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Redescription of the subgenus *Rhithrogeniella* Ulmer 1939 (Ephemeroptera, Heptageniidae, genus *Ecdyonurus*) based on reared specimens from India and Thailand

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Abstract

Rhithrogeniella Ulmer 1939 is treated here as a subgenus of the genus *Ecdyonurus* Eaton 1868 (s. l.). The subgeneric name *Rhithrogeniella* is a senior synonym of *Afghanurus* Demoulin 1964 **syn. n.**, *Paracinygmula* Bajkova 1975 **syn. n.** and *Nixe* Flowers 1980 **syn. n**. Additional description of *Ecdyonurus* (*Rhithrogeniella*) *ornatus* (Ulmer 1939) is given based on imagines and subimagines of both sexes reared from larvae in India and Thailand; lectotype of this species name is designated. Synonymy of *E.* (*Rh.*) *ornatus* and *E.* (*Rh.*) *tonkinensis* Soldán & Braasch 1986 is established (**syn. n.**). Male and female imagines and subimagines of an unnamed species of *Rhithrogeniella* are reported from India.

Key words: mayflies, systematics, India, Thailand

Introduction

The genus *Rhithrogeniella* Ulmer 1939 was originally established for a single species *Rh. ornata* Ulmer 1939 described as male and female imagines and subimagines from Java and Sumatra. Ulmer (1939: 575–576) assumed relation of this genus with *Rhithrogena* Eaton 1881. Holotype of *Rh. ornata* had not been designated; two specimens, a male imago and a female imago were reported as «Typen» (Ulmer 1939: 578), both from Bogor (former Buitenzorg). Sartori (2014) erroneously interpreted these two type specimens as «One male holotype, one female allotype». Lectotype of this species is designated below.

Soldán & Braasch (1986) described a second species of *Rhithrogeniella*, *Rh. tonkinensis* Soldán & Braasch 1986 as male subimago, female imago and larva from Vietnam. The winged stages were not reared from the larvae, and the reason for their placing in one and the same genus and species was not explained. Based on examination of the larval structure, these authors revealed closer relationship of *Rhithrogeniella* with *Ecdyonurus* Eaton 1868 and related taxa, rather then with *Rhithrogena*. Examination of eggs allowed them to assume its relationship with *Nixe* Flowers 1980. Currently (Kluge 1997), *Nixe* is regarded to be a junior synonym of *Afghanurus* Demoulin 1964, which is accepted as a subgenus in the genus *Ecdyonurus* s. l.

Braasch (1990) described male imagines from Thailand ascribed to *Rh. tonkinensis* and placed *Rhithrogeniella* in the newly established tribe Ecdyonurini.

Since association of larvae and winged stages proposed by Soldán & Braasch (1986) was not proven by rearing, Kluge (2004) reported *Rhithrogeniella* among «Radulapalpata *incertae sedis*».

Wang & McCafferty (2004) synonymized *Rhithrogeniella* with *Rhithrogena* and argued this by the single

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sentence: «The type species of *Rhithrogeniella*, *R. ornata* Ulmer, possesses the essential characteristics associated with *Rhithrogena*». They did not report any concrete «essential characteristics» which allowed them to make this conclusion. With placing *Rh. ornata* in the genus *Rhithrogena*, they transferred *Rh. tonkinensis* to the genus *Ecdyonurus*, regarding these species to be non-related.

Sartori (2014) and Sartori *et al*. (2016) redescribed type specimens of *Rh. ornata* (male and female imagines and subimagines) and described larvae from Sumatra associated with this species with the help of the egg structure. They concluded that *Rh. ornata* and *Rh. tonkinensis* belong to one and the same genus *Rhithrogeniella* belonging to Ecdyonurinae (that is equal to Ecdyonurini *sensu* Braasch 1990 and Ecdyonurus/fg1 *sensu* Kluge 2004). They characterized *Rhithrogeniella* as having titillators in the subimaginal stage, but lacking them in imaginal stage. They concluded that the male imago from Thailand with well-developed titillators, identified by Braasch (1990) as *Rh. tonkinensis*, was misidentified. Three species known as larvae from Taiwan and originally described as *Nixe* (*Nixe*) *littorosus* Kang & Yang 1994, *N.* (*N.*) *mitificus* Kang & Yang 1994 and *N.* (*N.*) *obscurus* Kang & Yang 1994, were transferred by them to the genus *Rhithrogeniella*.

Principles of the rank-free hierarchical nomenclature based on the International Code of Zoological Nomenclature, were introduced by Kluge (2004). The taxon under rank-free hierarchical name Ecdyonurus/fg1 (first published by Kluge 2004) is accepted either as the genus *Ecdyonurus* with several subgenera (Kluge 1988, 1997, 2022), or as a taxon of higher rank (either tribe Ecdyonurini *sensu* Braasch 1990, or subfamily Ecdyonurinae *sensu* Wang & McCafferty 2004) with several genera. In application to the faunas of Europe or Afrotropical Region the second approach is rather convenient, because these faunas contain few well-distinguished taxa belonging to Ecdyonurus/fg1. In contrast, in application to the Oriental Region and the East Palearctic the second approach is hardly applicable, because their faunas of Ecdyonurus/fg1 are more diverse and contain various natural groups, some of which are poorly outlined. In this situation ascribing generic ranks to natural groups smaller than Ecdyonurus/fg1, causes instability of binominal species names.

One of the taxa subordinated to Ecdyonurus/fg1, is known as subgenus or genus under the names *Afghanurus* Demoulin 1964 (*sensu* Kluge 1997, 2022), *Paracinygmula* Bajkova 1975 (*sensu* Jacob *et al*. 1996) and *Nixe* Flowers 1980. Till now (Kluge 2022), the subgenus or genus *Rhithrogeniella* was regarded as distinct from the subgenus or genus *Afghanurus* = *Paracinygmula* = *Nixe*.

Our recent examination of reared specimens from India and Thailand proves that the stage association made by Soldán & Braasch (1986) is correct, reveals failure of the characters formerly regarded as species-specific differences between *E*. (*Rh*.) *ornatus* and *E*. (*Rh*.) *tonkinensis* and reveals failure of the characters separating *Rhithrogeniella* from *Afghanurus*, *Paracinygmula* and *Nixe*.

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. Material is preserved in ethanol. Slides are made in Canadian balsam.

Material reported in this paper, is deposited in the following institutions: (1) **ZIN**: 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; (2) **AMC**: American College (Department of Zoology), Madurai, India.

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**♀/**O**—female imago reared from larva, with larval and subimaginal exuviae and eggs; **L-S**♂—male subimago reared from larva, with larval exuviae; **L-S**♀/**O**—female subimago reared from larva, with larval exuviae and eggs; **L/S**♀/**O**—female subimago extracted from larva, with eggs.

The term «microlepides» is used according to Kluge (2022); the term «protopteron» according to Kluge (2005); other terms according to Kluge (2004). The noun «blank» is used to describe an unpigmented area of cuticle. The terms «chromozone» and «achromozone» are determined in application to Leptophlebiidae by Kluge (2020), in application to *Teloganodes* by Kluge (2023). Here the term «chromozone» as applied to peculiar areas on subimaginal

mesonotum of *Ecdyonurus*, which has **anterior chromozone**, paired **lateroparapsidal chromozone** and paired ovoid **parascutellar chromozone** (Fig. 66). These chromozones have constant outlines in all *Ecdyonurus* s. l. and are variously pigmented in different species or in different individuals (Figs 66–67); areas of subimaginal cuticle between chromozones are usually colorless.

Genus *Ecdyonurus* Eaton 1868 s. l., or Ecdyonurus/fg1

(Figs 1–116)

Type species: *Ephemera venosa* Fabricius 1775 (with neotype designated by ICZN 2015: Opinion 2356).

Diagnosis (according to Kluge 2004)

Metathoracic nerve ganglion greatly transferred anteriorly, nearer to mesothoracic ganglion, being connected with it by short unpaired connective; due to this, imaginal and subimaginal median impression of furcasternum parallel-sided or widened toward its anterior part (not narrowed in anterior part, in contrast to all other Heptageniidae) (Fig. 107).

Left and right mandibles have incisors dissimilar: incisor of left mandible (with mola projected distally) pointed, with a row of denticles on inner margin; incisor of right mandible (with mola projected proximally) with large denticle at some distance from apex and row of smaller denticles proximad of it; denticles on outer margins of both incisors at a distance from apex (Figs 29–30).

Superlinguae of peculiar shape uniform for all representatives, with rounded apico-lateral projection (Fig. 32).

On maxilla, ventral row of setae transformed to field of irregularly situated setae (unique apomorphy) (Figs 28, 33). Proximal dentiseta always bifurcate (Fig. 33).

Vestige of segment 3 of maxillary palp triangular, larger than in Heptagenia/f6=g5 (Fig. 28).

Glossae rhomboid, with inner margin convex (Fig. 31).

Tergalii are differentiated as following: tergalius I narrowed, with concave anal margin (i.e. more or less banana-like); tergalii II–VII widened, with anal margin most convex (i.e. more or less roundish-triangular). Unique apomorphy.

Outer (posterior) margin of larval femur with regular row of long stout setae situated less dorsally, than similar setae in Rhithrogena/fg1 and *Cinygma*. (Figs 34–35).

Composition. The genus *Ecdyonurus* s. l. is divided into several subordinated taxa which can be treated as subgenera (Kluge 2004), with the subgenus *Rhithrogeniella* among them.

Subgenus *Rhithrogeniella* Ulmer 1939

(Figs 1–116)

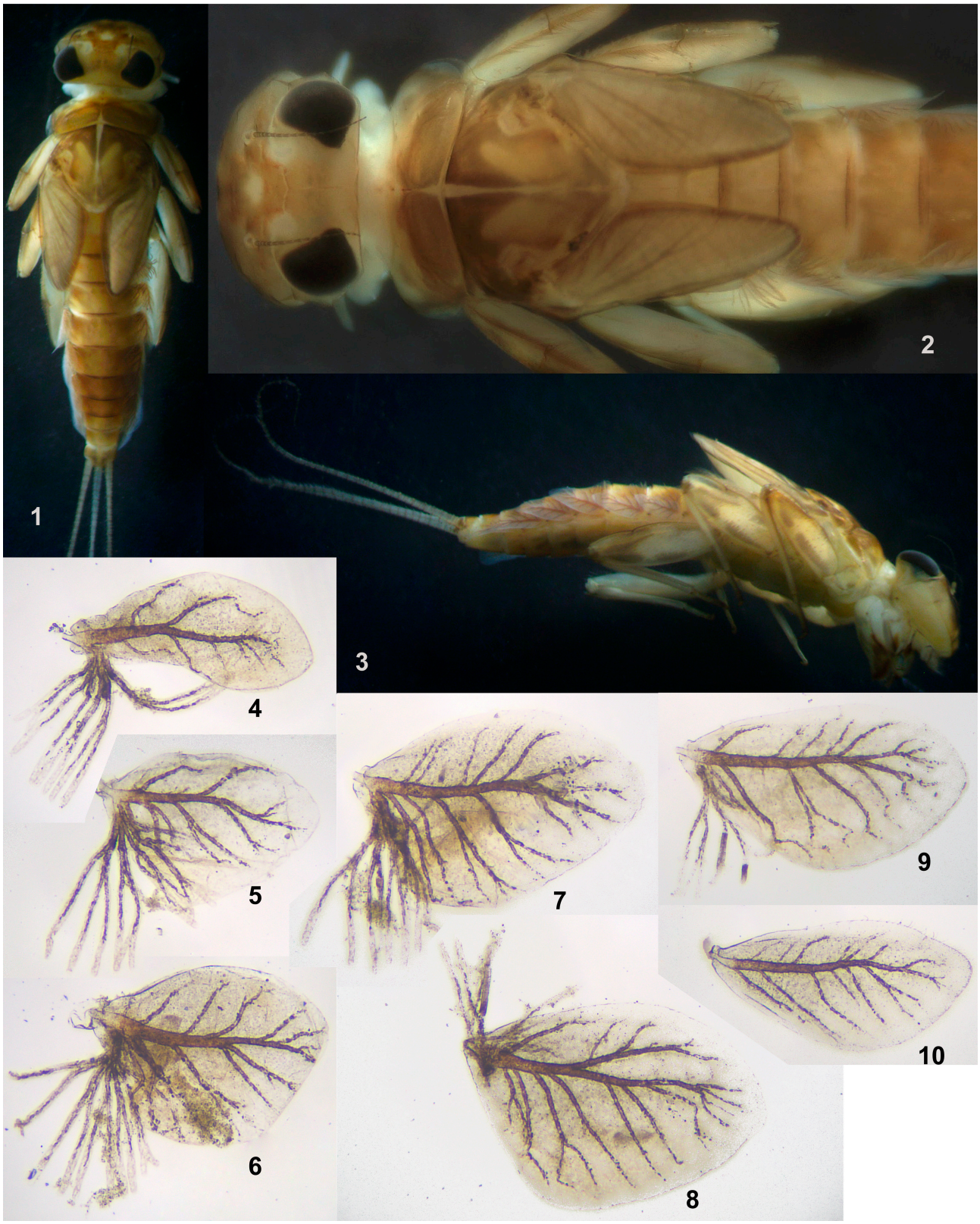
Rhithrogeniella Ulmer 1939 (type species: *Rh. ornata* Ulmer 1939);
= *Afghanurus* Demoulin 1964 (type species: *A. vicinus* Demoulin 1964) **syn. n.**;
= *Paracinygmula* Bajkova 1975 (type species: *P. zhiltzovae* Bajkova 1975) **syn. n.**;
= *Nixe* Flowers 1980 (type species: *Ecdyonurus lucidipennis* Clemens 1913) **syn. n.**
= *Akkarion* Flowers 1980 (type species: *Heptagenia simplicioides* McDunnough 1924) **syn. n.**

Diagnosis

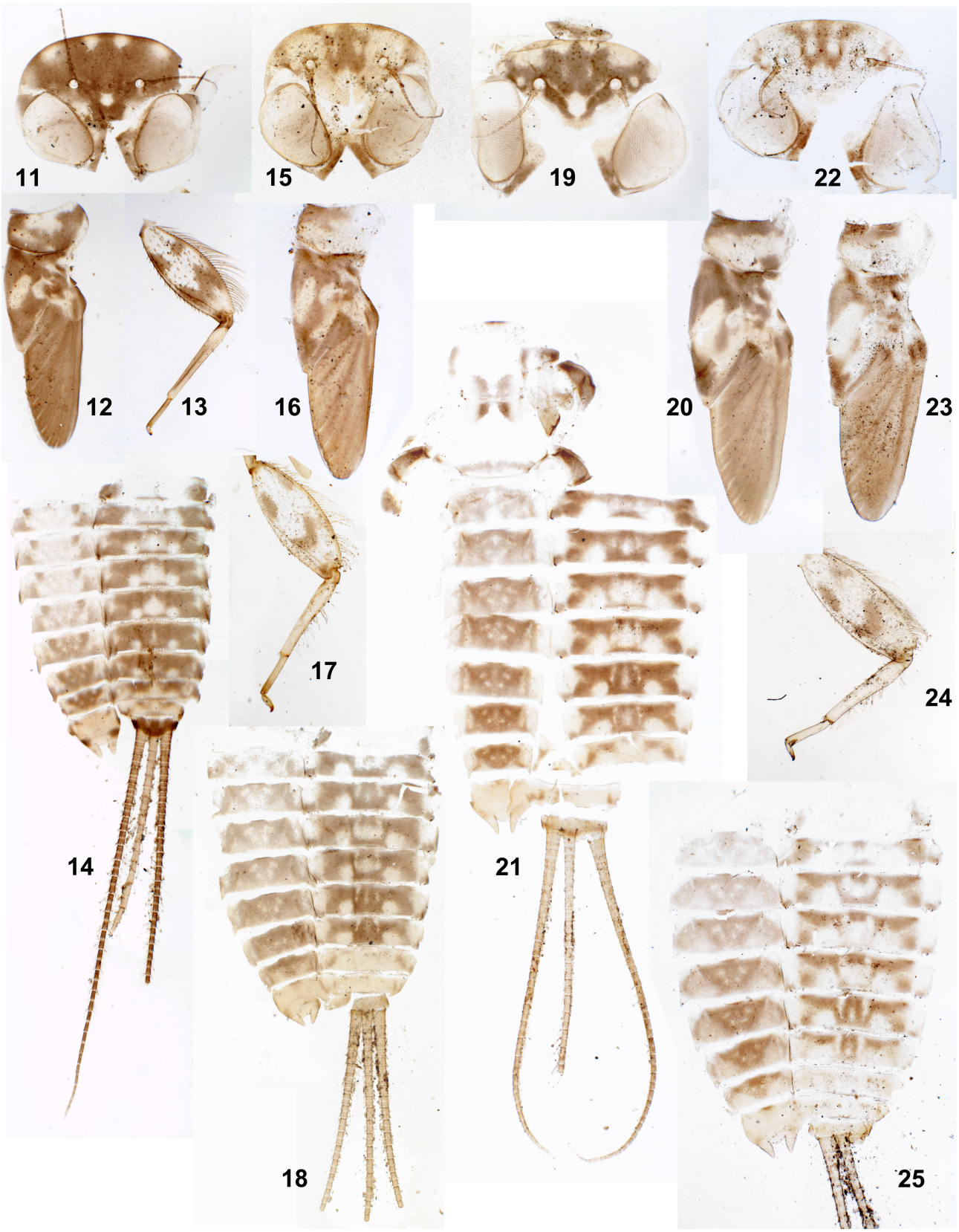
Maxilla with distal dentiseta simple, non-branched (Fig. 33) (the same in Ecdyonurus/fg2 *sensu* Kluge 2004, *Leucrocuta* Flowers 1980 and *Ecdyogymnurus* Kluge 2004; in contrast to Atopopus/fg1 *sensu* Kluge 2004).

Larval pronotum without lateral projections stretched laterad of mesonotum (Figs 1–3) (in contrast to Ecdyonurus/fg2).

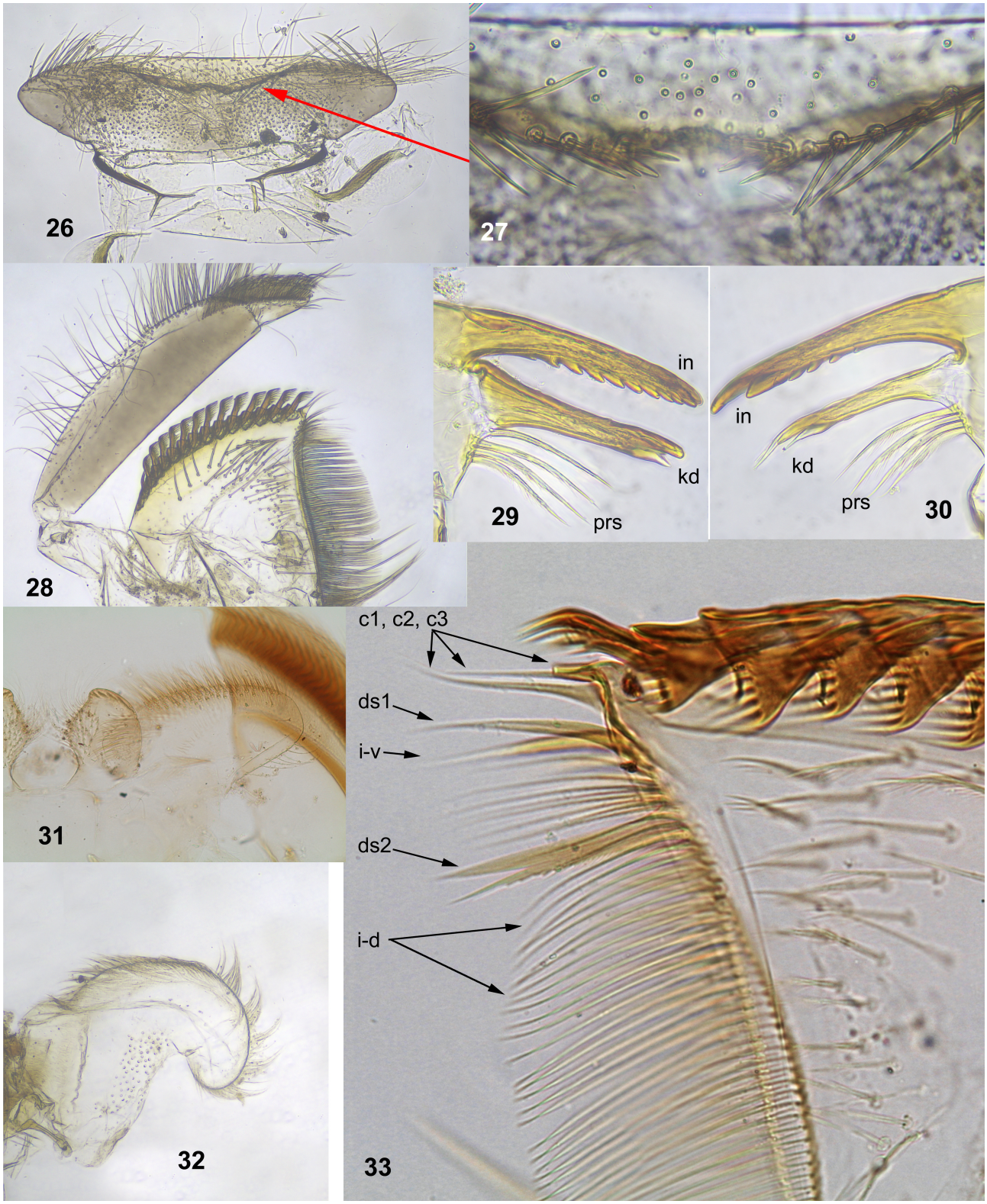
Larval caudalii with swimming setae: regular or irregular row of primary swimming setae is present at least on each lateral side of the paracercus and on median (i.e. inner) side of each cercus (Fig. 47) (the same in Ecdyonurus/fg2, in contrast to other taxa within Ecdyonurus/fg1). Similar secondary setae on lateral (i.e. outer) side of each cercus are either absent, or present: they are present in all individuals of *E.* (*Rh.*) *ornatus* (Figs 48–50) and in some individuals of *E.* (*Rh.*) *joernensis* Bengtsson 1909 (Fig. 52), but absent in other examined species.



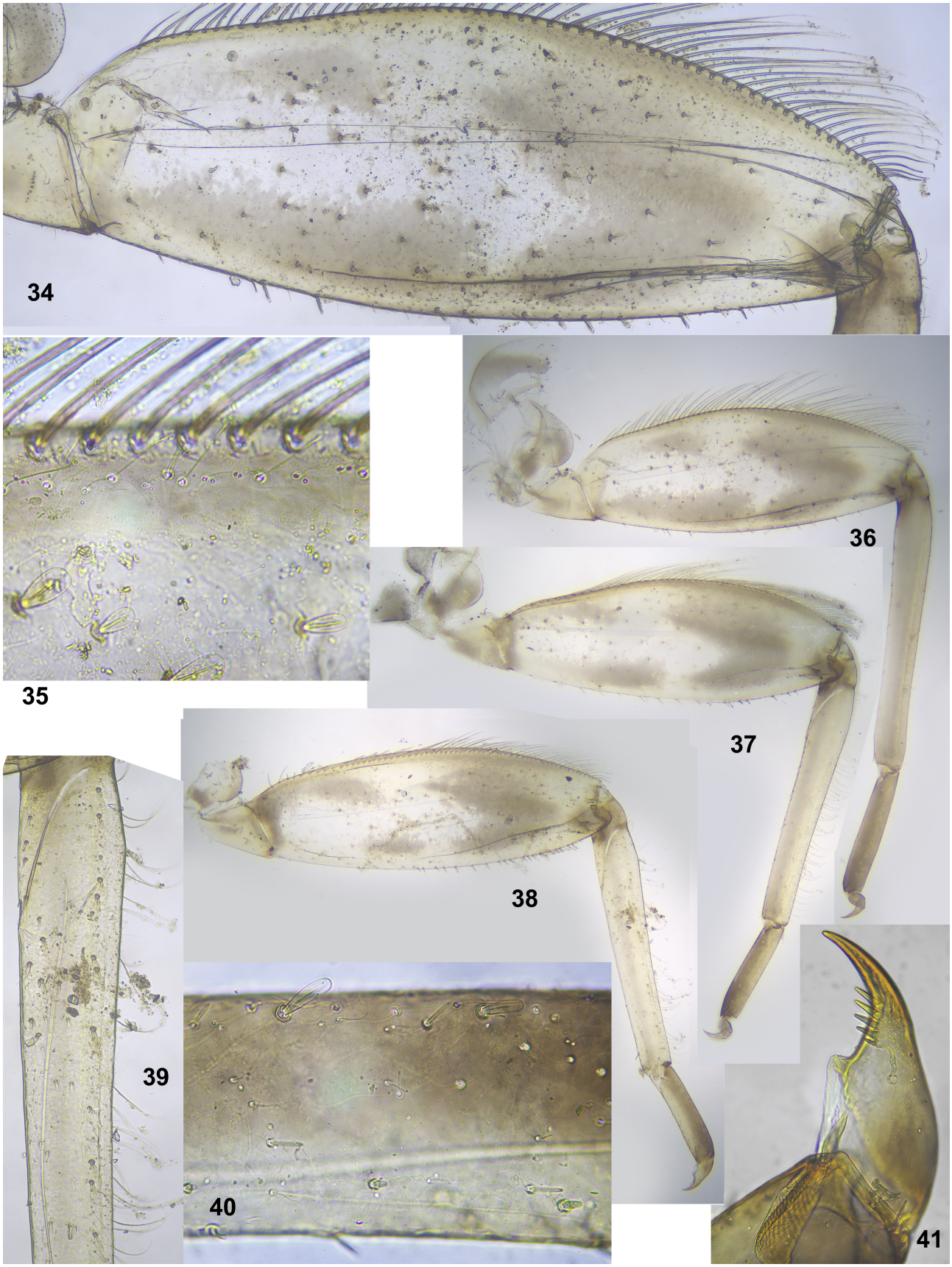
FIGURES 1–10. *Ecdyonurus* (*Rhithrogeniella*) *ornatus* from Kodaikanal (India). 1–3, larvae; 4–10, tergalii I–VII.



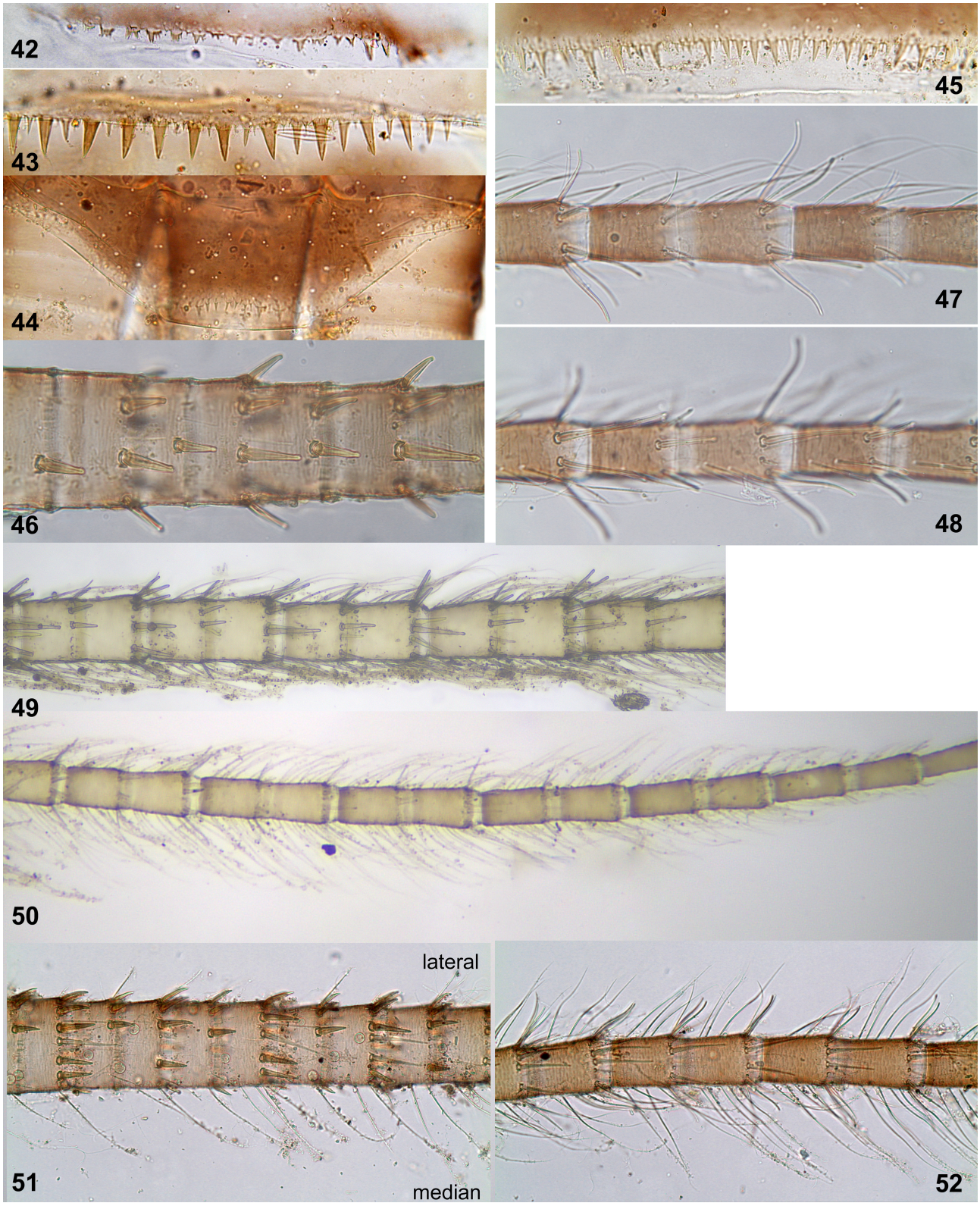
FIGURES 11–25. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, larval exuviae. 11–14, specimen from Agumbe (India); 15–18, 19–21 and 22–25, specimens from Pai (Thailand) (11, 15, 19, 22, head; 12, 16, 20, 23, half of pronotum and mesonotum; 13, 17, 24, hind leg; 14, 18, 21, 25, abdomen).



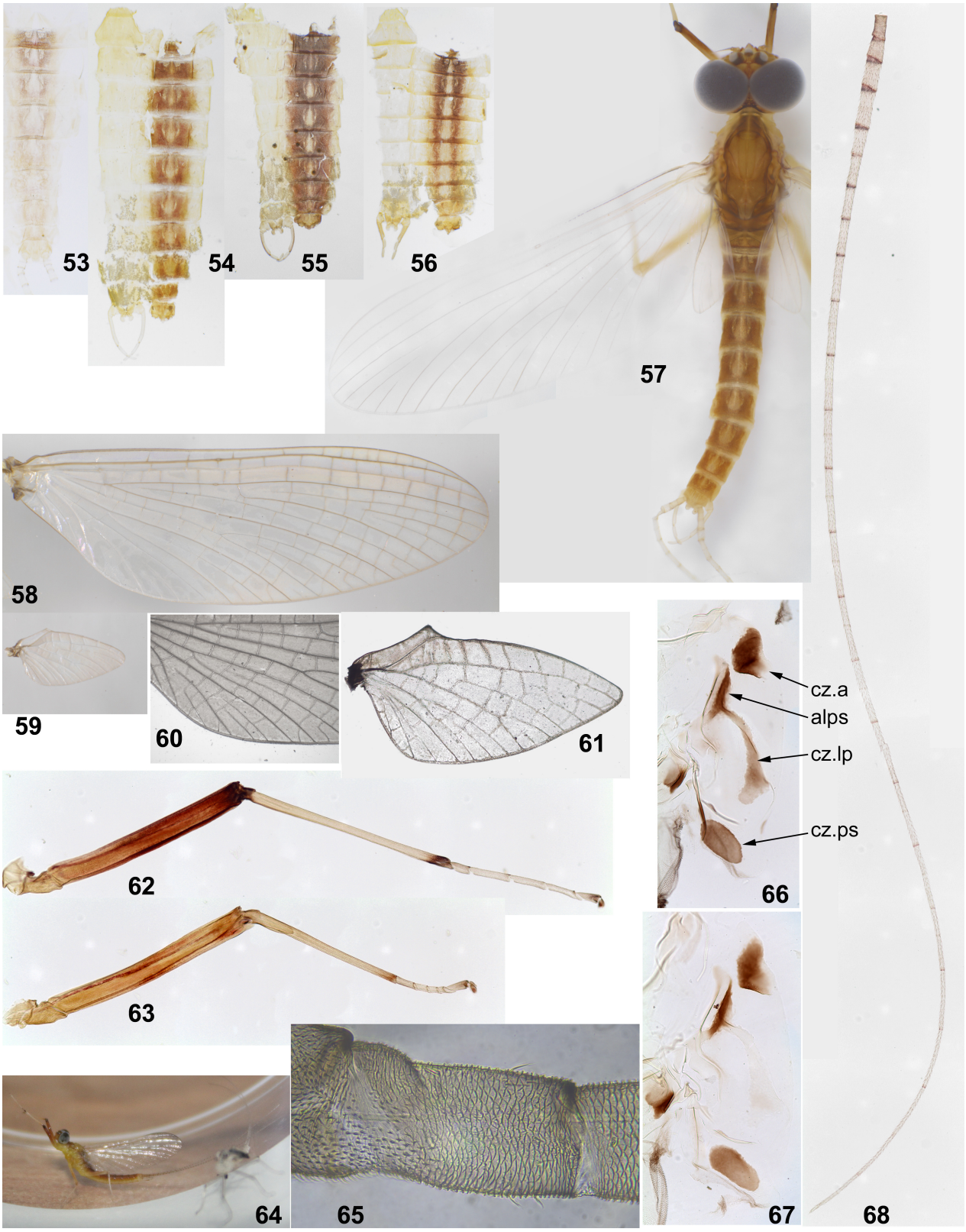
FIGURES 26–33. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, larval mouthparts. 26, labrum; 27, anterior margin of labrum bent ventrally; 28, maxilla; 29–30, apices of left and right mandibles; 31, glossa and paraglossa of labium; 32, hypopharynx and superlingua; 33, apex of maxilla, dorsal view. Abbreviations: c1, c2, c3, three maxillary canines; ds1, distal (first) dentiseta; ds2, proximal (second) dentiseta; i-d, inner-dorsal row of setae; i-v, first (largest) seta of inner-ventral setal row; in, incisor; kd, kinetodontium; prs, prostheca.



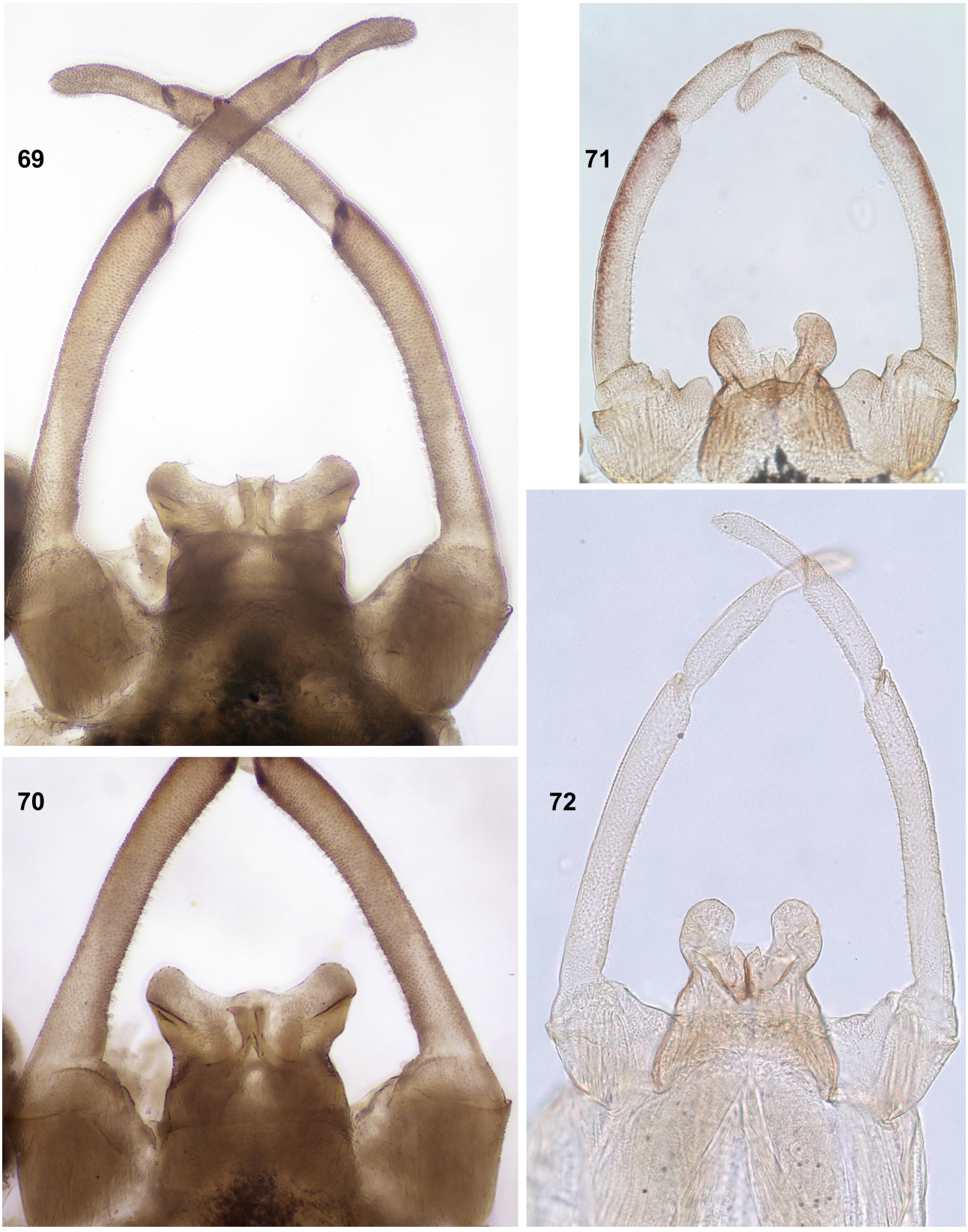
FIGURES 34–41. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, exuviae of larval legs (reared specimen from Kodaikanal). 34, fore femur; 35, outer margin of fore femur; 36–38, fore, middle and hind legs; 39, hind tibia; 40, hind tarsus; 41, claw.



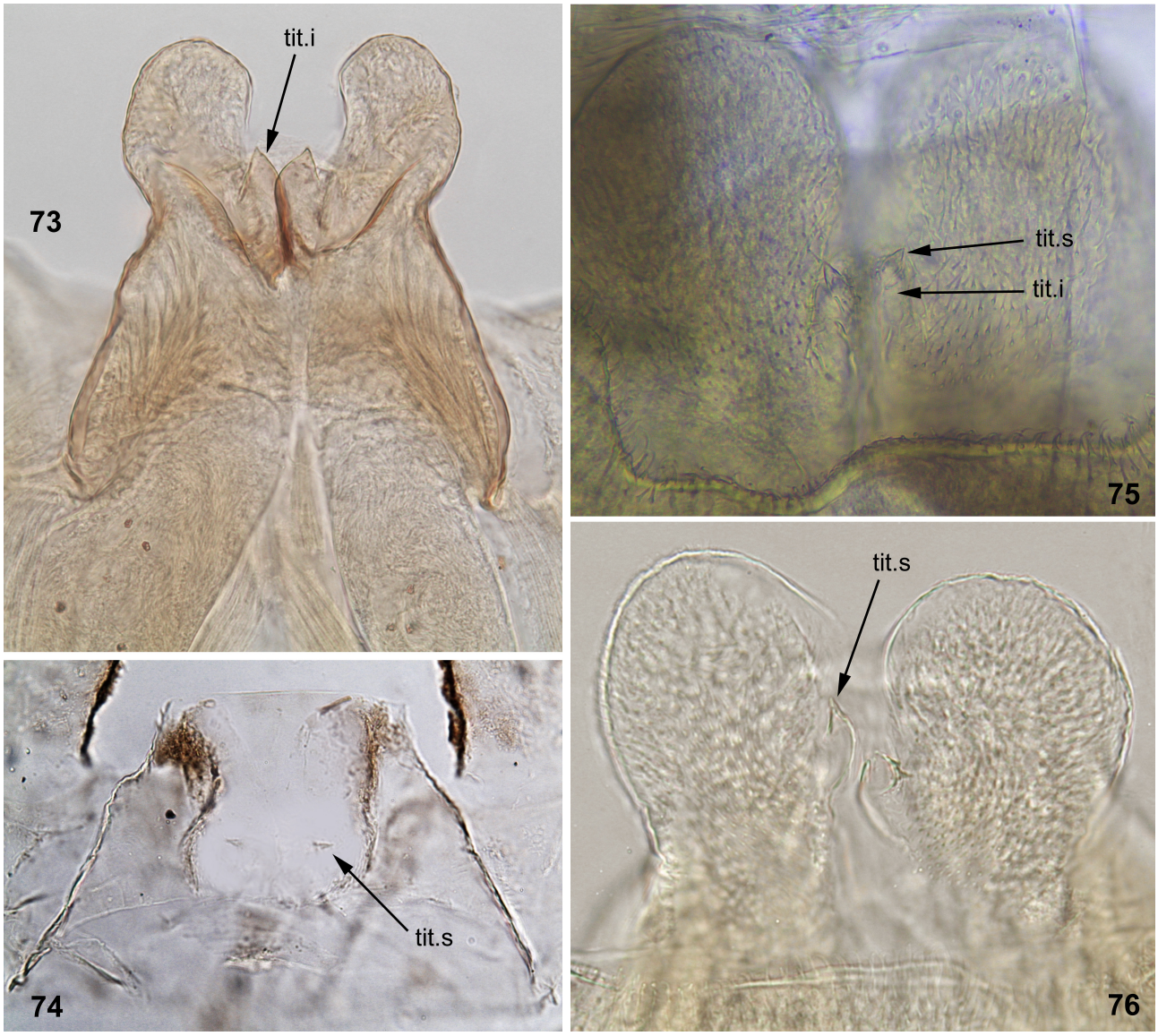
FIGURES 42–52. Larvae. 42–50, *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, larval exuviae: 42–44, specimen from Agumbe (India), posterior margins of abdominal terga I, VIII and X; 45, specimen from Pai (Thailand), posterior margins of abdominal tergum VI; 46–48, cercus of specimen from Agumbe: 46, proximal portion; 47, middle portion in median-ventral view, to show bases of primary swimming setae on inner (median) side; 48, the same portion with focus on lateral-dorsal side, to show bases of secondary swimming setae on outer (lateral) side; 49–50, cercus of specimen from Kodaikanal (India). 51–52, *Ecdyonurus* (*Rhithrogeniella*) *joernensis* (Russia, Orenburg province, Tashla, 16.VIII.1986, coll. N. Kluge): two portions of cercus, dorsal view.



FIGURES 53–68. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*. 53–56, male abdomina to show hypodermal coloration: 53, subimago extracted from mature larva; 54–55, imagines; 56, subimago; 57, male imago; 58–60, fore and hind wings; 61, hind wing; 62–63, fore and middle legs of male imago; 64, male imago with subimaginal exuviae; 65, 1st tarsal segment of male subimaginal exuviae; 66–67, exuviae of half of subimaginal mesonotum; 68, cercus of male imago (53, 54, 57–60, 66, from Pai; 56, 61, 67, from Kwai-Yai; 56, 61, 67, from Agumbe; 64–65, from Kodaikanal). Abbreviations: cz.a, anterior chromozone; cz.lp, lateroparapsidal chromozone; cz.ps, chromozone of parascutellum.



FIGURES 69–72. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, genitalia of male imagines, ventral view. 69–70, specimen from Kodaikanal (India) in tense condition; 71, specimen from Agumbe (India); 72, specimen from Pai (Thailand).



FIGURES 73–76. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, development of penis. 73–74, imaginal penis and its subimaginal exuviae with minute points of titillators; 75, subimaginal penis extracted from mature larva, with imaginal titillators developing under subimaginal cuticle; 76, subimaginal penis extracted from mature larva, without tissues under subimaginal titillators (73–74, 76, from Pai; 75, from Kodaikanal. Abbreviations: tit.i, imaginal titillator; tit.s, subimaginal titillator).

Species composition. Following species are placed in *Rhithrogeniella* (chronologically):

Ecdyonurus (*Rhithrogeniella*) *joernensis* Bengtsson 1909 (= *Ecdyonurus flavomaculatus* Aro 1928, = *Heptagenia mongolica* Bajkova & Varykhanova 1978, = *Heptagenia dentata* Braasch 1979, = *Ecdyonurus stubbei* Braasch 1979) (Eastern Palaearctic and north of Europe);

Ecdyonurus (*Rhithrogeniella*) *lucidipennis* Clemens 1913 (Nearctic);

Ecdyonurus (*Rhithrogeniella*) *simplicioides* (McDunnough 1924 [*Heptagenia*]) (= *Heptagenia rodocki* Traver 1935, = *Heptagenia werestschagini* Tshernova 1952, = *Rhithrogena imanica* Bajkova 1972) (Eastern Palaearctic and Nearctic);

Ecdyonurus (*Rhithrogeniella*) *inconspicuus* (McDunnough 1924 [*Heptagenia*]) (Nearctic);

Ecdyonurus (*Rhithrogeniella*) *perfida* (McDunnough 1926 [*Heptagenia*]) (Nearctic);

Ecdyonurus (*Rhithrogeniella*) *criddlei* (McDunnough 1927 [*Heptagenia*]) (= *Heptagenia otiosa* McDunnough) (Nearctic);

Ecdyonurus (*Rhithrogeniella*) *rubrofasciatus* Brodsky 1930 (= *Stenonema tianshanica* Kustareva 1984) (Central Asia);

Ecdyonurus (*Rhithrogeniella*) *rusticalis* (McDunnough 1931 [*Heptagenia*]) (Nearctic);

Ecdyonurus (*Rhithrogeniella*) *ornatus* (Ulmer 1939 [*Rhithrogeniella*]) (= *Rhithrogeniella tonkinensis* Soldán & Braasch 1986, **syn. n.**) (Oriental Region, see below);

Ecdyonurus (*Rhithrogeniella*) *vicinus* (Demoulin 1964 [*Afghanurus*]) (Central Asia and Siberia);

Ecdyonurus (*Rhithrogeniella*) *zhiltzovae* (Bajkova 1975 [*Paracinygmula*]) (= *Ecdyonurus bajkovae* Kluge (in Tshernova, Kluge, Sinitshenkova & Belov) 1986, = *Nixe subspinosa* Braasch & Soldán 1988) (Eastern Palaearctic);

Ecdyonurus (*Rhithrogeniella*) *littorosus* (Kang & Yang 1994 [*Nixe*]) (Taiwan) **comb. n.**;

Ecdyonurus (*Rhithrogeniella*) *mitificus* (Kang & Yang 1994 [*Nixe*]) (Taiwan) **comb. n.**;

Ecdyonurus (*Rhithrogeniella*) *obscurus* (Kang & Yang 1994 [*Nixe*]) (Taiwan) **comb. n.**.

Status of *Rhithrogeniella*

Sartori (2014) regarded *Rhithrogeniella* as a genus distinct from *Nixe* or *Paracinygmula* based on the fibrillose portion of tergalius VI, the setation of larval caudalii and the structure of imaginal penis structure. He stated that «nymphs of *Nixe*/*Paracinygmula* ... present gills with a weakly developed fibrillose part, either absent or reduced to a single filament in gill VI, which is not the case in *Rhithrogeniella* ...» (Sartori 2014: 58). However, some species placed in *Nixe* have well developed fibrillose portion on tergalii I–VI (Kluge 1980: figs 84, 95), and presence/absence of the fibrillose portion on tergalius VI was regarded as the subgeneric character separating the subgenera *Akkarion* and *Nixe* in the genus *Nixe* (Flowers 1980). Among examined individuals of *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, number of filaments or their branches on tergalii VI varies from 2 to 12.

Difference in caudalii setation was reported as: «The genus can be distinguished from all relatives by the peculiar structure of the cerci and terminal filament which possess a row of stout setae in the proximal part and bunches of long and thin setae in the medial and distal parts» (Sartori 2014: 48). However, caudalii of the Palaearctic species *E.* (*Rh.*) *joernensis* (placed by this author in *Nixe* or *Paracinygmula*) have the same structure (Figs 51–52).

Soldán and Braasch (1986) reported the following feature of the cerci as diagnostic for *Rhithrogeniella*: «segments with large blunt spines and bristles on anterior margin regularly alternate with those with very fine bristles and individual scales on posterior margin» and «(10) segments of cerci bearing stout spines regularly alternate with those without spines» (Soldán and Braasch 1986: 203–204, 205, figs 14, 15). Among specimens examined, this alternation is expressed in some individuals on some portions of cerci, but not expressed on others; sometimes such alternation is expressed on ventral side of the cercus segments (Fig. 47), but dorsal sides of these segments bear equally stout spine-like setae (Fig. 48).

Difference in penis structure was reported as following: «Contrary to *Nixe*/*Paracinygmula*, the male genitalia have a very different shape and lack well developed median titillators as well as basal sclerite spines» (Sartori 2014: 58). However, general shape of penis is quite different in the type species of *Nixe* (Burks 1953: fig. 372), the type species of *Paracinygmula* (Kluge 1983: fig. 2M) and other representatives of this taxon. As shown below, the median titillators are present in the type species of *Rhithrogeniella*. Thus, the single difference between the type species of *Rhithrogeniella* from one side, and the type species of *Afghanurus*, *Paracinygmula*, *Nixe* and *Akkarion* from other side, is the absence of the pair of spines on ventral side of the penis in the type species of *Rhithrogeniella*. Formerly (Kluge 2004) the presence of these spines was regarded to be a key autapomorphy of the taxon Afghanurus/g1 (incl. *Leucrocuta*). However, the same pair of spines occur in *Compsoneuriella* Ulmer 1939 which has the autapomorphy of the taxon Atopopus/g1 *sensu* Kluge 2004; this fact testifies that phylogenetic status of this character was wrongly estimated.

Ecdyonurus (*Rhithrogeniella*) *ornatus* (Ulmer 1939)

(Figs 1–102, 110)

Rhithrogeniella ornata Ulmer 1939: 576, figs 169–174 (♂ and ♀ imagines and subimagines); Sartori 2014: 49 (♂ and ♀ imagines and subimagines, eggs and larvae);

Rhithrogena ornata: Wang & McCafferty 2004: 21.

Rhithrogeniella tonkinensis Soldán & Braasch 1986: 206 (♀ imago, ♂ subimago, larva, egg) **syn. n.**; Boonsoong & Braasch 2013: 78 (larva, egg).

Ecdyonurus tonkinensis: Wang & McCafferty 2004: 21.
Ecdyonurus (*Rhithrogeniella*) *tonkinensis*: Kluge 2022: 168 (subimago).

Lectotype designation. Lectotype (designated here): male imago in alcohol, collected by Lieftinck in Buitenzorg (currently Bogor) in July 1932 and deposited in Zoologisches Museum und Biozentrum Grindel, Hamburg, Germany. This specimen is reported in literature as the following:

1) Ulmer 1939, p. 578: «1 ♂, 2 ♀. wohl frisch geschlüpft, in Spiritus, Buitenzorg, VII. 1932, Dr. LIEFTINCK leg. (1 ♂, 1 ♀ in meiner Sammlung, Typen)»;

2) Sartori 2014, p. 49: «One male holotype, one female allotype: Indonesia, Java, Buitenzorg, VII 1932, Dr. Lieftinck leg. [ZMH]»;

3) Sartori, Kubiak & Michalik 2016, p. 30: «The holotype of *Rh. ornata* is a specimen stored in ethanol and originating from Indonesia, Java, Buitenzorg, [Bogor], collected in July 1932 by Dr. Lieftinck».

Formerly (Sartori 2014, Sartori *et al*. 2016) this specimen was regarded to be the holotype. However Ulmer (1939) did not designate a single specimen as the holotype and did not distinguish two specimens (the male imago and the female imago) as holotype and allotype, but reported both them as types of equal status. According to Article 73 of the International Code of Zoological Nomenclature (4th edition), «73.1.1. If an author when establishing a new nominal species-group taxon states in the original publication that **one specimen, and only one**, is the holotype, or "the type", or uses some equivalent expression, that specimen is the holotype fixed by original designation» and «73.1.3. The holotype of a new nominal species-group taxon can only be fixed in the original publication and by the original author». Thus, according to the Article 73.2 of the Code, both specimens reported by Ulmer (1939) as «Typen» were syntypes, i.e. name-bearing types of equal status. Here one of them is designated as the lectotype.

Material examined. INDIA: state Karnataka, border of Shivamogga and Udupi districts, near Agumbe, rivers Modi-hole and Seethanadhi-hole, 11–31.I.2013, coll. N. Kluge & L. Sheyko: 1 L-S-I♂, 1 L-S♂, 1 S♂, 2 L-S-I♀, 1 S♀, 16 larvae (ZIN); state Tamil Nadu, Dindigul, Kodaikanal hills, Perumal malai stream, 28–30.XII.2022, coll. P. Srinivasan & R. Isack: 1 L-S-I♂, 2 L/S♂, 1 mature larva ♀, 5 larvae (AMC).

THAILAND: Kanchanaburi province, river Kwai-Yai (= Khwae Yai = Si Sawat) and river Taphoen, Lad-Ya (= Lat Ya), resort «Island Resort River Kwai», 29–30.I.2015, coll. N. Kluge & L. Sheyko: 1 L-S♂, 3 L-S-I♀, 3 larvae (ZIN); Mae-Hong-Son province, 90 km NW Chiang-Mai, river Pai upstream Pai, 5–14.II.2015, coll. N. Kluge & L. Sheyko: 2 L-S-I♂, 1 L-S/I♂, 1 S-I♂, 1 L/S♂, 2 L-S-I♀, 1 L-S♀ (ZIN).

Descriptions

***Larva*.** CUTICULAR COLORATION: Cuticle either pale ochre, or with more or less contrasting brown areas and ochre blanks (Figs 11–25). Head usually with pair of submedian blanks adjacent to anterior margin; often with more or less expressed pair of wider blanks laterad of them (Figs 11, 15, 19, 22; Soldán & Braasch 1986: fig. 16; Sartori 2014: fig. 6); rarely submedian blanks absent (Sartori 2014: fig. 7). Each femur mostly light, with 3 dark maculae originating from two initial transverse bands: initial proximal transverse band is separated into two longitudinal maculae; distal transverse band integral, either V-shaped (Fig. 17), or Z-shaped (Fig. 13). Tibia mostly light, with base darkened. Abdominal terga II–VII with following blanks: median blank and pair of submedian blanks (submedian sigilla) are either separated, or fused into integral median blank; pair of smaller or larger blanks are located laterad of it and adjacent to posterior margin; pair of smaller or larger lateral blanks are adjacent to anterior margin. Terga I and VIII–IX with more extensive blanks. Abdominal sterna with small blanks corresponding to sigilla.

HYPODERMAL COLORATION: Abdominal terga with or without reddish markings resembling that of winged stages (Figs 53).

SHAPE AND SETATION: Labrum moderately expanded laterally (Fig. 26); anterior portion sharply bent ventrally and invisible from above, with narrow median emargination; initial anterior margin (hidden on ventral side) with pair of regular setal rows separated by median emargination; setae of these rows stout, pointed, spine-like, inclined medially toward emargination (Fig. 27); dorsal surface of labrum with irregular, long, hair-like setae. Mandibles as described by Soldán & Braasch (1986: 208, figs 11–12) and Sartori (2014: 52); prostheca of left mandible consists of 3–4 setae, prostheca of right mandible consists of 2–4 setae (Figs 29–30). Maxilla with 10–15 comb-like setae, each with 4–11 denticles (Figs 28, 33). Distal dentiseta simple, proximal dentiseta bifurcate, with proximal branch pectinate (Fig. 33; Sartori 2014: fig. 12). Hypopharynx and superlinguae usual for *Ecdyonurus* s. l. (Fig. 32; Soldán & Braasch 1986: fig. 2; Sartori 2014: fig. 11). Labium with paraglossae sharply expanded; glossae with oblique ridges on apex (Fig. 31; Soldán & Braasch 1986: fig. 9; Sartori 2014: figs 9–10).

Spatulate setae on dorsal surface of each femur flat, colorless, with narrow base, divergent margins and rounded apex (Fig. 35). Tibia and tarsus of each leg with fewer similar setae (Fig. 40); middle and hind tibiae with sparse row of hair-like setae on outer margin (Fig. 39). Claw with rectangular projection at midlength and with one row of 3–6 denticles distad of it (Fig. 41; Soldán & Braasch 1986: fig. 13; Sartori 2014: fig. 18)

Denticles on posterior margins of abdominal terga irregular, either narrow and sharply pointed, or dentate; denticles on terga I and X very small (Figs 42, 44), denticles on terga II–IX larger (Figs 43, 45). Abdominal sterna without denticles. Tergalii increasing from II to V; tergalii I–VI with branched fibrillose portion, tergalii VII without fibrillose portion (Figs 4–10). Number of branches of fibrillose portion either subequal on all tergalii I–VI, or less on tergalius VI (Fig. 9); among individuals examined, number of branches on tergalius VI varying from 2 to 12.

***Subimago*.** CUTICULAR COLORATION: Head colorless, antennae light brown. Pronotum colorless. Mesonotum mostly colorless, with brown anterior chromozone (area anteriad of mesonotal suture), paired brown area including antelateroparapsidal suture and paired brown parascutellar chromozone (ovoid macula on parascutellum); paired lateroparapsidal chromozone (stretching along lateroparapsidal suture and widening posteriorly) either lighter brown (Fig. 66), or colorless (Fig. 67). Thoracic pleura and sterna colorless, with ventral ark of prealar bridge narrowly bordered with light brown (Fig. 110). Wing membrane colorless, microtrichia brown. Legs from light brown to nearly colorless; fore leg darker than middle and hind legs. Abdominal terga and sterna nearly colorless; gonostyli light brownish; cerci proximally colorless, distally light brownish.

HYPODERMAL COLORATION: As in imago.

TEXTURE: In both sexes, on all leg pairs, all tarsomeres covered with blunt microlepides; microtrichia occupy only ventral-proximal part of first tarsomere (Fig. 65) (Kluge 2022).

Imago, male (Figs 57, 64). Head ochre with brown. Eyes gray.

Pronotum ochre with brown macula medially (as in females — Figs 77–84). Mesonotum with ochre and light brown areas. Thoracic pleura and sterna light ochre (as in female — Fig. 77). Wing membrane colorless; veins mostly colorless, some longitudinal veins ochre or light brown (Figs 57, 64; as in Figs 58–61). Pterostigma with simple and complete crossveins perpendicular to Sc (Fig. 58). Hind wing narrowing toward apex, with small, pointed costal projection (Fig. 61). On fore leg, femur gradually changing color from light ochre base to dark reddish-brown apex, with reddish-brown darkening at midlength; tibia ochre with base and apex contrastingly dark brown; tarsus ochre with apex brown (Fig. 62). Middle and hind legs lighter (Fig. 63).

Abdomen mostly ochre, all terga I–X with reddish-brown paired submedian stripe and ochre submedian sigilla on its background (Figs 54–57). Penis with proximal ⅔ unpaired, distal ⅓ divided into pair of rounded lobes separated by wide space (Figs 69–73; Sartori *et al*. 2016: fig. 2); latero-dorsal and ventral (discal) spines absent. Pair of median titillators present or absent; if present, with single apical point (Fig. 73). Cerci ochre, in proximal part with brown articulations (Fig. 68).

Imago, female. Coloration similar to male (Figs 77–84).

***Egg*.** Chorion with net-like relief bearing knob-terminated coiled thread (KTC) in each cell. Among individual females, ridges forming cells vary from integral (Figs 85–92) to interrupted (Figs 96–97, 99–100) or irregular (Fig. 93, 95. 98); on eggs extracted from one female completely absent (Figs 101–102). Among individual females, KTC varying from small (Figs 85–87) to large (Fig. 91–94) or large on one pole and small on another pole (Figs 89–90). Micropyle varying from small (Figs 85–87) to large (Fig. 90).

Dimension. Fore wing length 5–6 mm (up to 7 mm according to Ulmer 1939).

Distribution. Oriental Region; known from Southern India, Indochina and Great Sunda Islands.

Confusion about labrum structure. Soldán and Braasch (1986) overlooked median emargination of labrum, and Sartori (2014) erroneously reported that labrum has «no anteromedian emargination ... ventral face with shorter and stout setae along the anterior margin». On the photo (Sartori 2014: fig. 8), focus is given on the dorsal side, but if enlarge the picture, it is possible to see the stout pointed setae bordering the initial anterior margin, which is bent ventrally; medially this paired setal row is interrupted by the median emargination of the initial anterior margin, but this emargination is invisible on the photo; shape of this labrum and its visible setal rows are exactly the same as in our specimens (Figs 26–27).

Disagreements about presence / absence of titillators. Originally, male imago of *Rhithrogeniella ornata* was described as lacking titillators (Ulmer 1939: 575, fig. 169); male subimagines of this species were reported, but their genital structure was not described (Ulmer 1939: 577).

Soldán and Braasch (1986) described subimagines placed by then in a new species of *Rhithrogeniella*, *Rh.*

tonkinensis, which have well developed medial titillators with sclerotized apices. In the same paper, they reported that «similar structures occur in subimagoes of *R. ornata* (material in the Zoological Museum, Hamburg)» and wrote: «Our opinion agrees with that of Jensen (pers. comm.) who supposes the existence of medial titillators as well».

FIGURES 77–84. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, female imagines. 77–78, specimen from Agumbe (India); 79–81, specimens from Kwai-Yai (Thailand); 82–84, specimens from Pai (Thailand).

Sartori (2014) and Sartori *et al*. (2016) reexamined the single male imago and the male subimagines which belong to the type series of *Rhithrogeniella ornata* and found out that the male imago has no titillators, and a male subimago has titillators which exist on subimaginal cuticle only, but are absent on imaginal penis developing under the subimaginal cuticle (Sartori 2014: fig. 4). Based on this fact, they concluded that *Rhithrogeniella* (both *Rh. ornata* and *Rh. tonkinensis*) have no titillators in imaginal stage, but have them in subimaginal stage only (Sartori 2014: 59).

Our recent examination of the specimens from India and Thailand reveals that presence/absence of titillators in imaginal stage varies individually (Table 1). All 6 examined males from India (two imagines, two subimagines and two larvae ready to molt to subimago) and one examined male subimago from Kwai-Yai in Thailand, have either imaginal titillators (Figs 69–71), or tissues of future imaginal titillators located under cuticle of subimaginal titillator (Fig. 75). Among specimens from Pai (Thailand), 4 reared male imagines also have imaginal titillators (Figs 72–73),

but one larva ready to moult to subimago, has only subimaginal cuticle of titillators, without tissues of imaginal titillators under it (Fig. 76).

TABLE 1. Presence/absence of imaginal titillators in the specimens examined

Locality	Collection number	Stage of development	Subimaginal titillators	Imaginal titillators	Fig.
India: Agumbe	[XII](1)2013	L-S♂	+	+	—
India: Agumbe	[XV](6)2013	L-S-I♂	+	+	71
India: Agumbe	slide 21.II.2023-1	S♂	+	+	—
India: Kodaikanal		L-S-I♂	+	+	69–70
India: Kodaikanal		L/S♂	+	+	75
India: Kodaikanal		L/S♂	+	+	—
Thailand: Pai	[XV](A)2025	S-I♂	+	+	—
Thailand: Pai	[XVI](1)A2015	L-S/I♂	+	+	—
Thailand: Pai	[XVI](2)A2015	L-S-I♂	+	+	—
Thailand: Pai	[XIX](1)	L-S-I♂	+	+	72–74
Thailand: Pai	slide 28.II.2023-1	L/S♂	+	–	76
Thailand: Kwai-Yai	[IV](2)B2015	L-S♂	+	+	—

Thus, in all cases subimaginal cuticle bears a pair of titillators in a form of very small, pointed denticles (Figs 74–76); tissues of imaginal penis developing under these pointed denticles, either have a pair of larger imaginal titillators (Fig. 75), or lack them (Fig. 76); in the last case imago will have no titillators.

Variability of egg structure. Presence of mesh-like reticulate ridges was reported as diagnostic character of the subgenus *Nixe* (Flowers 1980) and the genus *Rhithrogeniella* (Sartori 2014). Our recent examination of the specimens from India and Thailand reveals that presence/absence of this relief varies individually, at least among specimens from Thailand (Table 2).

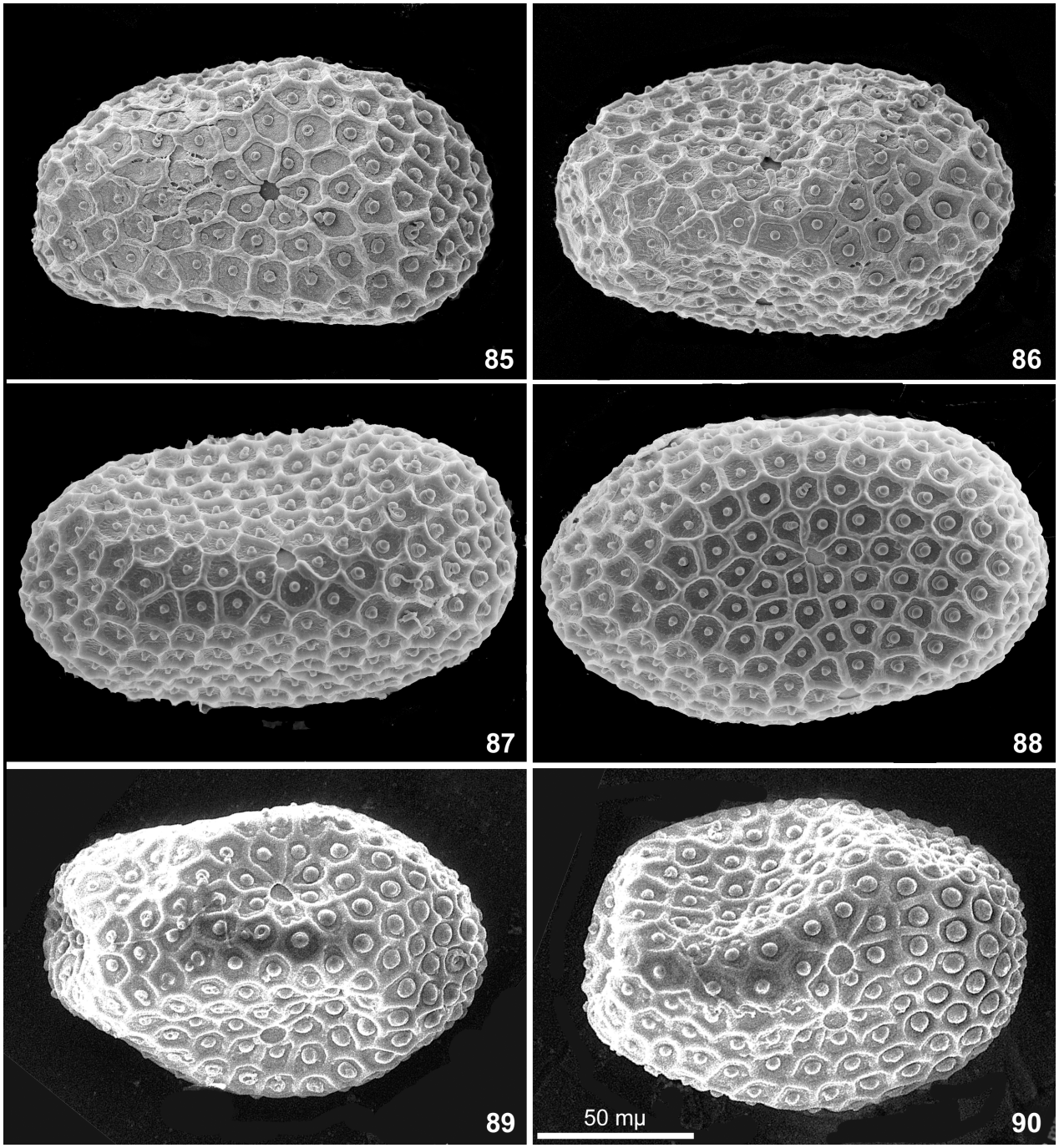
TABLE 2. Relief of egg chorion in the specimens examined

Locality	Collection number	Stage of development	Ridges forming net-like relief	Fig.
India: Agumbe	[XIII](2)2013	L-S-I♀	all regular	85–86
India: Agumbe	[IX](6)2013	L-S-I♀	all regular	87–88
India: Kodaikanal		L/S♀	all regular	89–90
Thailand: Pai	[XIII](4)2015	L-S-I♀	regular or broken	91–92
Thailand: Pai	[XIX](1)2015	L-S-I♀	regular or smoothed	93–94
Thailand: Pai	[XVIII](4)2015	L-S♀	broken or smoothed	95–96
Thailand: Kwai-Yai	[III](11)2015	L-S-I♀	broken or smoothed	97–98
Thailand: Kwai-Yai	[III](37)A2015	L-S-I♀	broken	99–100
Thailand: Kwai-Yai	[IV](2)B2015	L-S-I♀	completely absent	101–102

Geographical variability. Our small collection allows to make following assumptions about characters peculiar for certain geographical forms (Table 3).

TABLE 3. Larval cuticular coloration

Locality	Medio-posterior blanks on frontal shield	Anterior margin of pronotum
India (8 individuals)	absent	light
Thailand: Pai (7 individuals)	present	dark
Thailand: Kwai-Yai (7 individuals)	coloration not expressed	coloration not expressed
Vietnam (Soldán & Braasch 1986)	absent	dark
Sumatra (Sartori 2014)	absent	dark

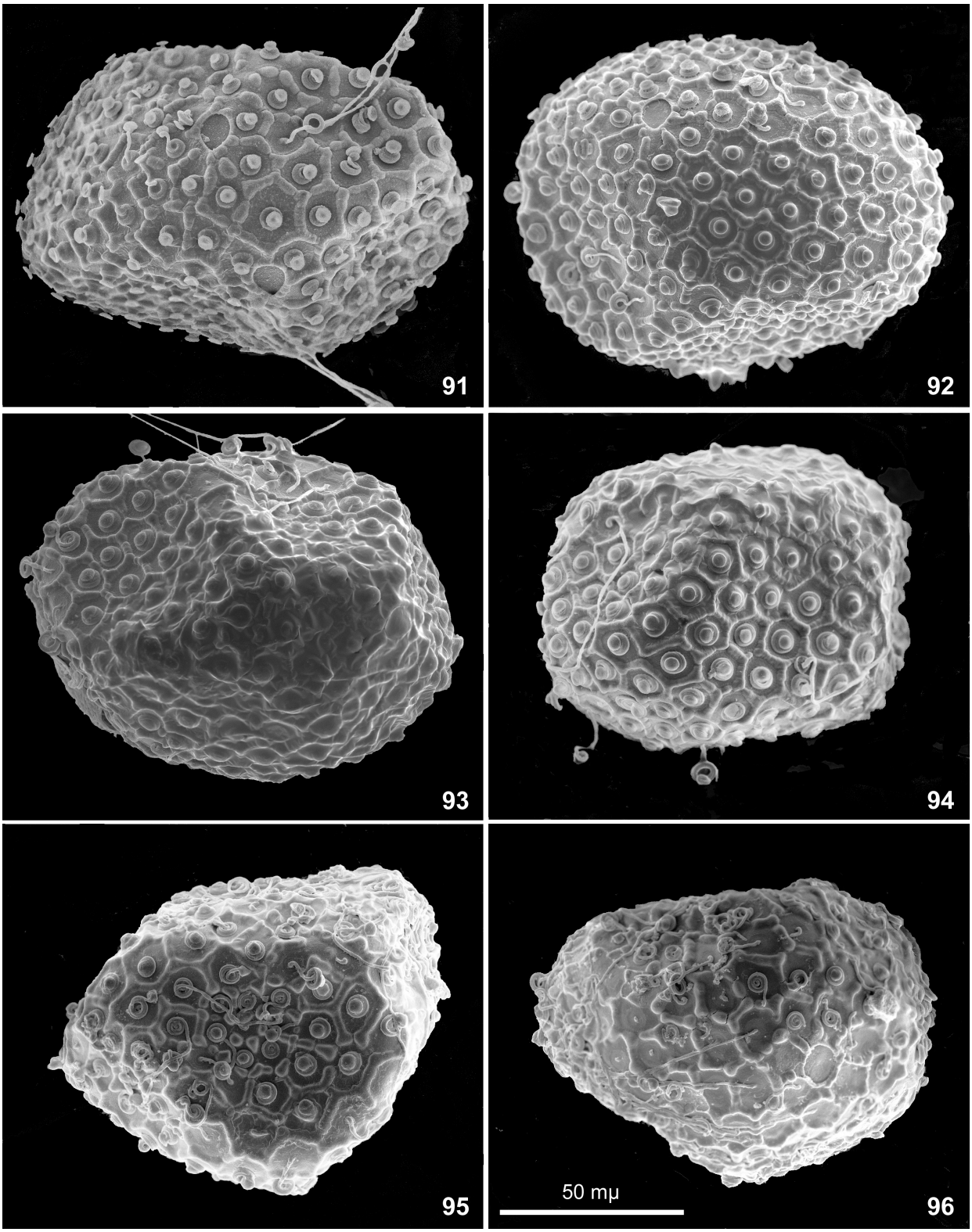


FIGURES 85–90. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, fully developed eggs from India. 85–86, reared imago from Agumbe, specimen [XIII](2)2013; 87–88, reared imago from Agumbe, specimen [IX](6)2013; 89–90, mature larva from Kodaikanal.

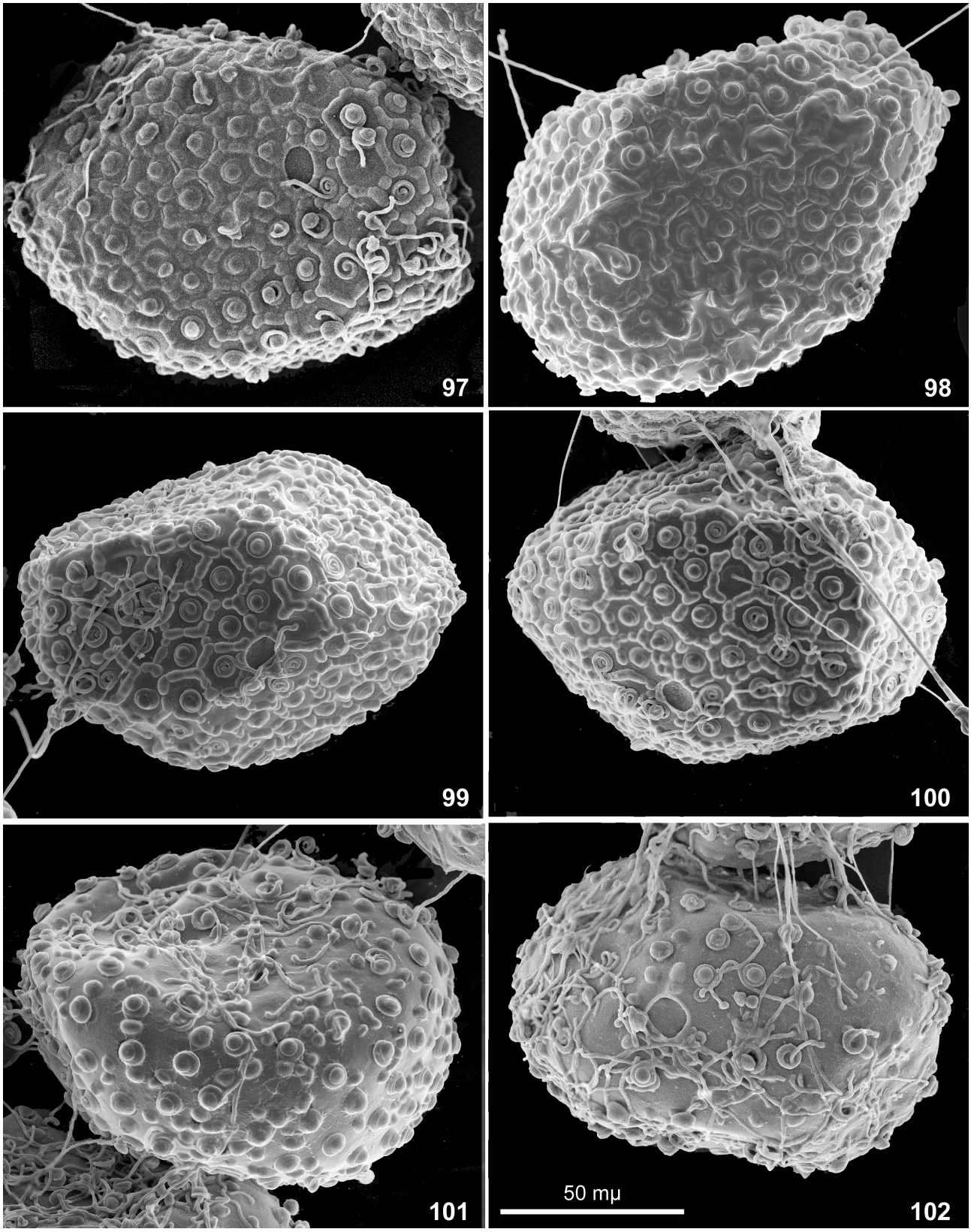
Thailand. Denticles on posterior margins of abdominal terga II–IX are irregular, small and thin (Fig. 45), on some of these terga can be as small as on terga I and X. In all specimens from Kwai-Yai, larval cuticle is very pale and nearly lacks pigmentation, so that the features of cuticular coloration characteristic for individuals from Pai and India, are not expressed. All examined mature larvae from Pai have well expressed cuticular coloration. Frontal shield has a pair of blanks behind the pair of submedian blanks adjacent to anterior margin (Figs 15, 19, 22), in contrast to the specimens from India (Fig. 11), Vietnam and Sumatra (Soldán & Braasch 1986: fig. 16; Sartori 2014: figs 6–7). Cuticle of larval pronotum has dark area of this or that shape adjacent to anterior margin (Figs 16, 20, 23); the same in larvae from Vietnam (Soldán & Braasch 1986: fig. 17) and Sumatra (Sartori 2014: figs 6–7).

India. Denticles on posterior margins of abdominal terga II–IX are regularly alternating as large and small (Fig 43), well different from small denticles on terga I and X (Figs 42 and 44). All examined mature larvae from both

localities in the states Karnataka and Tamil Nadu have well expressed cuticular pigmentation (in contrast to the specimens from Kway-Yai in Thailand). In contrast to the individuals from Pai in Thailand, frontal shield has no additional blanks behind the pair of submedian blanks adjacent to anterior margin (Fig. 11); the same is figured for the individuals from Vietnam (Soldán & Braasch 1986: fig. 16) and from Sumatra (Sartori 2014: figs 6–7). Cuticle of larval pronotum has paired light blank adjacent to anterior margin (Figs 2, 12); this differs from larvae from Pai in Thailand, Vietnam and Sumatra (see above).



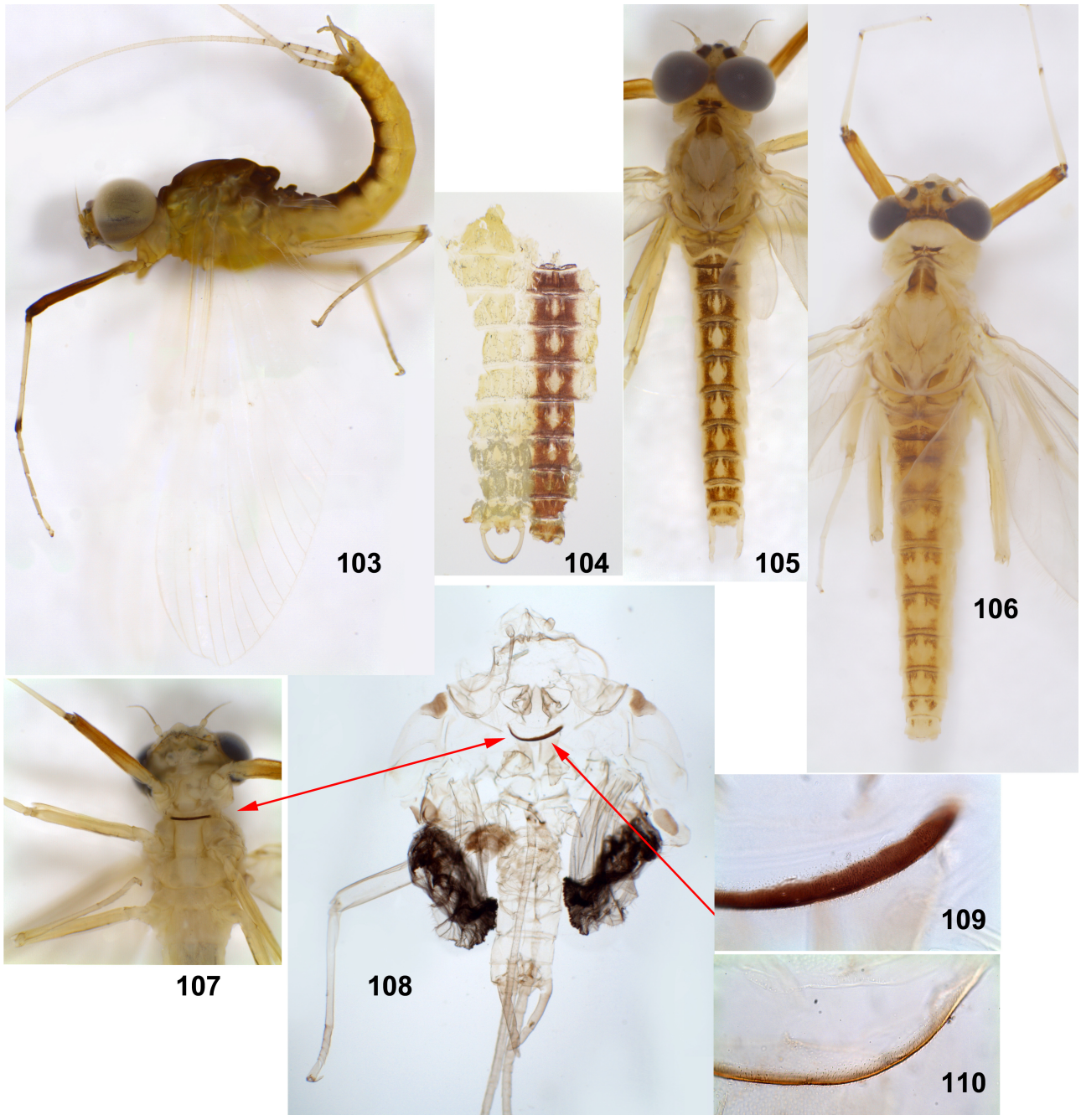
FIGURES 91–96. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, fully developed eggs from Pai (Thailand). 91–92, reared imago, specimen [XIII](4)2015; 93–94, reared imago, specimen [XIX](1)2015; 95–96, reared subimago, specimen [XVIII](4)2015.



FIGURES 97–102. *Ecdyonurus* (*Rhithrogeniella*) *ornatus*, fully developed eggs of reared imagines from Kwai-Yai (Thailand). 97–98, specimen [III](11)2015; 99–100, specimen [III](37)A2015; 101–102, specimen [IV](2)2015.

In all three examined females, all eggs have regular mesh-like relief consisting of non-interrupted ridges (Figs 85–90 and Table 2).

Synonymy of *E.* (*Rh.*) *ornatus* and *E.* (*Rh.*) *tonkinensis*. Originally *Rh. ornata* was described from Great Sunda Islands (Java and Sumatra), and *Rh. tonkinensis* was described from Indochinese Peninsula (Vietnam). The original differential diagnosis of *Rh. tonkinensis* contained the following statement: «Since the adult male of *Rhithrogeniella tonkinensis* sp. n. and nymphs of *R. ornata* Ulmer are unknown only subimagoes of these two species can be compared» (Soldán & Braasch 1986: 209).

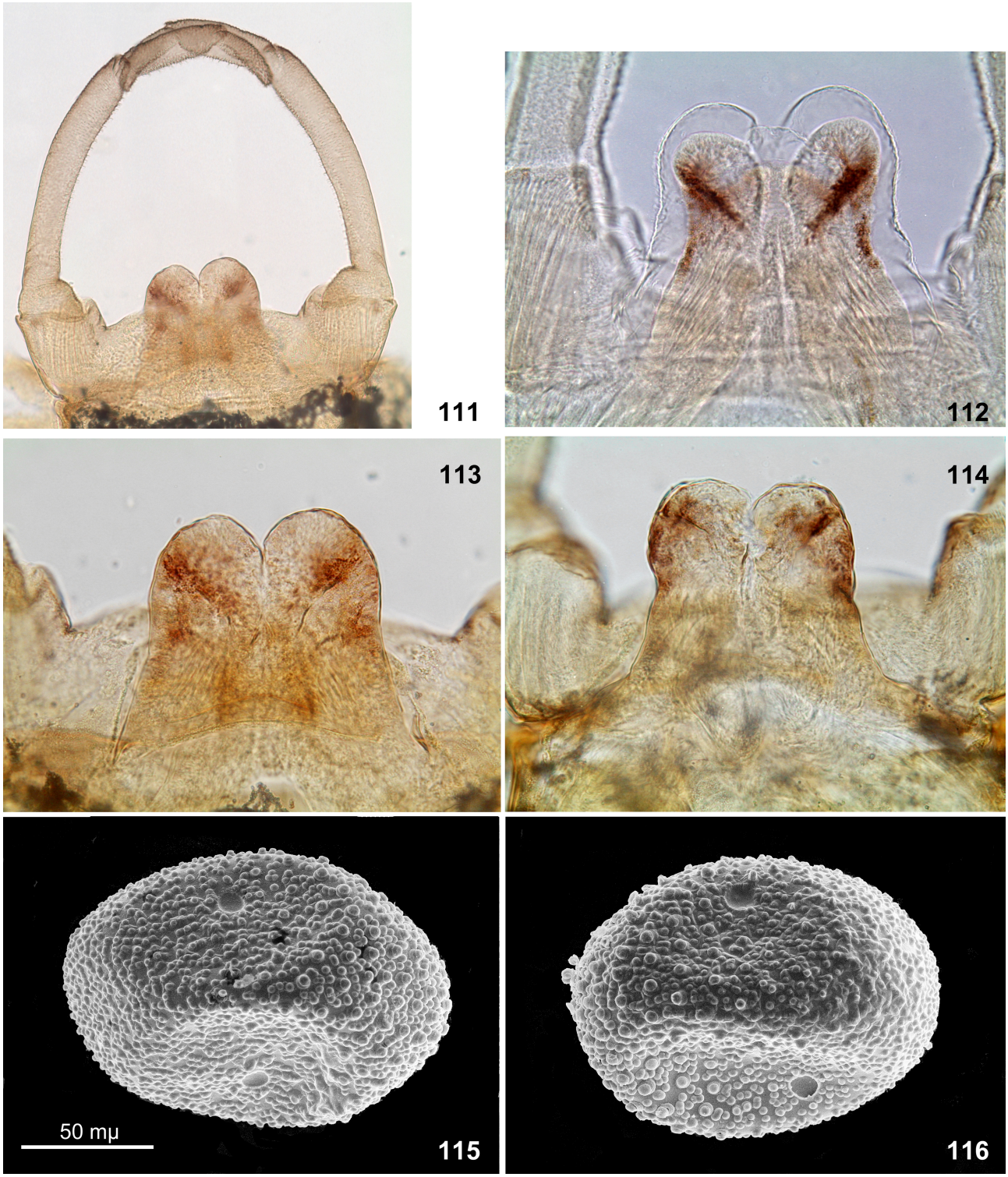


FIGURES 103–110. 103–109, *Ecdyonurus* (*Rhithrogeniella*) sp. 2: 103, male imago, 104, abdomen of male imago; 105, male subimago; 106, female subimago; 107, thorax of male subimago, ventral view; 108, male subimaginal exuviae; 109, enlarged part of its ventral arc of prealar bridge; 110, the same of *E.* (*Rh.*) *ornatus*.

Subimagines of these species were said to differ by abdominal coloration, leg proportions and shape of male genitalia.

The difference in abdominal coloration was caused by the fact that the Soldán's drawing of subimaginal abdomen (Soldán & Braasch 1986: fig. 19) was probably made from subimago just emerged and not fully colored; it resembles the subimaginal abdomen extracted from larva ready to molt (Fig. 53), while the Ulmer's drawing (Ulmer 1939: fig. 170) was probably made from an older subimago, whose coloration is approximated to the imaginal one

(Figs 54–57). Female abdomen of *Rh. tonkinensis* was said to be «without tergal markings», while abdomen of female *Rh. ornata* has tergal markings (Ulmer 1939: fig. 171). Actually abdominal markings of female are worse expressed than in male (Figs 78–84). Hypodermal coloration of male abdomen, female pronotum, mesonotum and abdomen of our specimens from India and Thailand are the same as in the paralectotypes of *E.* (*Rh.*) *ornatus* from Java and Sumatra (Ulmer 1939: figs 170–172).



FIGURES 111–116. *Ecdyonurus* (*Rhithrogeniella*) sp. 2: 111, genitalia of male imago; 112, penis of male subimago; 113–114, penes of male imagines; 115–116, eggs.

Comparison. Besides *E.* (*Rh.*) *ornatus*, three other Oriental species were described based on larvae and eggs from Taiwan, under the names *Nixe* (*Nixe*) *littorosus*, *Nixe* (*Nixe*) *mitificus* and *Nixe* (*Nixe*) *obscurus* (Kang &

Yang 1994). Originally, the subgenus *Nixe* was characterized by absence of fibrilliform portion on tergalius VI of larva and «mesh-like reticulate ridges» on egg (Flowers 1980). Kang & Yang (1994) reported only the «mesh-like reticular ridges» and ignored the structure of tergalii. It is unclear from the descriptions of these species, if they have the fibrilliform portion on tergalius VI or not. Characters reported as diagnostic for these species, vary individually in *E.* (*Rh.*) *ornatus*. Since imagines of these species are unknown, it is unclear if they really represent three different species distinct from *E.* (*Rh.*) *ornatus*, or not.

Among species examined, *E.* (*Rh.*) *joernensis* (widely distributed from Scandinavia and northern part of Russian Plain to Siberia, Kazakhstan, Mongolia and Russian Far East) is most closely related to *E.* (*Rh.*) *ornatus*. Eggs of *E.* (*Rh.*) *joernensis* have the same mesh-like ridges (Flowers 1986: fig. 3), larva has the same cuticular coloration and leg setation; in both species paraglossae are greatly projected laterally (Fig. 31; Kluge 1997: tab. 15: fig. 7). Both species have similar individual variability of subimaginal mesonotum (compare Figs 66–67 with Kluge 1980: figs 93–94). Imagines of these species have similar general appearance, including coloration of the body and legs, shape of hind wing, proportion of tarsal segments. Male imago of *E.* (*Rh.*) *ornatus* well differs from *E.* (*Rh.*) *joernensis* by more simple shape of penis and by absence of discal spines on ventral side. Larva of *E.* (*Rh.*) *ornatus* differs from *E.* (*Rh.*) *joernensis* by size of tergalii, which increase from tergalius II to tergalius V (Figs 4–10), while in *E.* (*Rh.*) *joernensis* (= *E. mongolicus*) they decrease from tergalius II to tergalius VII (Kluge 1980: fig. 84).

Ecdyonurus (*Rhithrogeniella*) sp. 2

(Figs 103–109, 111–116)

Material examined. INDIA, state Kerala, Erumeli, river Koratty, 20.I.2016, coll. N. Kluge & L. Sheyko: 4 S-I♂, 2 S♂, 1 S♀.

Characteristics

Larva. Unknown.

***Winged stages*.** Similar to *E.* (*Rh.*) *ornatus*. Male and female subimago differ from *E.* (*Rh.*) *ornatus* by contrasting dark brown ventral ark of prealar bridge (Figs 107–109) [in contrast to narrowly colored with lighter brown in *E.* (*Rh.*) *ornatus* — Fig. 110]. Male imago differs from *E.* (*Rh.*) *ornatus* and other species by penis lobes closely brought together (Figs 111, 113–114). Hypodermal coloration of abdominal terga of male and female imago and subimago is more composite than in *E.* (*Rh.*) *ornatus* (Figs 104–106).

***Egg*.** Chorion is densely and irregularly covered with roundish papilla and fewer knob-terminated coiled thread (KTC); micropiles wide and roundish (Figs 115–116). In contrast to *E.* (*Rh.*) *ornatus*, net-like relief or its traces are completely absent.

Dimension. Fore wing length 4–5 mm.

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