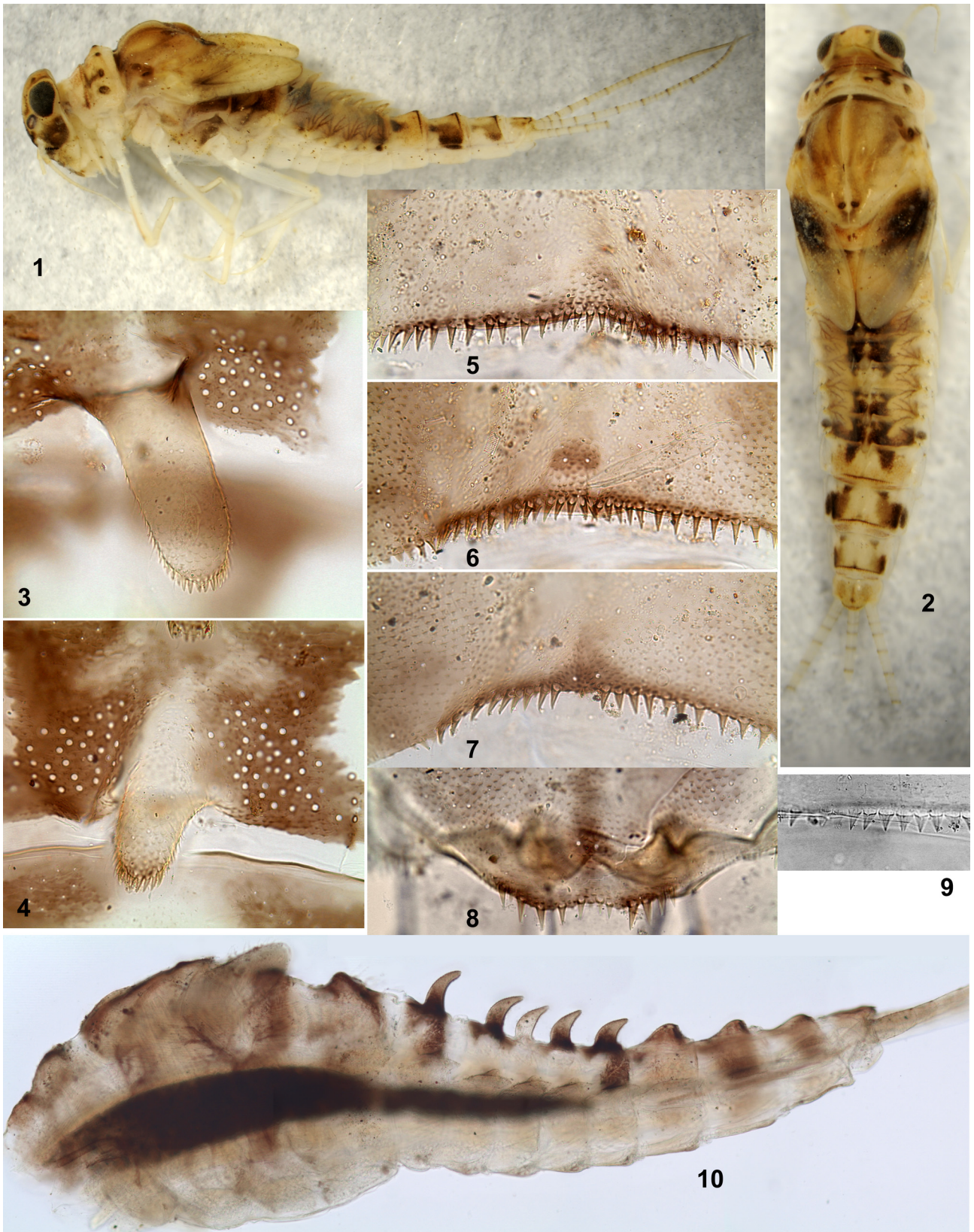
- 1(2) Abdominal segment VII with pair of wide, triangular lateral expansions similar to that of previous uromeres (Hill *et al.* 2010: fig. 8).....*W. dentatogriphus*
- 2(1) Abdominal segment VII without lateral expansions (Figs 28, 72)..... 3
- 3(4) Tergalium II without dorsal lamella (Fig. 74, 93); median protrusion of abdominal tergum II widened distally (Fig. 72, 88) . . .
..... *W. palifer* sp. n.
- 4(3) Tergalium II with dorsal lamella (Fig. 29); median protrusion of abdominal tergum II narrowed distally (Figs 3, 28).....
..... *W. pentacanthus* sp. n.

***Waynokiops pentacanthus* sp.n.**

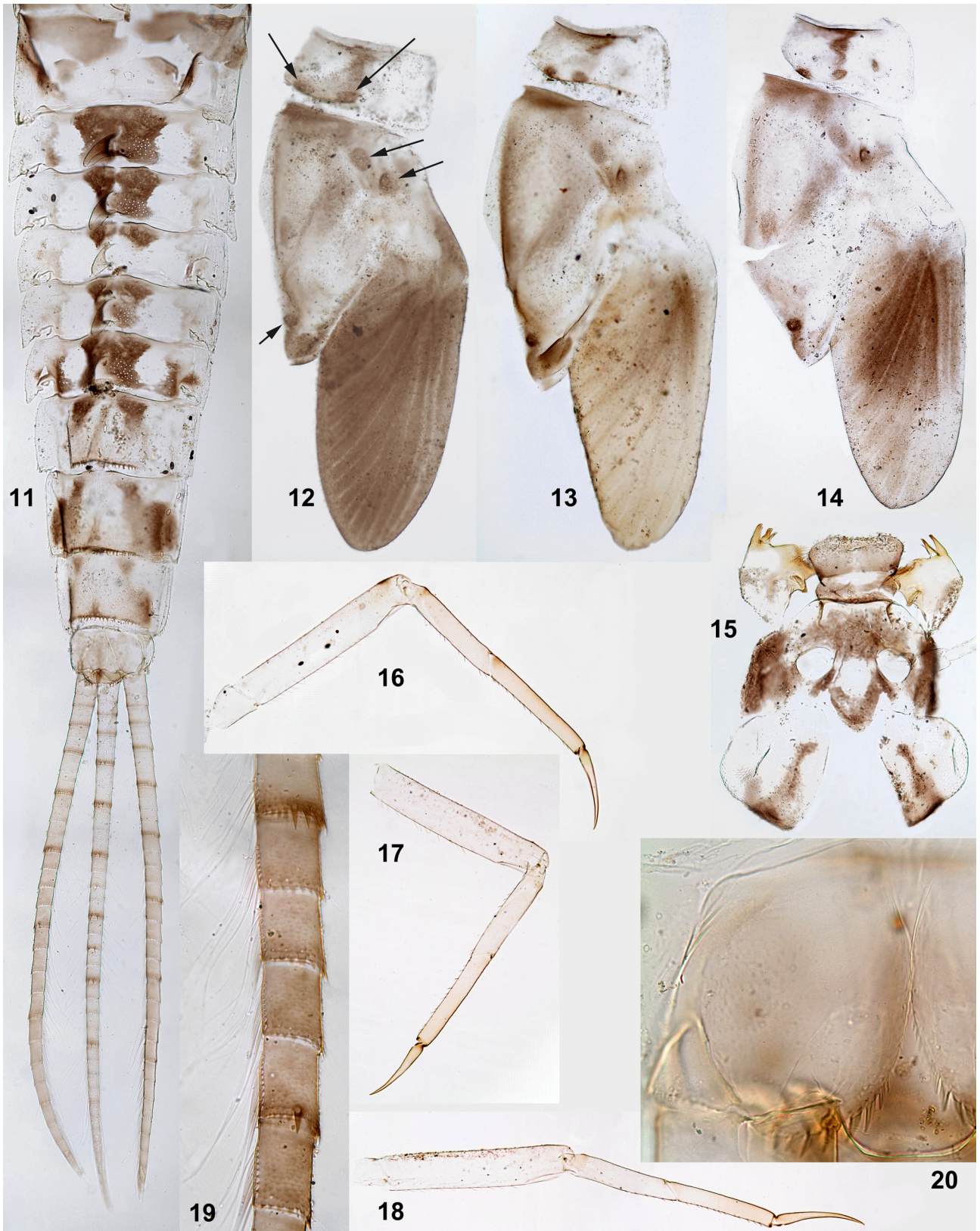
(Figs 1–61)

Etymology. From. *πεντ-* (Gr.)—five-, and *ακανθα* (Gr.)—thorn; allusion to five especially long protrusions of equal shape on abdominal terga II–VII of larva (Fig. 10).

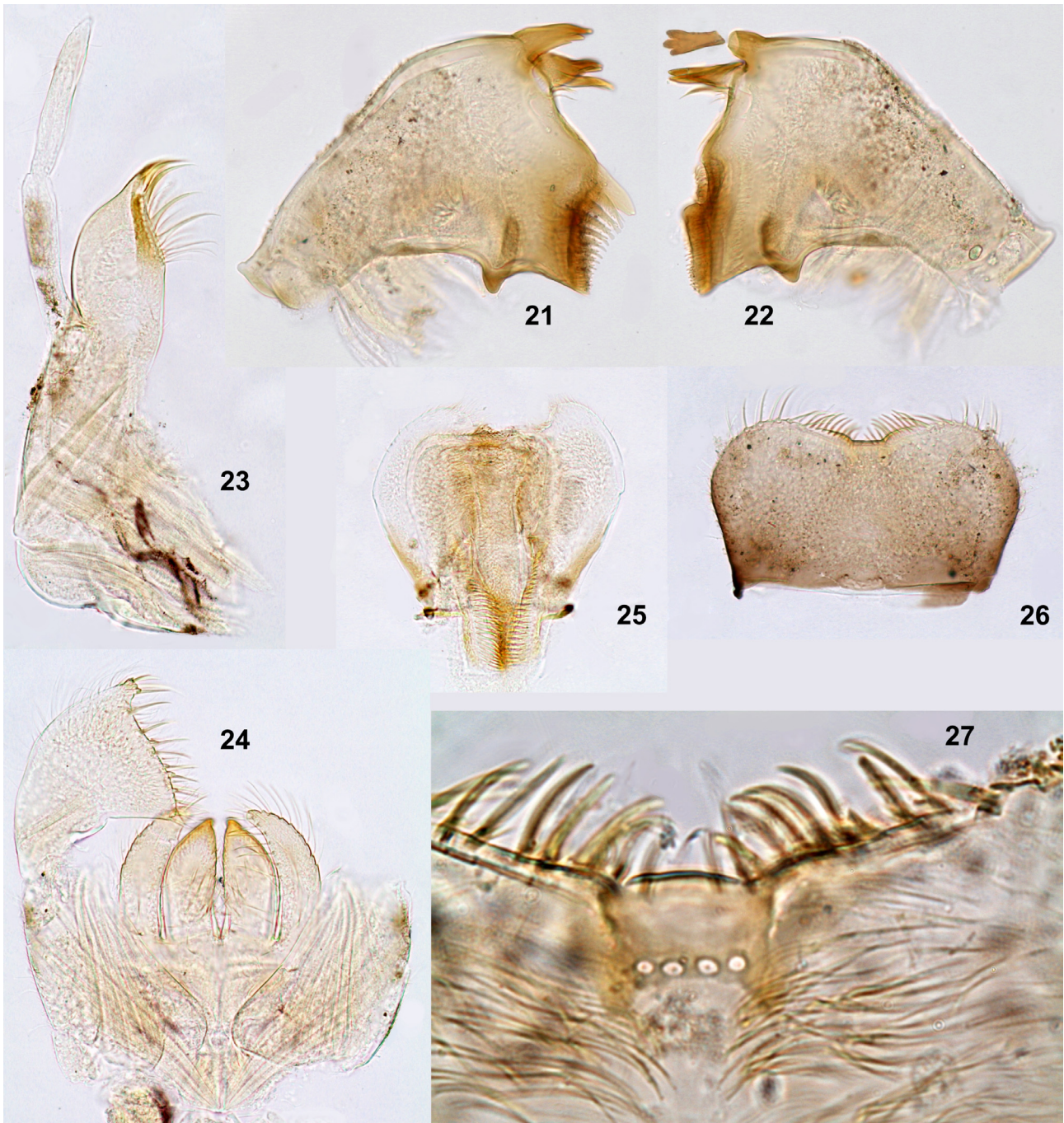
Material examined. Holotype: L-S-I♂ {specimen [XIII](2) 2015}, THAILAND, prov. Mae-Hong-Son, Pai, river Pai upstream Tan Jet Ton village, 9.II.2015, coll. N. Kluge & L. Sheyko. **Paratypes:** the same locality and collectors, 5–14.II.2015: 2 L-S-I♂, 1 L-S/I♂, 3 L-S-I♀, 16 larvae. **Additional material reported by D. Palatov:** INDIA, state Uttarakhand, Rudraprayag, Mandakini river 2 km from mouth, 30°18'8.83"N, 78°58'43.89"E, h=700 m, 5.II.2011, coll. D. Palatov: 1 larva.



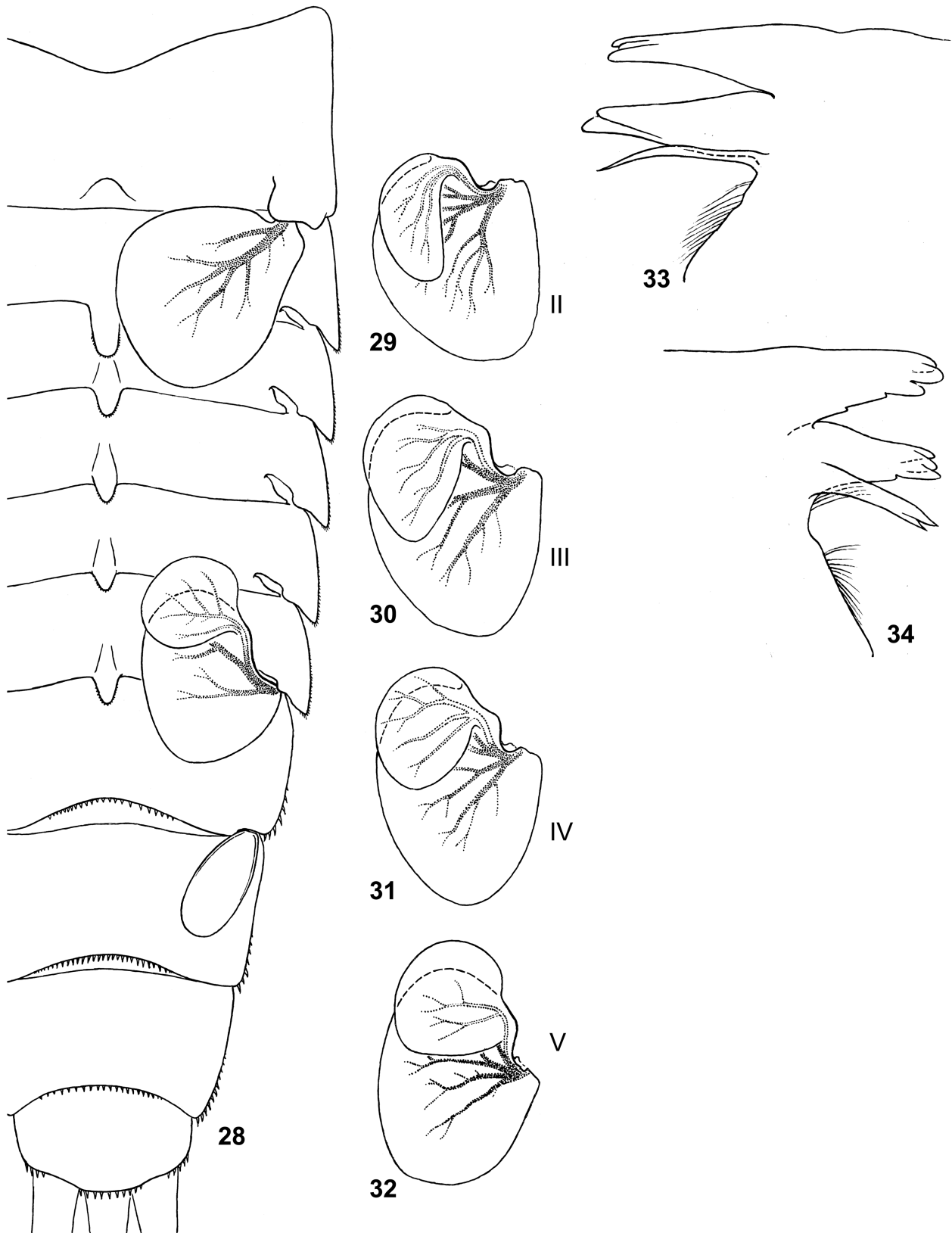
FIGURES 1–10. *Waynokiops pentacanthus* sp. n., larvae. 1–2, female larvae of last instar; 3–8, median part of abdominal terga II, VI, VII, VIII, IX and X; 9, median part of sternum VII; 10, thorax and abdomen of young larva.



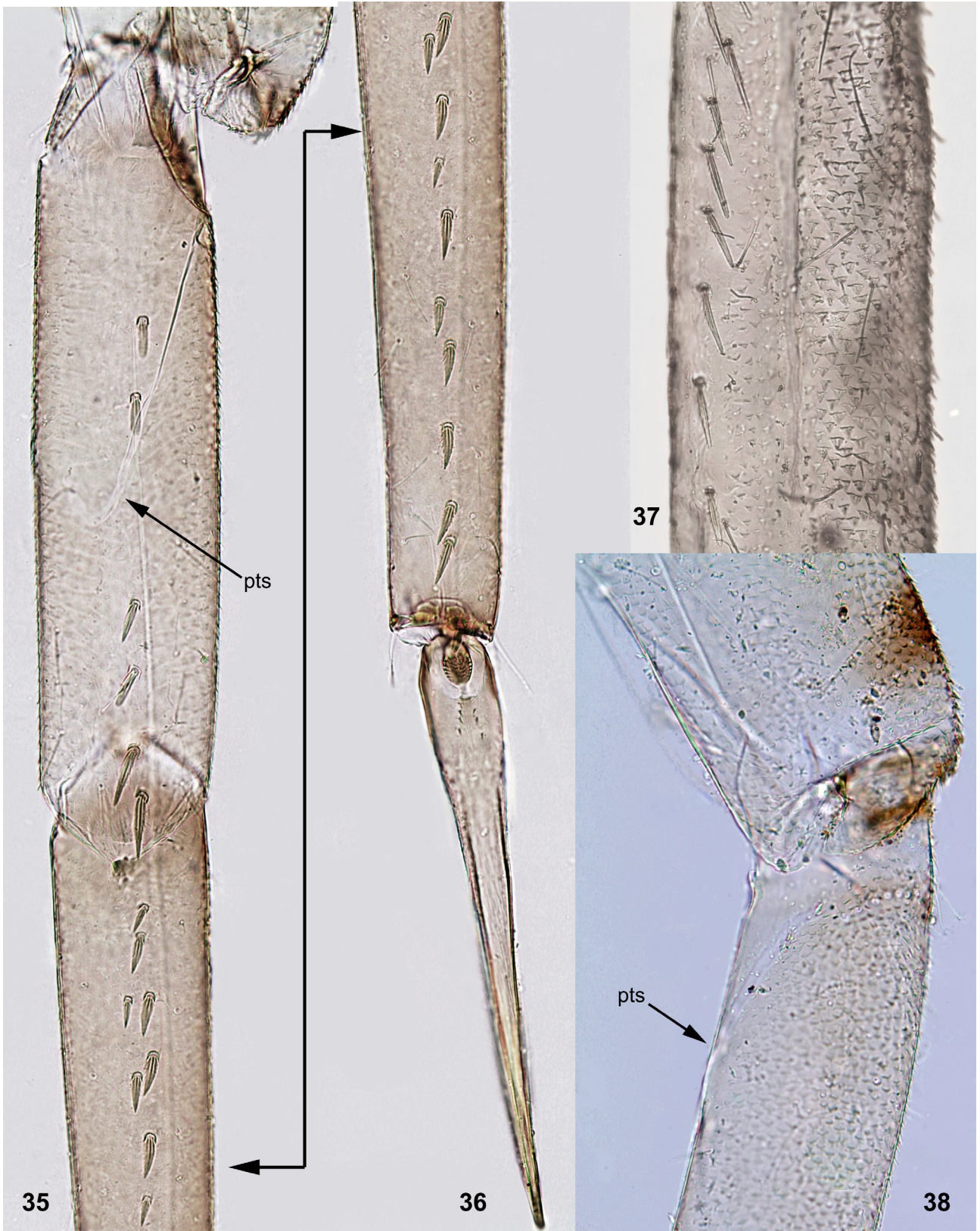
FIGURES 11–20. *Waynokiops pentacanthus* sp. n., larval exuviae (11–18 with same magnification). 11, abdomen; 12–14, half of pronotum and mesonotum (arrows show small prorerubances); 15, head; 16–18, fore, middle and hind legs; 19, fragment of cercus (dorsal view); 20, paraproct (11, 14, 16–19, holotype).



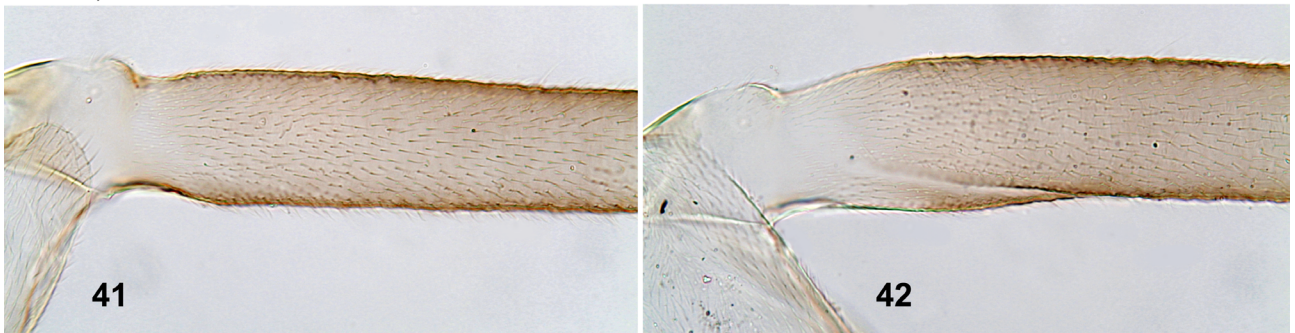
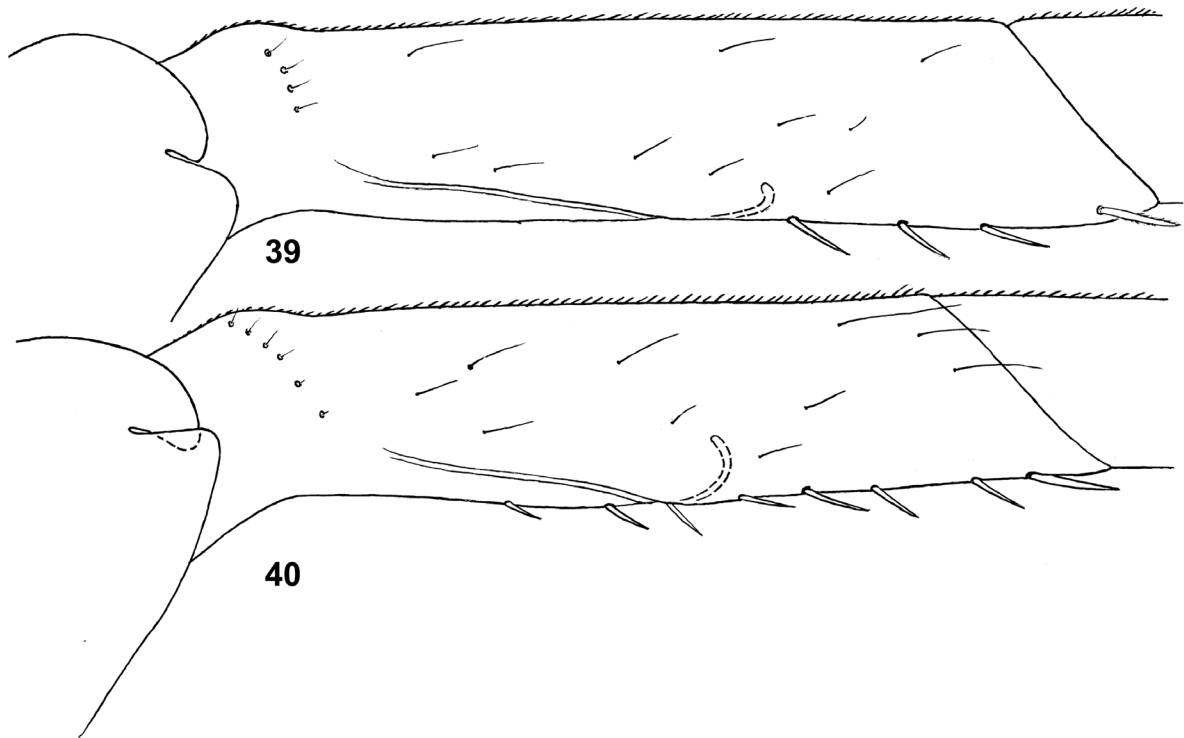
FIGURES 21–27. *Waynokiops pentacanthus* sp. n., larvae. 21–22, left and right mandibles; 23, maxilla; 24, labium (focus on ventral side); 25, hypopharynx with superlinguae; 26, labrum (focus on dorsal side); 27, the same, middle of anterior margin (focus on ventral side).



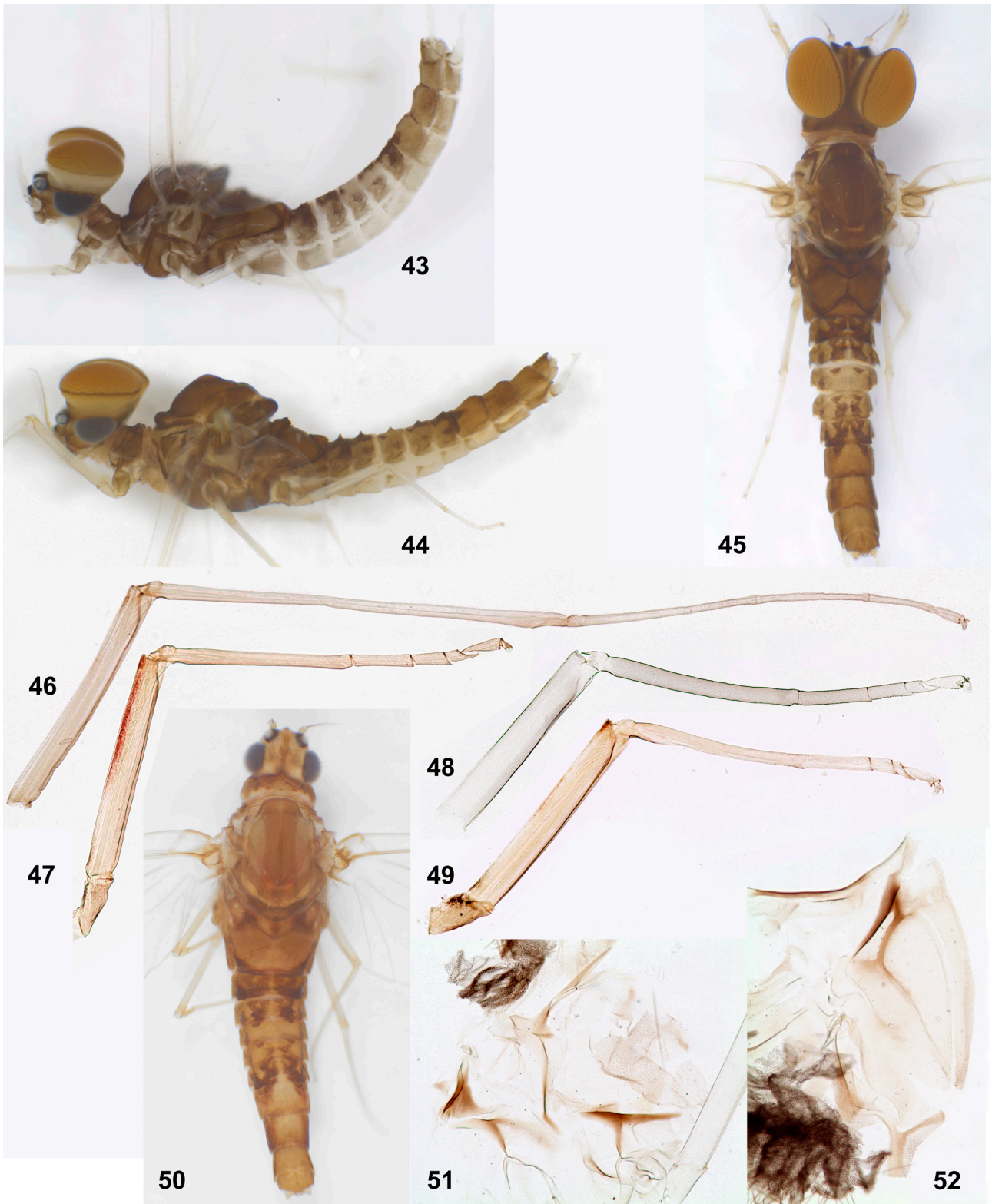
FIGURES 28–34. *Waynokiops pentacanthus* sp. n., larvae. 28, abdomen without tergali II–V; 29–32, tergali II–V; 33–34, apices of right and left mandibles.



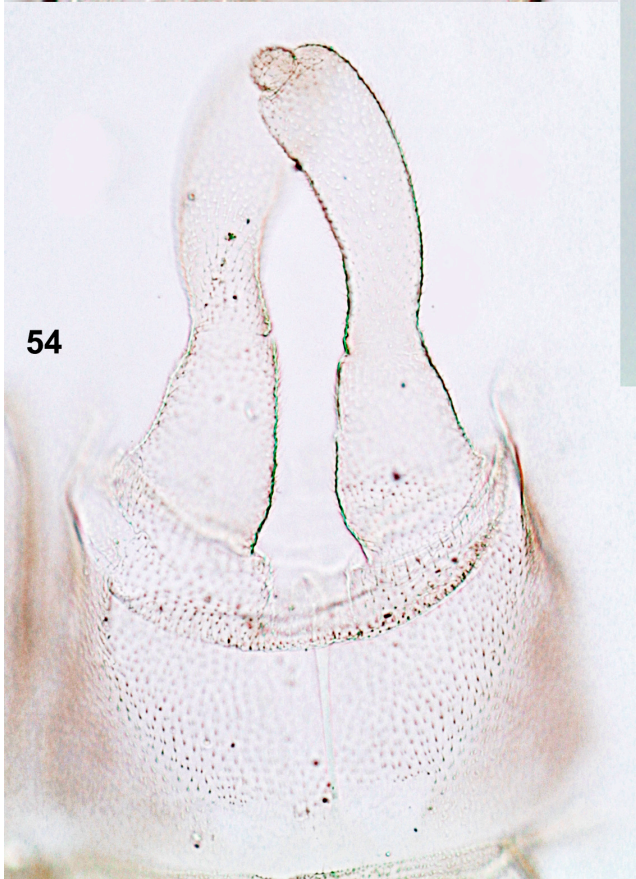
FIGURES 35–38. *Waynokiops pentacanthus* sp. n., exuviae of larval fore legs. 35–36, two fragments of tibia, tarsus and claw, ventral view; 37, femur; 38, apex of femur and base of tibia. Abbreviation: **pts**, patella-tibial suture crossing ventral side of tibia.



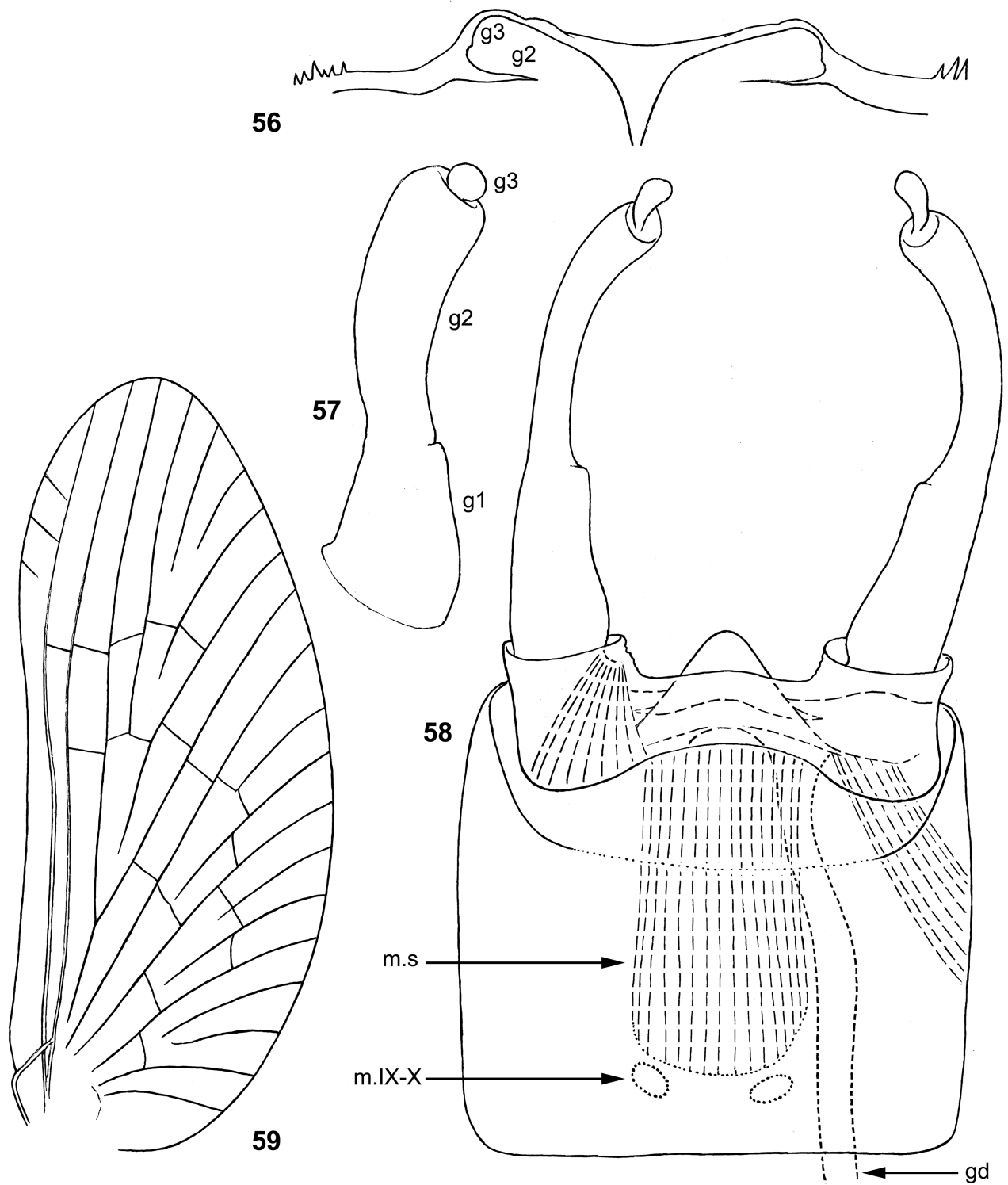
FIGURES 39–42. *Waynokiops pentacanthus* **sp. n.**, patella-tibial suture, anterior view. 39–40, fore and middle legs of larva; 41–42, fore and middle legs of female subimago.



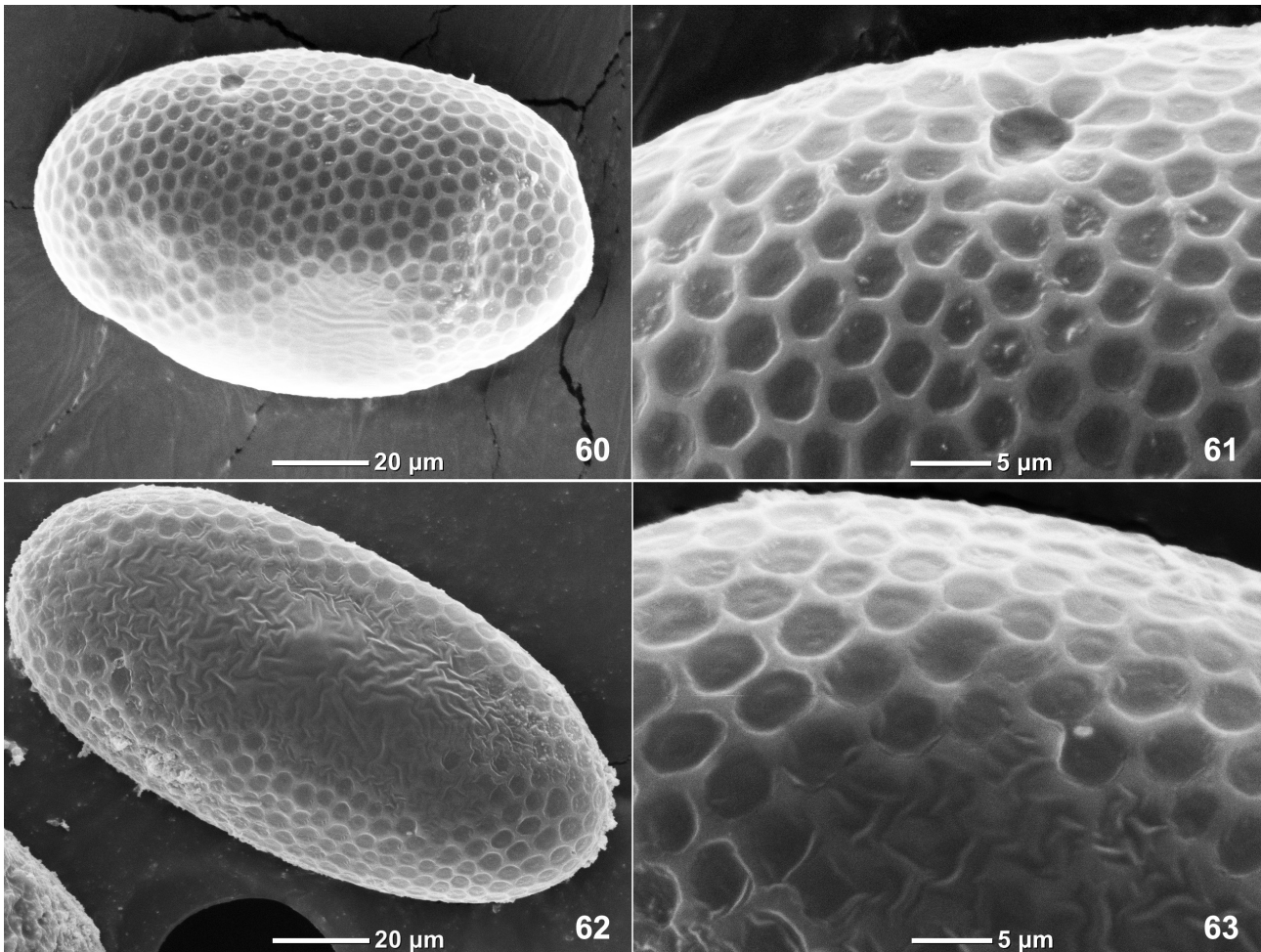
FIGURES 43–52. *Waynokiops pentacanthus* sp. n. 43–45, male imagines; 46, fore leg of male imago; 47, fore leg of female imago; 48, its subimaginal exuviae; 49, middle leg of female imago; 50, female imago; 51, subimaginal exuviae of meso- and metapleuron; 52, subimaginal exuviae of mesonotum (44–46, holotype).



FIGURES 53–55. *Waynokiops pentacanthus* sp. n. 53, genitalia of male imago, focus on dorsal side; 54, their subimaginal exuviae; 55, genitalia of male imago, focus on ventral side (holotype).



FIGURES 56–59. *Waynokiops pentacanthus* sp. n. 56, precursors of subimaginal gonostyli starting to develop under larval cuticle; 57, subimaginal exuviae of gonostylus; 58, genitalia of male imago; 59, wing. Abbreviations: **g1–g3**, segments of gonostylus; **gd**, gonoduct; m.IX-X, areas of anterior attachment of paired intersegmental muscles going to paraprocts base; **m.s.**, median sterno-styligeral muscle.



FIGURES 60–63. *Waynokiops* spp., eggs. 60–61, *W. pentacanthus* sp. n.; 62–63, *W. palifer* sp. n.

Descriptions

Larva. CUTICULAR COLORATION: Head with brown and colorless areas; antennae colorless (Fig. 15). Pronotum and mesonotum with darker and lighter brown and ochre areas; small protuberances (2 pairs on pronotum and 3 pairs on mesonotum) brown; proptera either entirely brown, or brown proximally and light distally (Figs 12–14). Pleura and sterna of prothorax and metathorax colorless. Metanotum and metapleura brown. Legs nearly colorless, with or without small brown markings on outer side near apex of femur, base of tibia and base of tarsus (Figs 16–18). Abdominal terga with brown and colorless areas, contrastingly outlined on terga II–IX and having different shape on different terga (Fig. 11). Abdominal sterna colorless. Caudalii light ochre, with brown band on posterior margin of each 4th segment; swimming setae on inner sides of cerci and lateral sides of paracercus entirely colorless (Fig. 19).

HYPODERMAL COLORATION: Fore femur with fine reddish stripe along outer margin (Fig. 1). Abdominal terga with contrasting brown markings partly coinciding with brown cuticular markings (Fig. 10).

SHAPE AND SETATION: Head and mouth apparatus as characterized for *Waynokiops* (see above).

Vestiges of hind proptera absent. Outer side of leg without stout setae, with numerous minute denticles directed distally (Fig. 37). One row of stout setae on inner sides of femur, tibia and tarsus; setae varying from blunt and non-pectinate to pointed and pectinate (Figs 35–37). Patella-tibial suture present on all legs, proximally far not reaching outer side of tibia, distally crossing inner side of tibia and bent backward on posterior side of tibia; bent portion on posterior side of tibia smaller on fore leg (Figs 35, 38, 39), larger on middle and hinds legs (Fig. 40). Base of each tibia with transverse row of round setal sockets (Figs 38–40). Claw of each leg slender, 1/2 length of tarsus;

two rows of denticles very short, each consisting of 3–4 very small denticles; most of claw with two longitudinal ridges on inner side (Fig. 36).

Abdominal terga and sterna without scales and their sockets, with numerous minute denticles directed posteriorly (Figs 3–8).

Uromere I longer than next ones; lateral margins straight or slightly convex, smooth; posterolateral projections very short (Fig. 28), with small pointed denticles. Tergum I medially with protuberance inclined anteriorly and lacking denticles (Fig. 10). Posterior margins of tergum I and sternum I smooth, without denticles.

Each uromere II–VI shortened, with expressed posterolateral projections (Fig. 28); lateral margins and posterolateral projections covered with small pointed denticles directed posteriorly. Each tergum II–VI medially with high, hooked protrusion narrowing toward apex; all 5 protrusions similar in shape and decreasing in size from tergum II to tergum VI (Fig. 10). Tips of protrusions covered with small pointed denticles; other posterior margins of these terga and posterior margins sterna II–VI smooth, without denticles (Figs 3–4).

Each uromere VII–IX not shortened, without posterolateral projections; lateral margin entirely covered with small pointed denticles directed posteriorly (Fig. 28). Each tergum VII–IX medially with protuberance adjacent to posterior margin (Fig. 10); posterior margins of these terga with conic, pointed denticles (Figs 5–7); on tergum IX row of denticles interrupted behind pair of submedian setae (Fig. 7). Posterior margin of each sternum VII–IX with smaller, flat, triangular denticles (Fig. 9) (on sternum IX of male denticles present only laterad of protogonostyli—Fig. 56).

Abdominal tergum X with conic, pointed denticles on posterior margin (Fig. 8). Paraprocts with pointed denticles (Fig. 20)

Tergalii I–VI with well-developed tracheae; tergalii I without dorsal lamella, tergalii II–VI with dorsal lamella arising from posterior margin at distance from base; tergalii VII narrowed, oval, without dorsal lamella (Figs 28–32). All tergalii rest on dorsal surface of abdomen (as in Fig. 28) or raised perpendicular to it (Fig. 1), capable of rhythmic respiratory movements, but unable to turn laterally; attached more firmly than in most mayflies.

Caudalii with primary swimming setae, without secondary swimming setae on lateral sides of cerci. Posterior margin of each segment dorsally with flat denticles; each 4th segment with larger, conic, pointed denticles; on cerci conic denticles located mostly on outer side (Fig. 19), on paracercus—both on dorsal and ventral sides.

POSE OF SUBIMAGINAL GONOSTYLI: Folding of developing subimaginal gonostyli in last instar male larva of «*Cloeon-type*», i.e. with 2nd segment directed laterally (Fig. 56).

Subimago. CUTICULAR COLORATION: Cuticle mostly nearly colorless, with microtrichia brown (Figs 47–48, 53); small areas of mesonotum and thoracic pleura brown (Figs 51–52).

HYPODERMAL COLORATION: As in imago.

TEXTURE: In both sexes, all tarsomeres of all leg pairs covered with sharply pointed microlepidies (as in Kluge 2022: fig. 6).

Imago, male (Figs 43–45). Head brown. Antennae ochre. Turbinate eyes high, with faceted surface long; faceted surface dull orange and bordered with narrow brown ring, stem paler. Thorax uniformly brown. Fore wings with membrane colorless, veins ochre. Pterostigma with several simple, oblique veins; marginal intercalaries absent (Fig. 59). Hind wing absent. Legs of all pairs pale ochre, femur either with narrow reddish-brown stripe along outer side (as in Fig. 47), or without it (Fig. 46). Middle and hind tarsi with one apical spine on initial 3rd segment (actual 2nd segment) (as in Fig. 49). Abdominal segments II–VI shorter than segments VII–IX (like in larva); terga II–VI either with unpaired median protuberances corresponding to larval protrusions (Fig. 44), or without them (Fig. 43); terga VII–IX convex medially. Abdominal terga with composite pattern of brown and ochre areas (Fig. 45), similar to larval hypodermal and cuticular colorations; sterna lighter. Cerci and gonostyli pale ochre.

Male genitalia (Figs 53–55, 57–58). External part of penial bridge triangular. 1st segment of gonostylus in imago long, slightly thickened proximally and nearly parallel-sided in distal part, with distinctly expressed medio-distal angle (Figs 53, 55, 58); in subimago conic, without distinct medio-distal angle (Figs 54, 57).

Imago, female (Fig. 50). Head and thorax light brown with ochre. Coloration of legs as in male (Figs 47, 49). Fore tarsus 5-segmented, with small apical spine on 3rd segment (Fig. 47); middle and hind tarsi 4-segmented, with apical spine on initial 3rd segment (actual 2nd segment) (Fig. 49). Shape and coloration of abdomen as in male.

Patella-tibial suture of winged stages. In subimago and imago, both in male and female, patella-tibial suture present on middle and hind legs (Figs 42, 49), completely absent on fore legs (Figs 41, 47–48).

Egg (Figs 60–61). Oval; most part of chorion covered with regular net-like relief; smaller area lacking relief and crumpled.

Dimension. Fore wing length 3.5 mm.

Distribution. From north of India to north of Thailand.

Habitat. All specimens collected in Thailand were found in the upper part of river Pai, where it runs among mountain slopes, has clean water, moderate current and bottom consisted mostly of stones, gravel and sand (Fig. 64); the larvae were collected from places with gravel, sand and abundant woody detritus. The specimen collected in Uttarakhand (India) was found in a large mountain river Mandakini with general water current 0.6–1.5 m/s and stony bottom; the single larva was collected from silty sand in the place with water current not exceeding 0.2 m/s.

Comparison. The larva of *W. pentacanthus* **sp.n.** differs from *W. dentatogriphus* by the absence of lateral expansions on abdominal segment VII and by less projected lateral expansions of previous segments (Fig. 28). It differs from *W. palifer* **sp.n.** by presence of patella-tibial suture, by non-widened dorsal protrusion on tergum II (Fig. 3), by absence of slender processes on postero-lateral projections of abdominal segments II–VI and by presence of dorsal lamella of tergalii II (Fig. 29).



FIGURE 64. Collecting site of *Waynokiops pentacanthus* **sp. n.** on river Pai (Thailand).

***Waynokiops palifer* sp. n.**

(Figs 62–63, 65–94)

Etymology. From *pala* (Lat.)—scoop, and *fero* (Lat.)—to bear; allusion to scoop-like median protrusion of abdominal tergum II of larva (Fig. 88).

Material examined. Holotype: Mature female larva ready to molt to subimago, INDIA, Karnataka state, Udupi district, river Seethanadhi near Seethanadhi, 6 km from Someswar, 30.I.2013, coll. N. Kluge & L. Sheyko.

Descriptions

Larva. CUTICULAR COLORATION: Cuticle mostly colorless, with few brown markings. Each femur with dark brown spot at distal part of outer margin, proximad of reddish dot on subimaginal tissues visible through cuticle; each tibia with dark brown spot at patella-tibial concavity of outer margin (Fig. 79, 84–86). Abdominal terga with scattered brown spots (Fig. 72).

HYPODERMAL COLORATION: As in subimago (see below).

SHAPE AND SETATION: Head and mouth apparatus as characterized for *Waynokiops* (see above).

Vestiges of hind protoptera absent. Outer side of leg without stout setae, with numerous minute denticles directed distally. One irregular sparse row of subequal spine-like setae on inner sides of femur, tibia and tarsus (Fig. 79). Patella-tibial suture absent from all legs; base of each tibia with transverse row of round setal sockets (Fig. 72). Claw of each leg slender, 1/2 length of tarsus; proximal 3/7 wider than distal portion, with 2 rows of minute denticles (Fig. 87).

Abdominal terga and sterna without scales and their sockets, with numerous minute denticles directed posteriorly (Figs 88–91).

Uromere I longer than next ones; lateral margins convex and posterolateral angles rounded, both smooth (Fig. 72). Posterior margins of tergum I and sternum I smooth, without denticles.

Each uromere II–VI shortened, expanded laterally, with expressed posterolateral projections; each posterolateral projection with serrate margin, terminating as slender, soft, pointed process (Figs 73, 89). Each tergum II–VI medially with high, hooked protrusion, blunt in dorsal view and pointed in lateral view; protrusion of uromere II scoop-likely widened toward apex (Fig. 88); other protrusions narrowing toward apex, decreasing in size from tergum III to tergum VI (Fig. 89). Surfaces of protrusions covered with minute denticles; other posterior margins of these terga and posterior margins sterna II–VI smooth, without denticles.

Uromere VII not shortened, not expanded and without posterolateral projections; insertions of tergalii distant from lateral margins; its tergum with small median convexity (Fig. 72). Uromeres VIII–IX with small, sclerotized, postero-lateral denticles and small denticles on lateral margins. Posterior margins of terga VII–IX with triangular, pointed denticles; on tergum IX row of denticle interrupted behind pair of submedian setae (Fig. 90). Posterior margins of each sternum VII–IX with smaller, blunt denticles (Fig. 91)

Abdominal tergum X with triangular, pointed denticles on posterior margin (as in Fig. 90). Paraprocts with pointed denticles (Fig. 80).

Tergalii I without dorsal lamella, widened distally, lacking tracheae, with cuticle somewhat hardened and forming distinct reticulate relief (Figs 72, 92). Tergalii II without dorsal lamella, with tracheae (Fig. 74, 93). Tergalii III–VI with dorsal lamella, both lamellae with tracheae (Figs 10–13, 93–94). Tergalii VII without dorsal lamella, narrow, lacking tracheae (Fig. 72).

Caudalii missing, except for few basal segments.

Subimago, female (extracted from larva).

CUTICULAR COLORATION: Pale or absent. Wings pale.

HYPODERMAL COLORATION: Head, thorax and abdomen yellowish with red markings (Figs 81–83). Legs very pale; each femur with small reddish dot on outer side near knee; each tarsal segment with brown dot apically on outer side (Figs 84–86). Abdominal terga I–VI yellowish with red paired and unpaired maculae; terga VII and VIII mostly red, with margins yellowish; terga IX and X yellowish with red maculation (Fig. 83). Abdominal sternum I pale reddish; sterna II–VI mostly yellowish, each with pair of sublateral pale reddish maculae; sterna VII and VIII pale reddish; sternum IX pale (Fig. 82).

SHAPE: Fore tarsus 5-segmented, with small apical spine on 3rd segment; middle and hind tarsi 4-segmented, with apical spine on initial 3rd segment (actual 2nd segment) (Fig. 79).

TEXTURE: All tarsomeres of all leg pairs covered with sharply pointed microlepidies (as in Kluge 2022: fig. 6).

Male. Unknown.

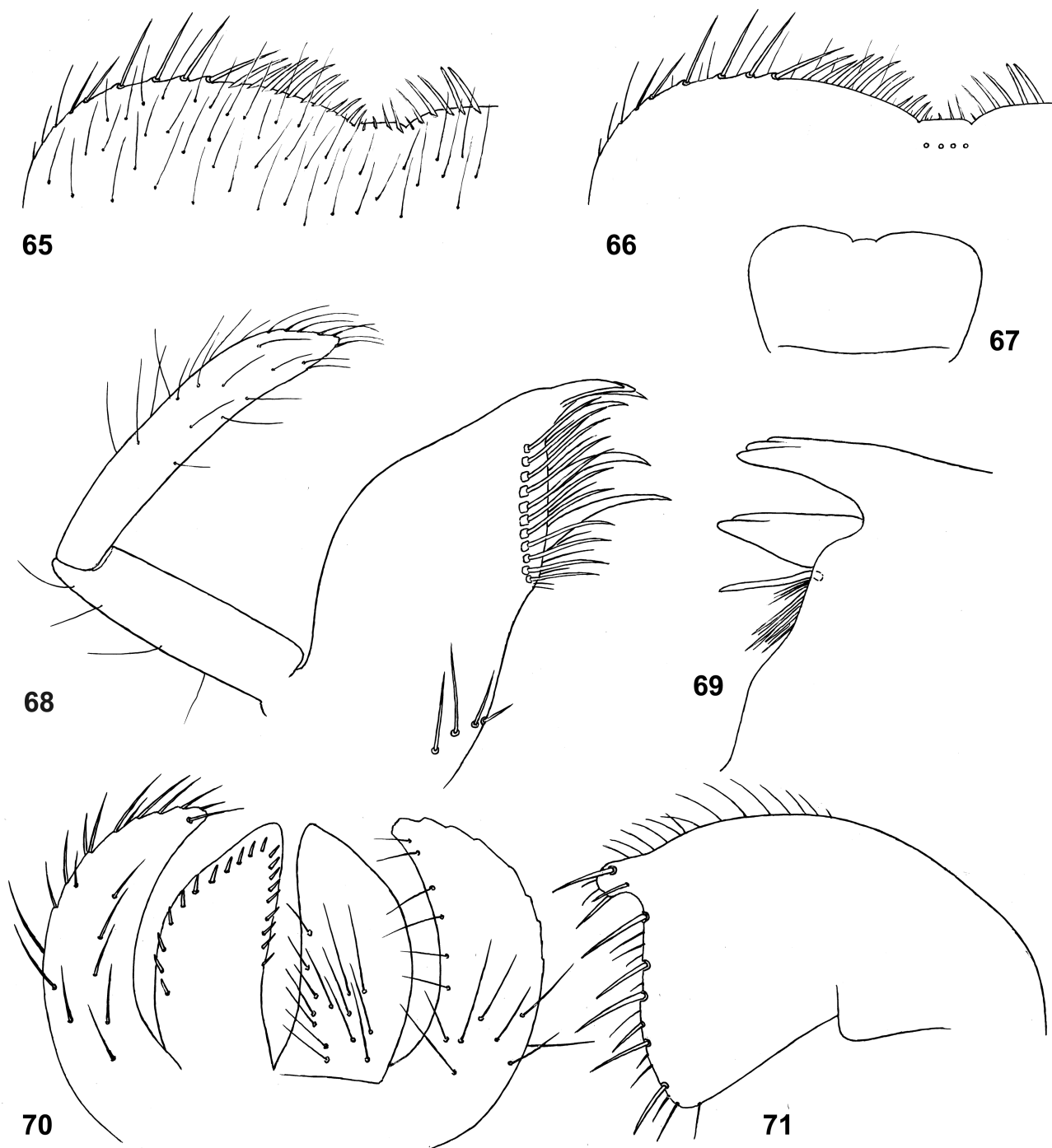
Egg (Figs 62–63). Oval, elongate; most part of chorion covered with regular net-like relief; smaller area lacking relief and crumpled.

Dimension. Body length 3 mm.

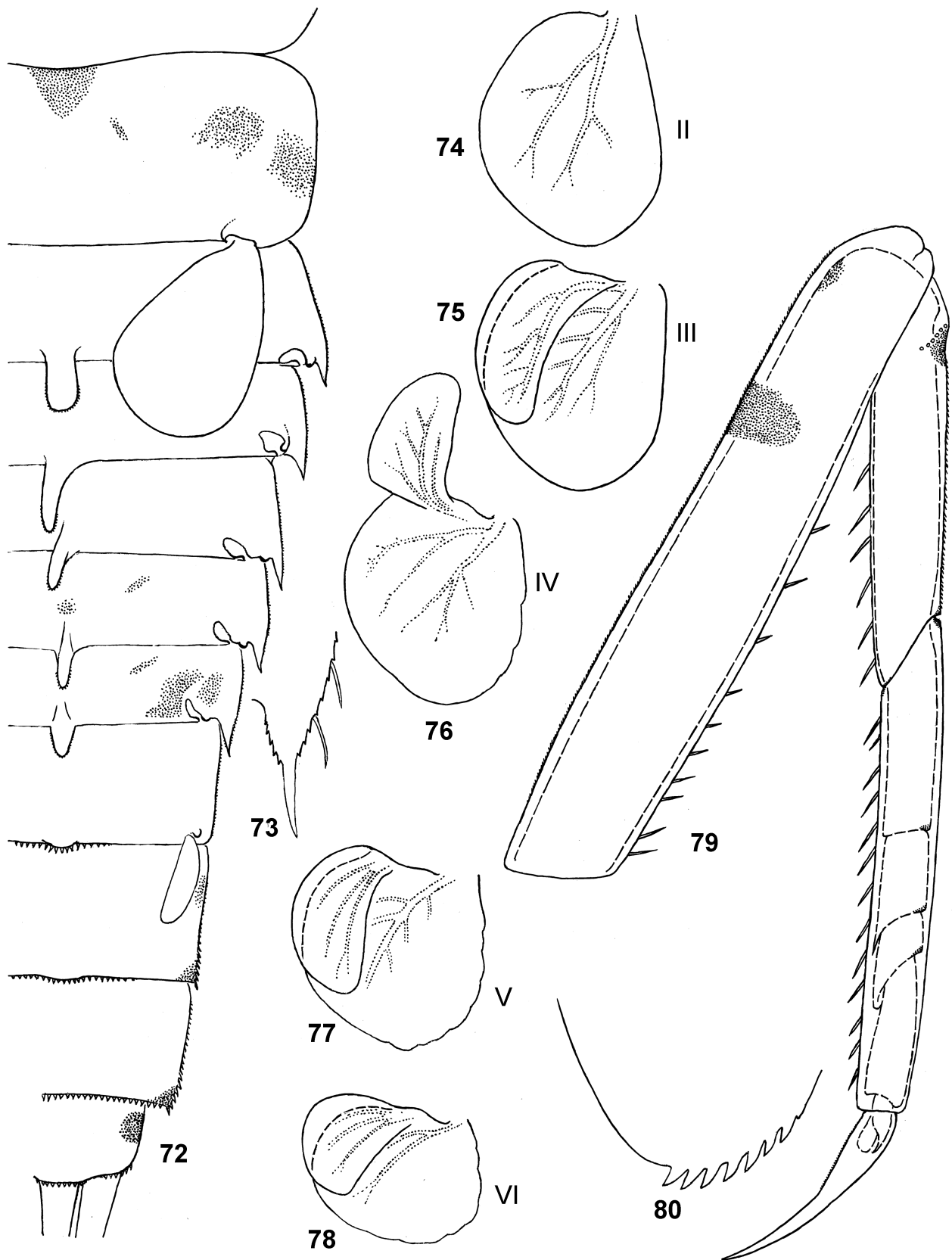
Distribution. Southern India.

Habitat. The single larva was collected close to the foot of the steep western slope of the Western Ghats, in the submountain river Seethanadhi, which at this place is rather wide and shallow, with moderate current. The larva was collected by net from bottom that consisted of sand and gravel, with sparse vegetation. Intensive attempts to collect more specimens at this place were not successful.

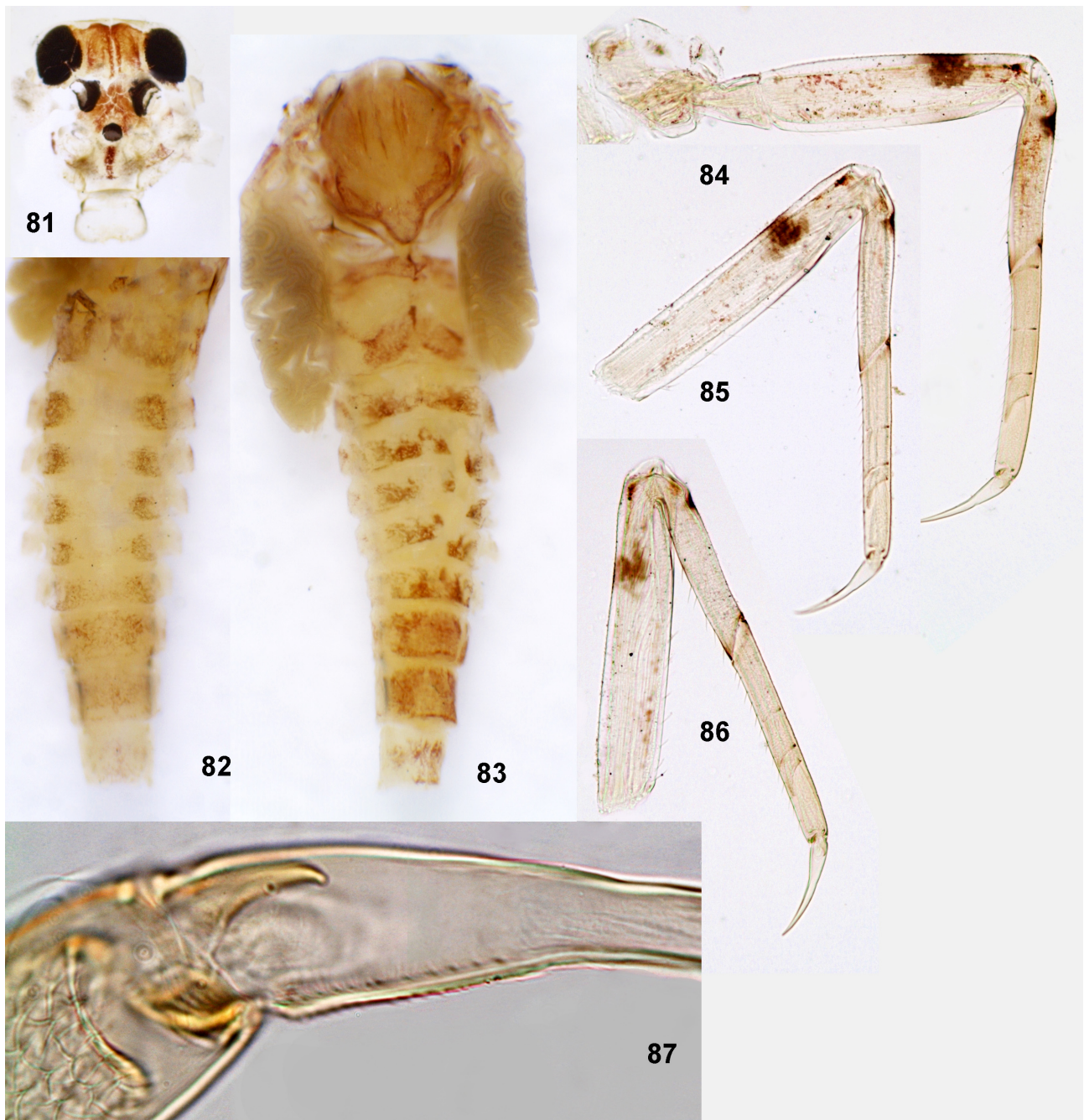
Comparison. The larva of *W. palifer* sp.n. differs from the two other known species by absence of patella-tibial suture on all legs (Fig. 79), by apically widened dorsal protrusion on abdominal tergum II (Figs 72, 88), by narrowly stretched postero-lateral angles of abdominal segments II–VI (Figs 73, 89) and by absence of dorsal lamella on tergalius II (Figs 74, 93). *W. palifer* sp.n. differs from *W. dentatogriphus* also by the absence of lateral expansions on abdominal segment VII (Fig. 72).



FIGURES 65–71. *Waynokiops palifer* sp. n., larva. 65–66, anterior margin of labrum, with focus on dorsal and ventral sides; 67, outline of labrum; 68, maxilla; 69, apex of left mandible; 70, glossae and paraglossae (at left dorsal view, at right ventral view); 71, 2nd and 3rd segments of labial palp.



FIGURES 72–80. *Waynokiops palifer* sp. n., larva. 72, abdomen without tergalii II–VI; 73, enlarged posterolateral spine of uromere VI; 74–78, tergalii II–VI; 79, hind leg with subimaginal leg inside; 80, paraproct.



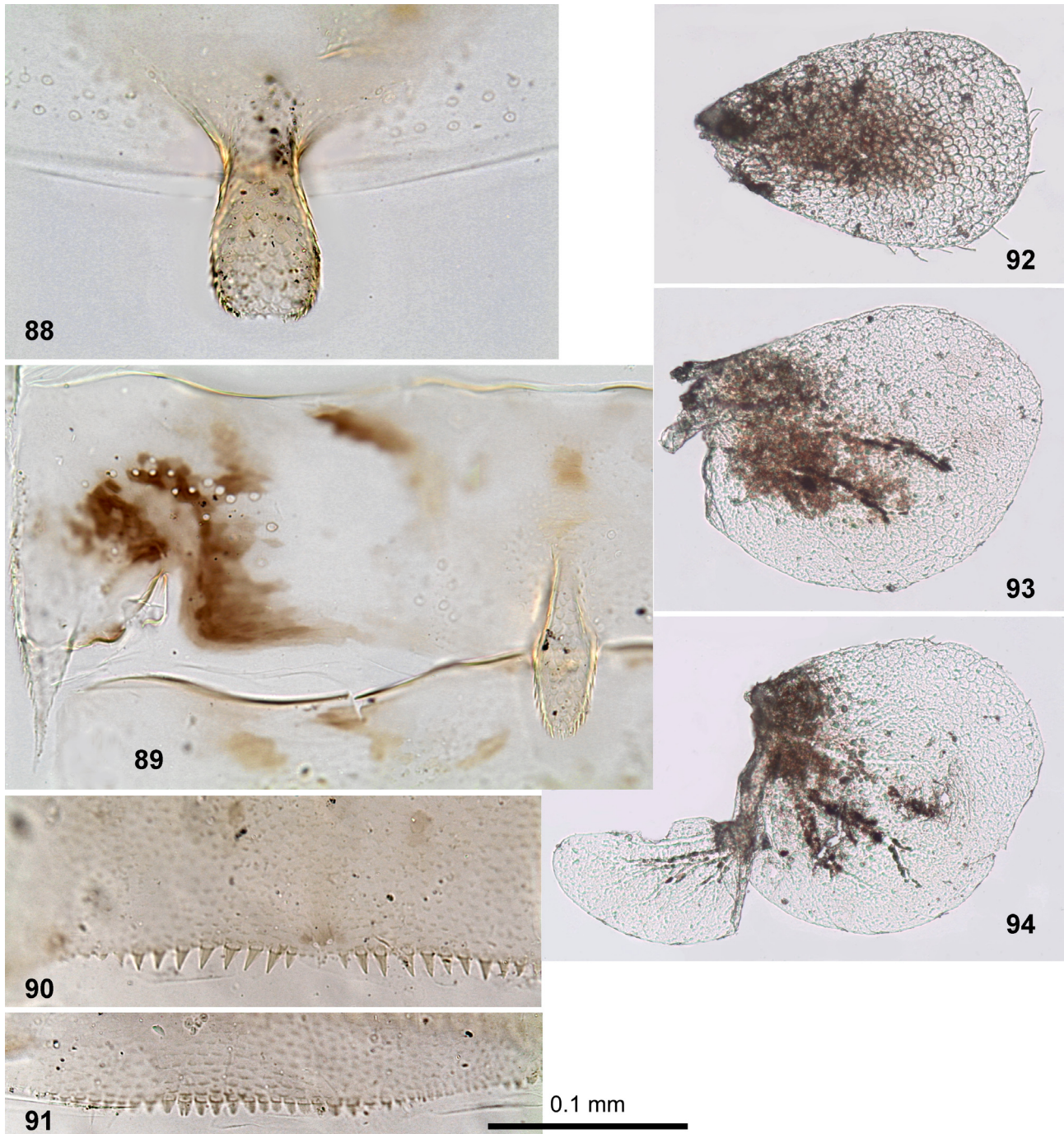
FIGURES 81–87. *Waynokiops palifer* sp. n. 81, head of female subimago in larval cuticle; 82–83, thorax and abdomen of female subimago extracted from larval cuticle, ventral and dorsal view; 84–86, larval fore, middle and hind legs with subimaginal legs inside; 87, proximal part of claw.

Discussion

Patella-tibial suture. *Waynokiops* has a complex of apomorphies testifying about its belonging to the taxon Cloeon/fg1, i.e. widened and truncate third segment of labial palp, lateral denticles on posterior abdominal segments of larva, additional dorsal lamella of tergalii, darkened and denticulate posterior margin of each fourth segment of larval caudalii, fused gonovectes of male imago and characteristic shape of gonostyli (characters 7, 14, 15, 17, 21 and 22 in the diagnosis given above) and a number of plesiomorphies in agreement with this (characters 4, 6, 11, 16, 19, 20 in the same diagnosis).

However, Cloeon/fg1 belongs to the taxon Anteropatellata Kluge 1997, which is characterized by restoring of

the patella-tibial suture on fore legs of larva and on fore legs of winged stages (subimago and imago) of female: in Anteropatellata the patella-tibial suture is present on all legs of larvae and females; only in male subimago and imago this suture is absent on fore legs and present on middle and hind legs (Kluge & Novikova 2011: 7, table 1). In its turn, Cloeon/fg1 is characterized by a peculiar form of larval patella-tibial suture, which is equal on all legs: on the anterior side of tibia, the proximal end of the patella-tibial suture is bent distally and connected under acute angle with the row of long thin hairs (Kluge & Novikova 1991: figs 1: 1–2; Kluge 2020a: figs 30–31).



FIGURES 88–94. *Waynokiops palifer* sp. n., larval exuviae. 88–90, fragments of abdominal terga II, VI and IX; 91, fragment of female sternum IX; 92–94, tergites I, II and IV.

These characters of Cloeon/fg1 and Anteropatellata are absent in *Waynokiops*. If larval patella-tibial suture is developed (in *W. dentatogriphus* and *W. pentacanthus* sp. n.), its proximal end is reduced, so that the bent in distal direction is absent; the row of setal sockets also is not bent distally (Figs 38–40; Hill *et al.* 2010: fig. 13); the patella-tibial suture is not equal on all larval leg pairs, but is better developed on middle and hind legs and less

developed on fore legs (Figs 39–40), so that demonstrates structure intermediate between typical Anteropatellata and Protopatellata. In *W. palifer* sp. n., the patella-tibial suture is lost on all larval legs (Fig. 79), so that its ancestral structure is unknown. Leg structure of winged stages is known for *W. pentacanthus* sp. n. only. In contrast to other Cloeon/fg1 and Anteropatellata in general, its fore legs of the female subimago and imago have no patella-tibial suture (Figs 41, 47–48), while this suture is well-developed on middle and hind legs (Figs 42, 49). Such a winged female can be taken as representative of Protopatellata, if the structure of its legs in the larval stage is unknown.

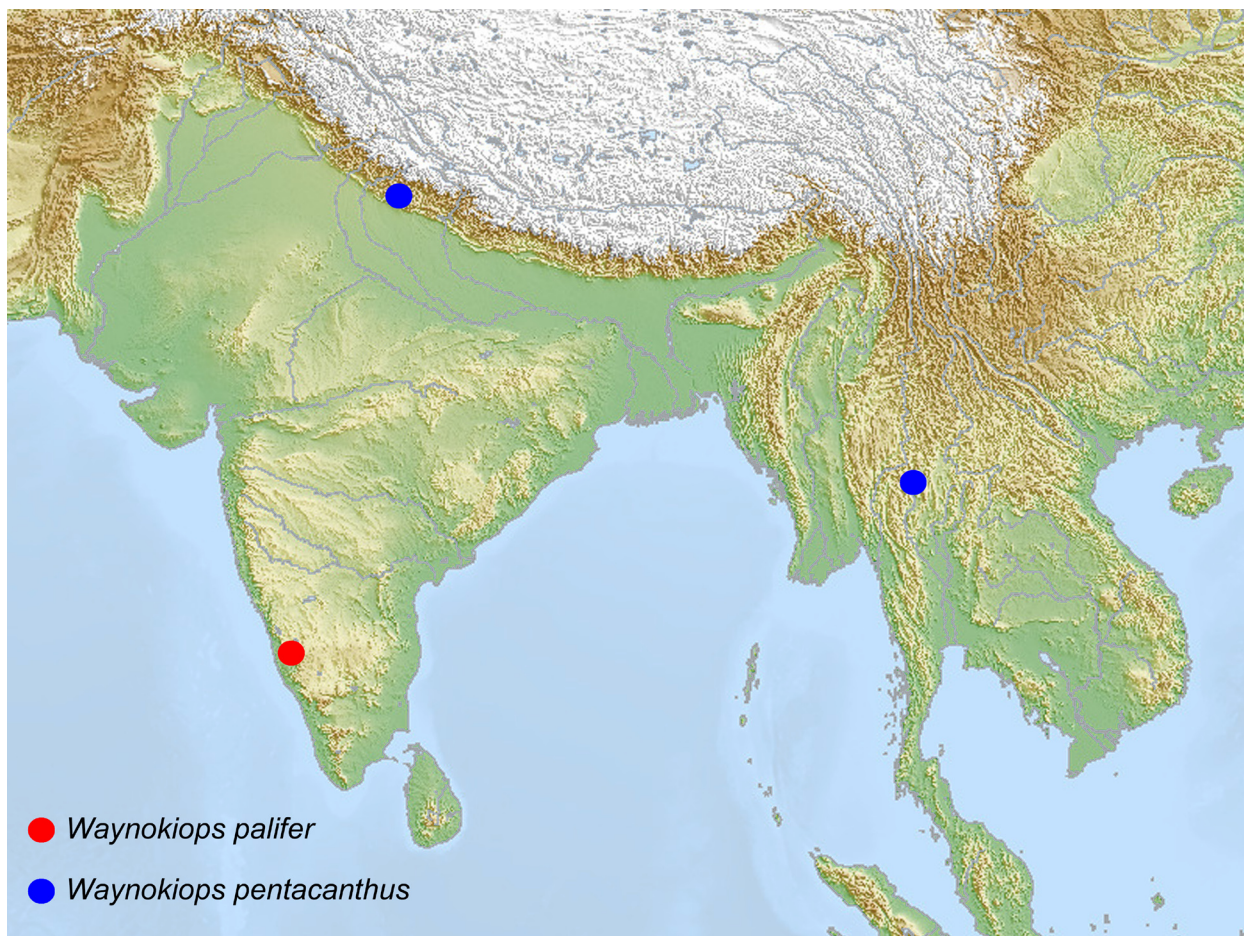


FIGURE 95. Known distribution of *Waynokiops* in Asia.

Distribution. The single formerly known species of *Waynokiops*, *W. dentatogriphus* has been reported as 14 larvae collected in 6 lakes located far apart, in 5 different states of the USA—Arkansas, Kentucky, Indiana, Ohio and Virginia. All these larvae were found in 2007, and never had been found before (Hill *et al.* 2010). Taking into account the facts that (1) the aquatic fauna of the USA has been intensively investigated for a long time, and (2) larvae of *Waynokiops* cannot be confused with any other mayflies, one is left to assume that this species was introduced to the American continent not long ago from some other part of the world. The recent discovery of representatives of *Waynokiops* in the Oriental Region suggests that natural area of *W. dentatogriphus* is also located somewhere in the Oriental Region, whose fauna is poorly investigated.

The two Oriental species described here are found at 3 very distant points (Fig. 95). All three points are located in mountain regions. Among them, two localities of *W. pentacanthus* sp. n. lie in an integral mountain system comprising the Himalayas and Shan highland of Indochina, while the single locality of *W. palifer* sp. n. lies in the well-separated mountains of the Western Ghats, which have an endemic mayfly fauna.

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References

- Bengtsson, S. (1915) Eine Namensänderung. *Entomologisk Tidskrift*, 36 (1), 34.
- Bogoescu, C. (1947) Un genre nouveau d'Ephéméroptère trouve en Roumanie. *Bulletin de la Section Scientifique de l'Académie Roumaine*, 29, 602–606.
- Eaton, A.E. (1869) On *Centroptilum*, a new genus of the Ephemeridae. *Entomologist's Monthly Magazine*, 6, 131–132.
- Hill, M.A., Pfeiffer, J. & Jacobus, L.M. (2010) A new genus and new species of Baetidae (Ephemeroptera) from lakes and reservoirs in eastern North America. *Zootaxa*, 2481 (1), 61–68.
<https://doi.org/10.11646/zootaxa.2481.1.4>
- Jacob, U. & Glazaczow, A. (1987) *Pseudocentroptiloides*, a new baetid genus of Palaearctic and Oriental distribution [sic] (Ephemeroptera). *Aquatic Insects*, 8 (4), 197–206.
<https://doi.org/10.1080/01650428609361254>
- Jacobus, L.M., McCafferty, W.P. & Gattolliat, J.-L. (2006) Taxonomy of Afrotropical *Securiops*, new genus, and *Cloeodes Traver* (Ephemeroptera: Baetidae). *African Entomology*, 14 (1), 129–140.
- Kluge, N.J. (1997) Classification and phylogeny of the Baetidae (Ephemeroptera) with description of the new species from the Upper Cretaceous resins of Taimyr. In: Landolt, P. & Sartori, M. (Eds.), *Ephemeroptera & Plecoptera. Biology-Ecology-Systematics*. Mauron+ Tinguely & Lacht SA, Fribourg, pp. 527–535.
- Kluge, N.J. (2004) *The phylogenetic system of Ephemeroptera*. Kluwer Academic Publishers, Dordrecht, 456 pp.
<https://doi.org/10.1007/978-94-007-0872-3>
- Kluge, N.J. (2005) Larval/pupal leg transformation and a new diagnosis for the taxon *Metabola Burmeister*, 1832 = *Oligoneoptera Martynov*, 1923. *Russian Entomological Journal*, 13 (4), 189–229. [2004]
- Kluge, N.J. (2012) Non-African representatives of the plesiomorphon *Protopatellata* (Ephemeroptera: Baetidae). *Russian Entomological Journal*, 20 (4), 361–376.
<https://doi.org/10.15298/rusentj.20.4.02>
- Kluge, N.J. (2016) A new subgenus *Oculogaster* subgen. n. for viviparous representatives of *Procloeon* s. l., with discussion about status of the generic name *Austrocloeon* Barnard 1932 and the species name *africanum* Esben-Petersen 1913 [*Cloeon*] (Ephemeroptera, Baetidae). *Zootaxa*, 4107 (4), 491–516.
<https://doi.org/10.11646/zootaxa.4107.4.2>
- Kluge, N.J. (2020a) New subgenus *Monilistylus* subgen. n. and a new species *Procloeon (Monilistylus) ornatipennis* sp. n. (Ephemeroptera: Baetidae: *Procloeon*). *Zootaxa*, 4742 (3), 573–587.
<https://doi.org/10.11646/zootaxa.4742.3.11>
- Kluge, N.J. (2020b) *Demoulinia* Gillies 1990 and two unnamed genera of the plesiomorphon *Protopatellata* (Ephemeroptera, Baetidae) from South Africa. *Zootaxa*, 4820 (3), 438–464.
<https://doi.org/10.11646/zootaxa.4820.3.2>
- Kluge, N.J. (2022) Taxonomic significance of microlepidides on subimaginal tarsi of Ephemeroptera. *Zootaxa*, 5159 (2), 151–186.
<https://doi.org/10.11646/zootaxa.5159.2.1>
- Kluge, N.J. & Novikova, E.A. (1992) [Revision of the Palaearctic genera and subgenera of mayflies of the subfamily Cloeoninae (Ephemeroptera, Baetidae) with description of new species from the USSR]. *Entomologicheskoe Obozrenie*, 71 (1), 60–83. [in Russian] *Entomological Review*, 71 (9), 29–54. [English translation]
- Kluge, N.J. & Novikova, E.A. (2011) Systematics of the mayfly taxon *Acentrella* (Ephemeroptera, Baetidae), with description of new Asian and African species. *Russian Entomological Journal*, 20 (1), 1–56.
<https://doi.org/10.15298/rusentj.20.1.01>
- Kluge, N.J. & Novikova, E.A. (2014) Systematics of *Indobaetis* Müller-Liebenau & Morihara 1982, and related implications for some other Baetidae genera (Ephemeroptera). *Zootaxa*, 3835 (2), 209–236.
<https://doi.org/10.11646/zootaxa.3835.2.3>
- Kluge, N.J. & Novikova, E.A. (2017) Occurrence of *Anafroptilum* Kluge 2012 (Ephemeroptera: Baetidae) in Oriental Region. *Zootaxa*, 4282 (3), 453–472.
<https://doi.org/10.11646/zootaxa.4282.3.2>
- Leach, W.E. (1815) Entomology. *Brewster's Edinburgh Encyclopedia*, 1st Edition, 9 (1), 57–172.
- Müller, O.F. (1776) *Ephemera*. In: *Zoologiae Danicae Prodrromus*. s.n., Havniae, pp. 142–143.
- Newman, E. (1853) Proposed division of Neuroptera into two classes. *Zoologist*, 11 (appendix), 181–204.