

Styloperlidae, stat. nov. and Microperlinae, subfam. nov. with a revised system of the family group Systellognatha

(Plecoptera)

By Shigekazu Uchida and Yu Isobe

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The subfamily Styloperlinae Illies is elevated to the rank of a family; the sister group is Peltoperlidae. A new subfamily of Peltoperlidae, Microperlinae, is established for *Microperla* Chu as the sister group of another subfamily, Peltoperlinae, which includes the other genera of the family. The superfamily Pteronarcyioidea is proposed for Pteronarcyidae, Styloperlidae and Peltoperlidae as the sister group of Perloidea. *Cerconychia flectospina* Wu and *Nogiperla obtusispina* Wu are transferred to *Styloperla* Wu. The egg, nymph and internal organs of *Cerconychia livida* Klapálek and the egg of *C. brunnea* Klapálek are described. The males and females of *Cerconychia livida* and *C. brunnea* and the males of *Styloperla inae* Chao and *S. wui* Chao are re-described. Some external and internal features of many stonefly families are described to support the new system.

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Introduction

The genera *Cerconychia* Klapálek, 1913, and *Styloperla* Wu, 1935, are known only from Taiwan and southern China and were originally placed in Perlidae s. l. But they have never been firmly placed in the system. Wu (1935) suggested the affinity of *Styloperla* with *Nogiperla* which was later assigned to Peltoperlidae. Kohno (1945) denied Wu's suggestion and assumed that *Cerconychia* and *Styloperla* could be assigned to Neoperlinae in Perlidae s. str., although she mentioned the analogy of the male cercus between proper Peltoperlidae and the two genera. Illies (1966) cited her paper (in Japanese) as if she had placed the two genera into Peltoperlidae. On the basis of this misunderstanding, he assigned *Cerconychia* and *Styloperla* to Peltoperlidae and presented no reason for it. He established, at that time, its second subfamily, Styloperlinae, for the two genera. Zwick (1973) followed Illies' system and proposed the shaft-like basal segments of the cercus as the second autapomorphy of Peltoperlidae (later deleted, Zwick 1980), in addition to another autapomorphy: cockroach-like nymph.

The difficulty of the placement simply arises from the lack of knowledge of *Cerconychia* and *Styloperla*: the nymphs have been unknown and descriptions of the adults are not detailed.

The senior author collected nymphs of *Cerconychia livida* from Taiwan, which were associated with the adults by rearing. The nymphs are not at all cockroach-like but long and slender (Fig. 1). It

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shows clearly that *Cerconychia* does not belong to Peltoperlidae. Further study of specimens in European museums and institutes and our collections leads to the elevation of Styloperlinae to the rank of a family. The family Styloperlidae with *Cerconychia* and *Styloperla* is the 16th of the order Plecoptera and is placed in Systellognatha.

On the other hand, the current phylogenetic system of Systellognatha by Zwick (1973, 1980) is, though well accepted, not yet doubtless. He could not examine enough material to establish a reliable system. Our examination of extended material, especially from East Asia, suggested that the current system necessitates some improbable reversals for the argumentation. Accordingly, we reexamined all the characters that are concerned with the controversy and some further characters through many families of Plecoptera including Styloperlidae. It results in a revision of the system in Systellognatha with the proposal of a superfamily, Pteronarcyioidea, for Pteronarcyidae, Styloperlidae and Peltoperlidae and a new subfamily of Peltoperlidae, Microperlinae.

Styloperlidae and Microperlinae can be identified using the key of Zwick (1980) with the following modifications:

Adults

- 5. Large or medium-sized. Wings with many crossveins everywhere except anal areas of hind wings. Abdominal segments 1–2 or 1–3 with gill remnants Pteronarcyidae
- Small or medium-sized. Wings with crossveins only in small areas. Abdomen without gill remnant 15
- 15. Frontoclypeal suture present (Fig. 2). Male abdominal sternite 9 with a brush (Figs 7, 14, 51, 55, 56, 60) but without vesicle or hammer. Radial area of wing with many crossveins (Fig. 6) Styloperlidae
- Frontoclypeal suture absent. Male abdominal sternite 9 with a vesicle (Figs 95–97) or a hammer but without brush. Radial area of wing with few crossveins (Peltoperlidae) 16
- 16. Three ocelli. Apex of tibia with a pair of spurs Microperlinae
- Two ocelli. Apex of tibia without spur Peltoperlinae

Nymphs

- 4. Habitus cockroach-like, thorax far wider than head and abdomen. Spinasternum of prothorax combined with the furcasternum (Fig. 98) (Peltoperlidae) 14
- Habitus normal or slender (Fig. 1), thorax not far wider than head and abdomen. Spinasternum of prothorax separated from the furcasternum (Fig. 29) 4'
- 4'. Apex of tibia without spur, with trifurcate setae (Fig. 36) Styloperlidae
- Apex of tibia with or without spur, without trifurcate setae 5
- 14. Head typical, with three ocelli (Fig. 110). Gills absent. Furcal pits of pro- and mesothoraces exposed (Fig. 98). Apex of tibia with a pair of spurs. Coxa without flap-like lobe. Mandible extended longitudinally (Figs 99, 101), lacinia with many teeth, galea with a large band of hairs (Fig. 100) Microperlinae
- Head strongly shortened, with two ocelli. Gills present always on thorax and, in some genera, on cervix or on tip of abdomen. Furcal pits of pro- and mesothoraces covered by posteriorly extended basisterna. Apex of tibia without spur. Form of mandible typically phytophagous, lacinia with two or three teeth, galea with a small tuft of hairs apically Peltoperlinae

Material and methods

Specimens examined in this study are deposited in the Institut für Pflanzenschutzforschung der Akademie der Landwirtschaftswissenschaften (Abt. Taxonomie der Insekten), formerly the Deutsches Entomologisches Institut, Eberswalde-Finow, German Democratic Republic (IPE), the Museum Alexander Koenig in Bonn, Federal Republic of Germany (MKB), the National Museum in Prague, Czechoslovakia (NMP), the Limnologische Flußstation

des Max-Planck-Institutes für Limnologie, Schlitz, Federal Republic of Germany (LFS) and the personal collections of the authors (SU, YI).

SEM micrographs were prepared by the method of Uchida & Isobe (1988), except the times of sonication (5–15 seconds) and gold-coating (2–3 minutes). The penis of *Cerconychia livida* was everted by squeezing live males between fingers just prior to fixing in alcohol. The other external genitalia were examined after KOH treatment. Head and thoracic tracheal systems were examined after KOH treatment of the whole segments whose dorsal sclerites had been removed. Internal organs were examined both in nymphs and adults in most cases. We found no conspicuous difference between the two stages, unless mentioned in the text. Morphological terms follow those of Wittig (1955, musculature and nervous system in occiput and thorax), Brinck (1956, genitalia) and Zwick (1973, 1980) unless the author is cited.

Family Styloperlidae Illies, stat. nov.

Styloperlinae Illies, 1966: 17; Zwick 1973: 218; 1980: 14.

Type genus *Styloperla* Wu.

The following features are shared by all the representatives of the family that we examined. The females, nymphs and eggs of *Styloperla* were inaccessible for our examination and therefore the features below are limited to those of the male. We assume, however, that the female, nymph and egg of *Styloperla* share most characteristics of *Cerconychia* that are described below, because of the great similarity in the males.

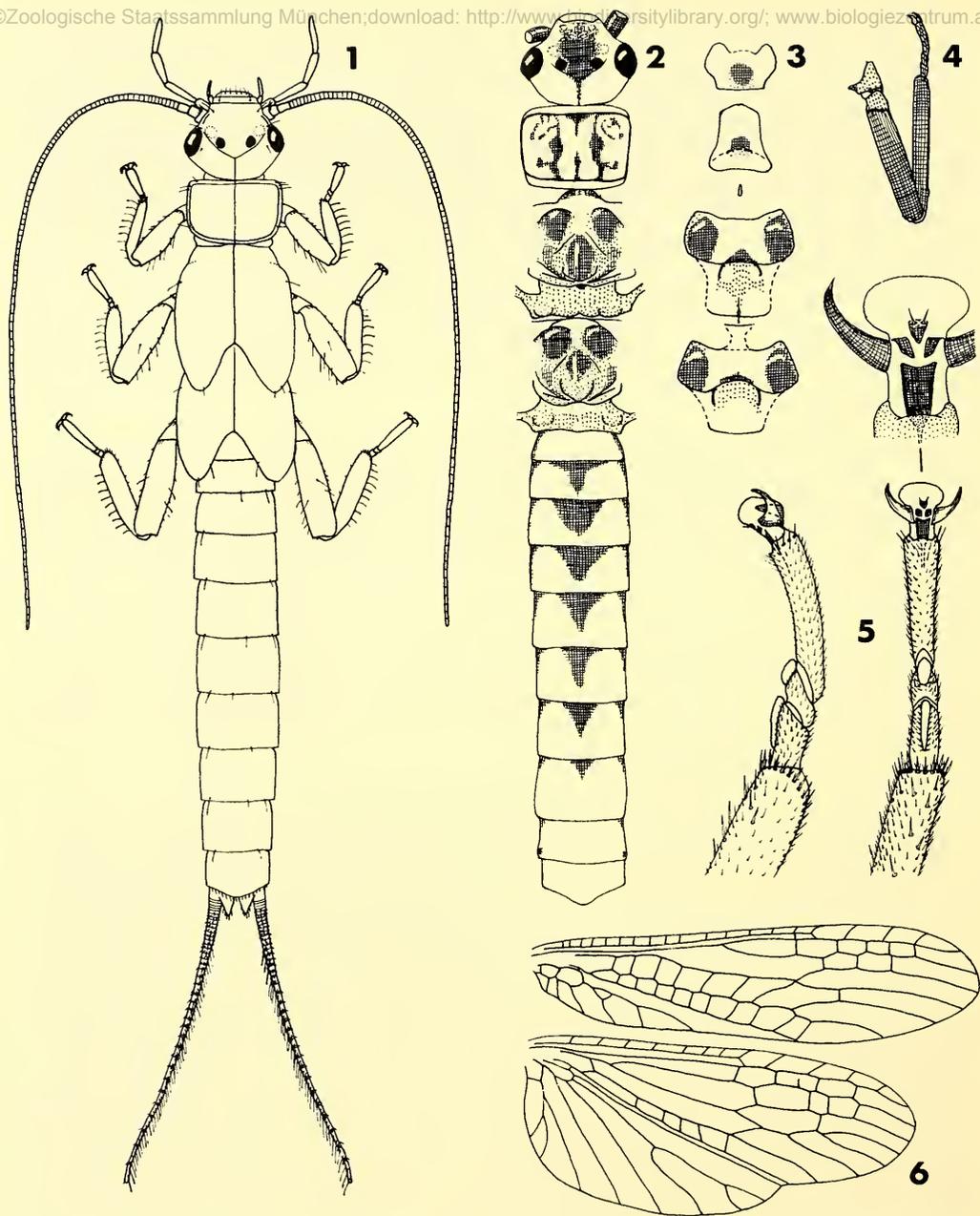
Male

General color yellow with brown markings which are dark in aged ones.

Head (Fig. 2) directed forward, with two ocelli and with a brown marking between the ocelli. Frontoclypeal suture present. Coronal suture marked by a narrow brown band. Antenna brown and long, about four-fifths of body length. Mouthparts reduced, membranous; maxillary palpus long, about as long as head width; all palpi brown.

Pronotum (Fig. 2) with a pair of median yellow stripes and edged by a distinct dark brown line all around. Spinasternum of prothorax (Fig. 3) separated from the furcasternum by a wide membranous swelling. Meso- and metanota (Fig. 2) brown except yellow praescuta. Pleura (Fig. 49) brown anterior half of anepisterna darker. Pre-episterna of meso- and metathoraces (Fig. 3) with large brown markings. Aged adult with brown central markings on postmentum and all thoracic sterna, but young one without them. Meso- and metathoraces with postalar bridges between pleura and postnota (Fig. 49). Leg (Fig. 4) brown, coxa and trochanter paler. The apex of tibia (Fig. 5) without spur, with a fringe of trifurcate setae. First tarsal segment long, about one-third as long as the third. The ventral bases of claws (Fig. 5, above) with a pair of auxilia and a median sclerite which is bearing a pair of minute hairs. Radial area of wing (Fig. 6) with many crossveins and divided into uniform quadrangular cells.

Abdominal tergites 2–8 (Fig. 2) with lateral and median triangular brown markings in the anterior parts. Sternite 1 fused to metasternum. Sternite 9 (Figs 7, 14, 51, 55, 56, 60) with a dense patch of long thick hairs (brush) anteriorly or centrally. Tergite 10 (Figs 9, 52, 57) often with a mesal cleft on the posterior margin; the depth of the cleft variable even within a single species (Fig. 15). Sternite 10 (Figs 14, 19, 55, 60) with a median X-shaped sclerite. The rudiment of epiproct (Figs 7, 9, 16, 52, 57) weakly or scarcely sclerotized, flat. The basal segments of cercus (Figs 7–10, 14, 16, 51–53, 56–58) fused into a long stout shaft, with a long spur which originates at the dorso-mesal side of the apex and curves postero-laterally; the next few segments with small dorsal spines, whose arrangement is variable even within a single species (Fig. 9, below); the apical segments (Fig. 7) with fringes of long hairs dorsally in the basal half and ventrally in the apical half. Penis (Figs 11–13, 17, 18, 54, 59) membranous, with dorsal striae, a ventral pair of slender sclerites and scattered spinules near the gonopore.



Figs 1–6. Nymphal habitus (1) and adult (2–6) of *Cerconychia livida*. 2. dorsum; 3. ventral sclerites of head (postmentum) and thorax; 4. right midleg, dorsal view; 5. apex of tibia and tarsal segments, lateral (left) and ventral (right) views with details of pretarsus (above); 6. right wings.

(Females presently indistinguishable. Nymphs and eggs of *Styloperla* unknown.)

- 1. Sternite 9 with a transversely elongate brush anteriorly (Figs 7, 14) *Cerconychia*
- Sternite 9 with a longitudinally elongate brush centrally (Figs 51, 55, 56, 60) *Styloperla*

Genus *Cerconychia* Klapálek

Cerconychia Klapálek, 1913: 124.

Type species, *Cerconychia livida* Klapálek, design. Kimmins, 1941.

The following characteristics are shared by adults and eggs of *brunnea* and *livida* and nymphs of *livida* and an unidentified species (*brunnea*?). The internal organs were examined in adults and nymphs of only *livida*.

Cerconychia represents more primitive features than *Styloperla*; they are, 1) the brush on sternite 9 located near the front margin like the vesicles of Nemouroidea and Peltoperlidae which may be the ground plan within Arctoperlaria, 2) tergite 10 with posterior hemitergal lobes (sensu Nelson & Hanson 1971) as in Pteronarcyidae, 3) the rudiment of epiproct much sclerotized. See also the part on phylogeny below.

Male

Abdominal sternite 8 (Figs 7, 14) with a posteromedian patch of long hairs. Brush on sternite 9 transversely elongate, located on a swelling at the anterior part of the sternite and delimited from the central and posterior flat part by a weak U-shaped fold. Tergite 10 (Figs 7, 9, 16) with posterior hemitergal lobes. The rudiment of epiproct more strongly sclerotized than in *Styloperla*, with a membranous swelling posteriorly which bears hairs. The basal shaft of cercus (Figs 7–10, 14, 16) with a fringe of long hairs on the mesal side; the spur with a pointed tip, not furcate. Penis (Figs 11–13, 17, 18) small, without sclerite dorsally; the ventral sclerite ca. 0.5 mm long.

Female

All the features except genitalia as in *Styloperlidae* male above.

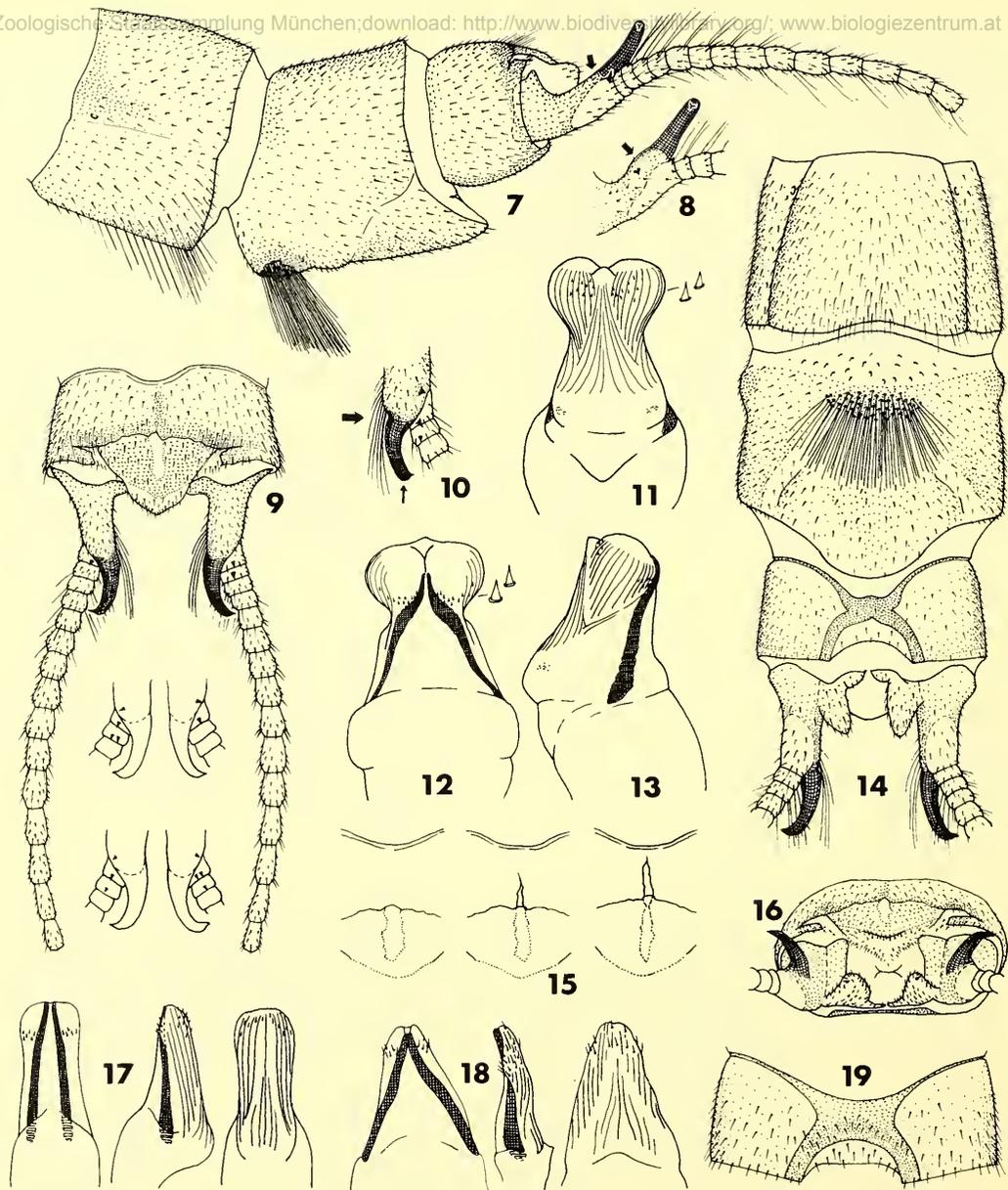
Abdominal sternite 8 (Fig. 20) not extended posteriorly. Sternite 9 with a pair of sclerotized bars directed posterolaterally and with an antero-median patch of spinules which is extended anteriorly into the membrane behind the vaginal opening. The membrane between sternites 9 and 10 with a band of anteriorly directed minute setae. Vagina (Figs 21, 22) membranous, constricted at two-thirds from the base and with a small sclerite dorsally. Spermatheca small, with five to eight accessory glands.

Nymph

Slender (Fig 1), uniformly light brown, without gill. Sclerites and membranes covered by short fine hairs which are easily abraded. Chloride cells (Fig. 35) coniform.

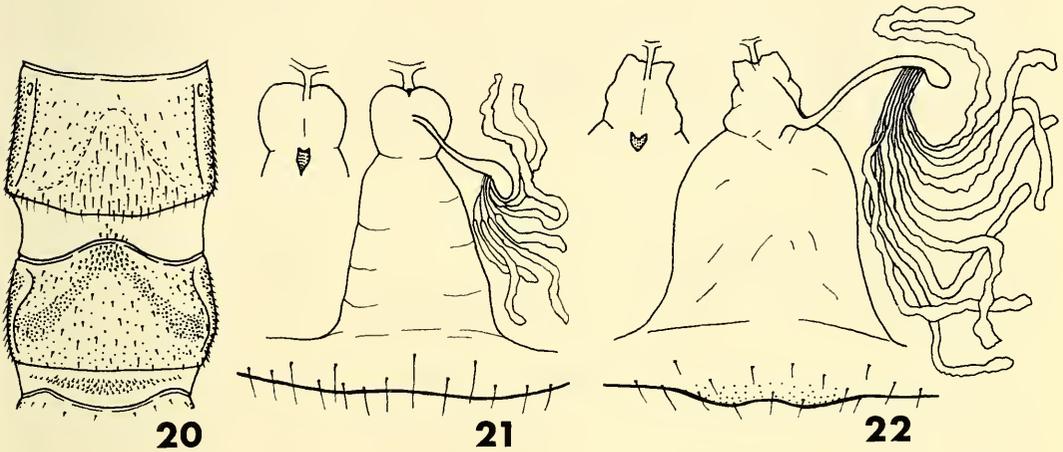
Head directed forward, with two ocelli and with a pair of indistinct light markings on tentorial callosities. Frontoclypeal suture (Fig. 23) present. Clypeus with a pair of long setae. Frons with three pairs of long setae; 1) near tentorial pits, 2) near frontoclypeal suture medially, 3) just before compound eyes. Parietals with a pair of long setae posteromesad from compound eyes. Antenna long and slender, longer than two-thirds of body length; scapus (Fig. 25) with an apical fringe of stout setae.

Mouthparts phytophagous. Labrum (Fig. 23) with an anterior fringe of short fine hairs and with a posterior transverse band of long setae which are bent ventrad. Left mandible (Figs 24 left, 26 right) with four teeth arranged on a single ridge whose line is prolonged posteriorly into the ventral row of three humps on the mola. Right mandible (Fig. 24 right, 26 left) with three teeth arranged on a single ridge whose line is prolonged posteriorly into the ventral ridge of the mola. Mandibles without hair



Figs 7–19. Male genitalia of *Cerconychia*. 7, 9, 11–17. *C. livida*; 8, 10, 18, 19. *C. brunnea*. 7, 9, 14, 16. abdominal terminal segments, lateral (7), dorsal (9, with variation in the spinules on basal cercal segments), ventral (14) and posterior (16) views; 8, 10. shaft and spur on cercus, lateral (8) and dorsal (9) views; 11–13, 17, 18. penes, everted in live male (11. dorsal; 12. ventral; 13. lateral views) and with KOH treatment (17, 18. left, ventral; middle, lateral; right, dorsal views); 15. variation in the cleft on tergite 10; 19. sternite 10.

band at the bases of teeth. Molae (Figs 32, 33) broad, without thorn carpet surface ("comb-like surface" of Stark & Stewart 1981); the left one (Fig. 33) with a sharp anterodorsal edge which bears short comb-like teeth and is produced into a blade in the anterior part; the right one (Fig. 32) cuplike, surrounded by a sharp edge, but the antero-dorsal side with a low hump instead of the edge. Postero-dorsal bases of molae with bands of long hairs; the left band (Fig. 24 left) arranged on a single continuous line with anterior sparse row of short setae. Lacinia (Figs 28, 34) with three apical teeth, the ventral one small, all pointed; with many long hairs on the inner base; and fringed with a row of long setae on the dorsal edge and with 10 small teeth on the ventral edge. Galea with a dorso-lateral sparse fringe of fine hairs which are bent dorsad. Maxillary palpus long (Fig. 1), slightly longer than head width. Paraglossae (Fig. 27) small, slightly larger than glossae which are separated from each other by a median sclerotized band (arrow in Fig. 27).



Figs 20–22. Female genitalia of *Cerconychia*. 20, 21. *C. livida*; 22. *C. brunnea*. 20. sternites 8 and 9; 21, 22. dorsal views of vaginae and spermathecae with ventral views of apical parts of vaginae.

Pronotum (Fig. 1) with two to four long setae on the anterior corner and with one or two on the posterior corner. Thoracic sterna (Fig. 29) without setae, smooth. Spinasternum of prothorax separated from the furcasternum. Lateral margin of meso- and metanotum (Fig. 1) each with a long seta; the seta of mesonotum longer than that of metanotum. Hind margin of meso- and metanotum each with two to four long setae. Coxa, trochanter and femur with distal fringes of short setae. Femur and tibia with sparse hind fringes of stout setae and long fine hairs. Tibia with a distal fringe of stout trifurcate setae (Figs 30, 36), but without spur; its distal part also with fine trifurcate setae (Fig. 37). The first tarsal segment shorter than in the adult, about one-fourth as long as the third which bears bud-like setae (Fig. 38) ventrally.

Abdominal sternite 1 fused to metasternum. Sternite 2 separated from the tergite by membrane; on the other segments the sternite and the tergite fused. Both tergites and sternites with hind fringes of short fine hairs and sparse long setae (Fig. 1). Paraproct slender, with dense stout setae apically. Cercus slender, about half body length, with ventral and dorsal fringes of long fine hairs (Fig. 31) and with stout setae on hind margins of the segments.

Egg.

Ellipsoidal (Figs 39, 41), without collar and anchor. Chorion hard; the surface smooth. Micropyles (Fig. 40, 42) without conspicuous structure, arranged circumlinearly at one-third from a pole which is directed toward the oviduct in the ovariole.

Nervous system. – The paired median tegumental nerves of head (Fig. 88, see also the character 2 in the part on phylogeny below) fused with each other at their end. Prothoracic ganglion (Fig. 43) not connected to suboesophageal ganglion in head. Seven individual abdominal ganglia present: the 1st one completely fused to metathoracic ganglion; the 2nd (Fig. 44) also connected to the metathoracic but clearly bordered by a suture; the 3rd to 8th free; the 9th to 11th fused into one ganglion. Retrocerebral system (Figs 45–47). – Corpora allata paired, in contact with each other mesally and with corpora cardiaca anteriorly. Corpora cardiaca also paired, but fused widely together mesally and dorsally to the ventral wall of aorta whose lateral and dorsal walls are also innervated. Musculature. – Tergal depressor muscle of trochanter present behind the bridge that connects furca with endopleural apodeme, the sternal depressor muscle absent. The muscle *I ism* 24 (Fig. 48, arrow) present. The muscle *II ppm* 56 (Fig. 49) originating at the posterior end of epimeron. Atypical longitudinal muscles of thorax (Fig. 48, white) well developed, especially in nymphs. Mesodermal genitalia. – Testes (Fig. 50) divided into a pair; each with ca. six follicles. A pair of seminal vesicles connected anteriorly to form an arch; accessory gland at the base of the vesicles absent. Ovaries connected anteriorly to form an arch. Alimentary canal. – Proventriculus without conspicuous sclerites or teeth bands. Midgut without caecal sacs.

Species list

1. *brunnea* Klapálek, Taiwan.
2. *livida* Klapálek, Taiwan.

Keys to the species of *Cerconychia*

(Nymph of *brunnea* unknown.)

Males

1. Basal shaft of cercus with a dorsal swelling posteriorly (Fig. 8, arrow), spur on the shaft constricted at the mesal side of the base (Fig. 10, thick arrow) and with an angle (fine arrow) near the tip *brunnea*
- Basal shaft of cercus without dorsal swelling (Fig. 7, arrow), spur on the shaft (Fig. 9) not constricted and gently curved postero-laterally *livida*

Females with eggs

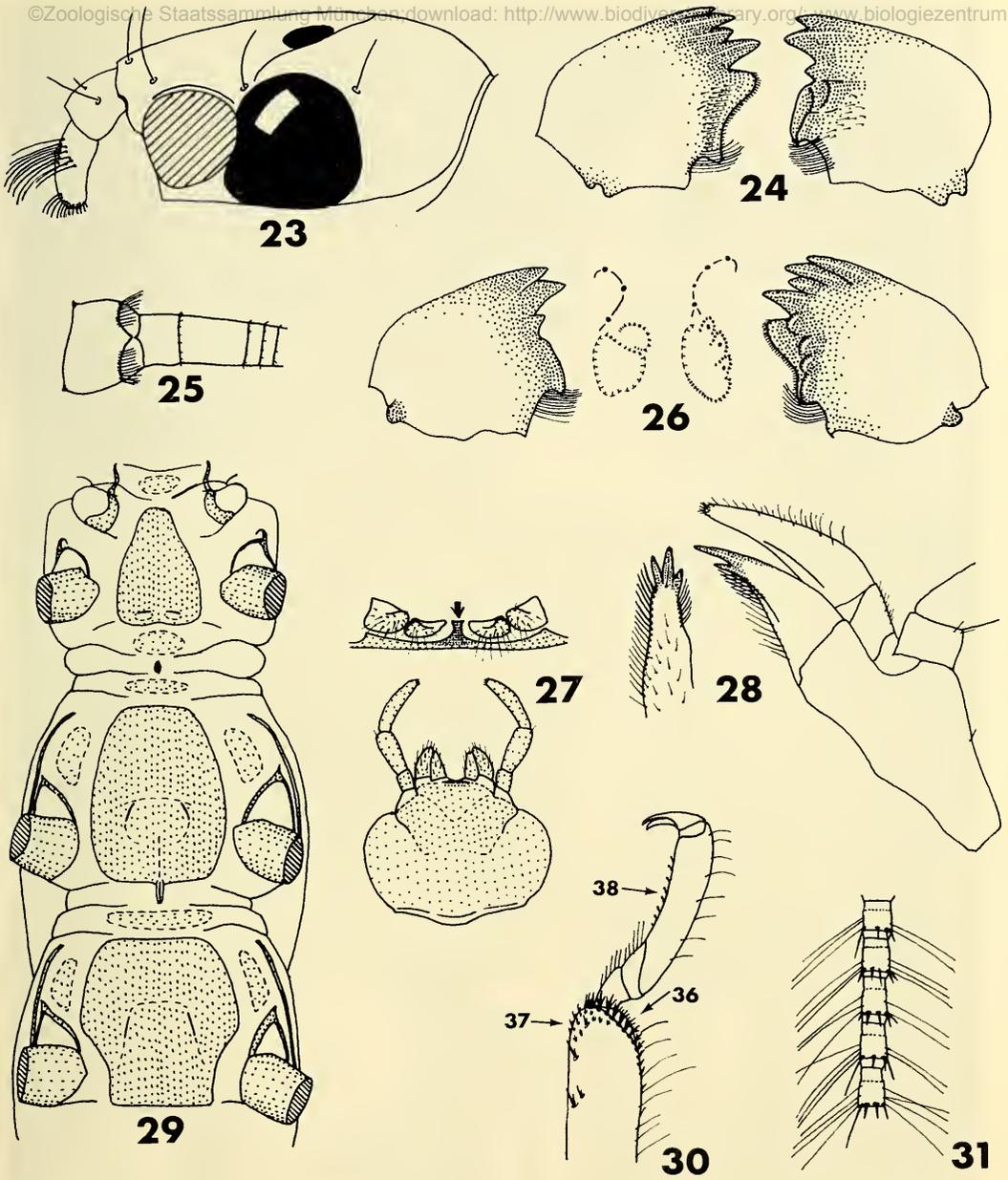
1. Vagina wide (Fig. 22), about three-fourths as wide as the length at the base. Egg large, 0.34–0.35 mm (pinned) or 0.40–0.41 mm (in alcohol) long *brunnea*
- Vagina narrow (Fig. 21), about two-thirds as wide as the length at the base. Egg small, 0.27–0.29 mm (pinned) or 0.31–0.33 mm (in alcohol) long *livida*

Cerconychia brunnea Klapálek

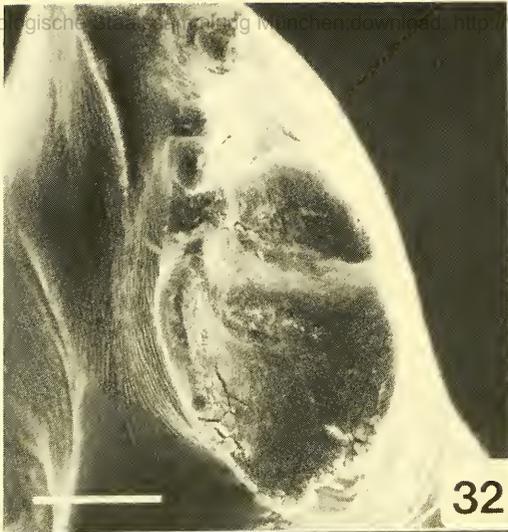
(Figs 8, 10, 18, 19, 22, 41, 42)

Cerconychia brunnea Klapálek, 1913: 126.

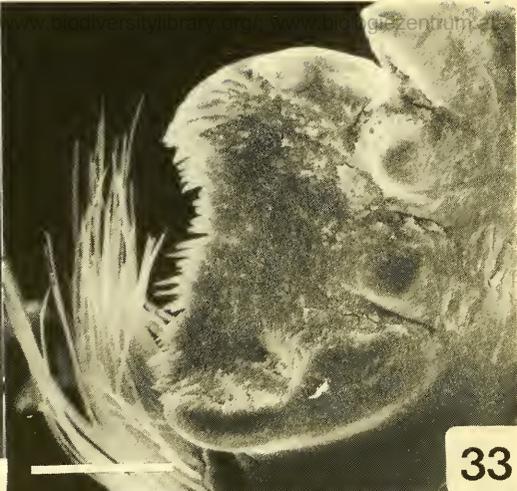
Material examined. Types: lectotype ♂, here designated, CHINA: Taiwan, Chiai-hsien, Suisharyo, X.1911 (Sauter) (IPE); paralectotypes, 1 ex. (without most of wings and abdomen), same data, (IPE); 1 ♂, same data, (NMP). Additional material: 1 ♂ paralectotype of *C. livida*, Taiwan, Kaohsiung-hsien, Kosempo, V.1912 (Sauter) (IPE); 1 ♀, same locality, VII.1911 (Sauter) (IPE); 1 ♀, Chiai-hsien, Alishan, 24. VI.1980 (Shimizu) (SU).



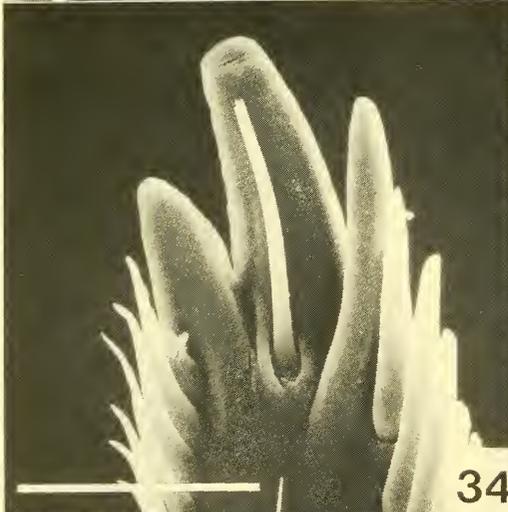
Figs 23–31. Nymph of *Cerconychia livida*. 23. head, lateral view; 24, 26. mandibles, dorsal (24) and ventral (26. left and right) views with schematic inner views of tooth arrangement (26. middle); 25. basal segments of right antenna; 27. labium, anterior (above) and ventral (below) views; 28. left maxilla, ventral view with inner view of lacinia; 29. thoracic sternae; 30. apex of tibia and tarsal segments, arrows refer to the locations of the setae in Figs 36–38; 31. details of cercal segments, lateral view.



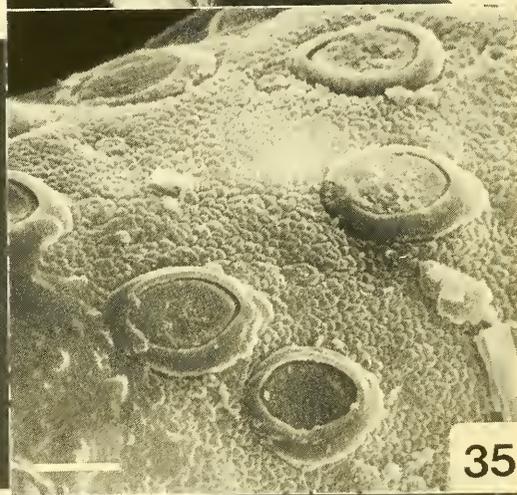
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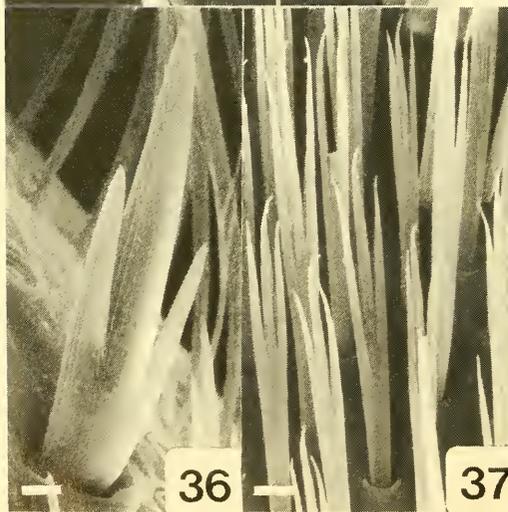
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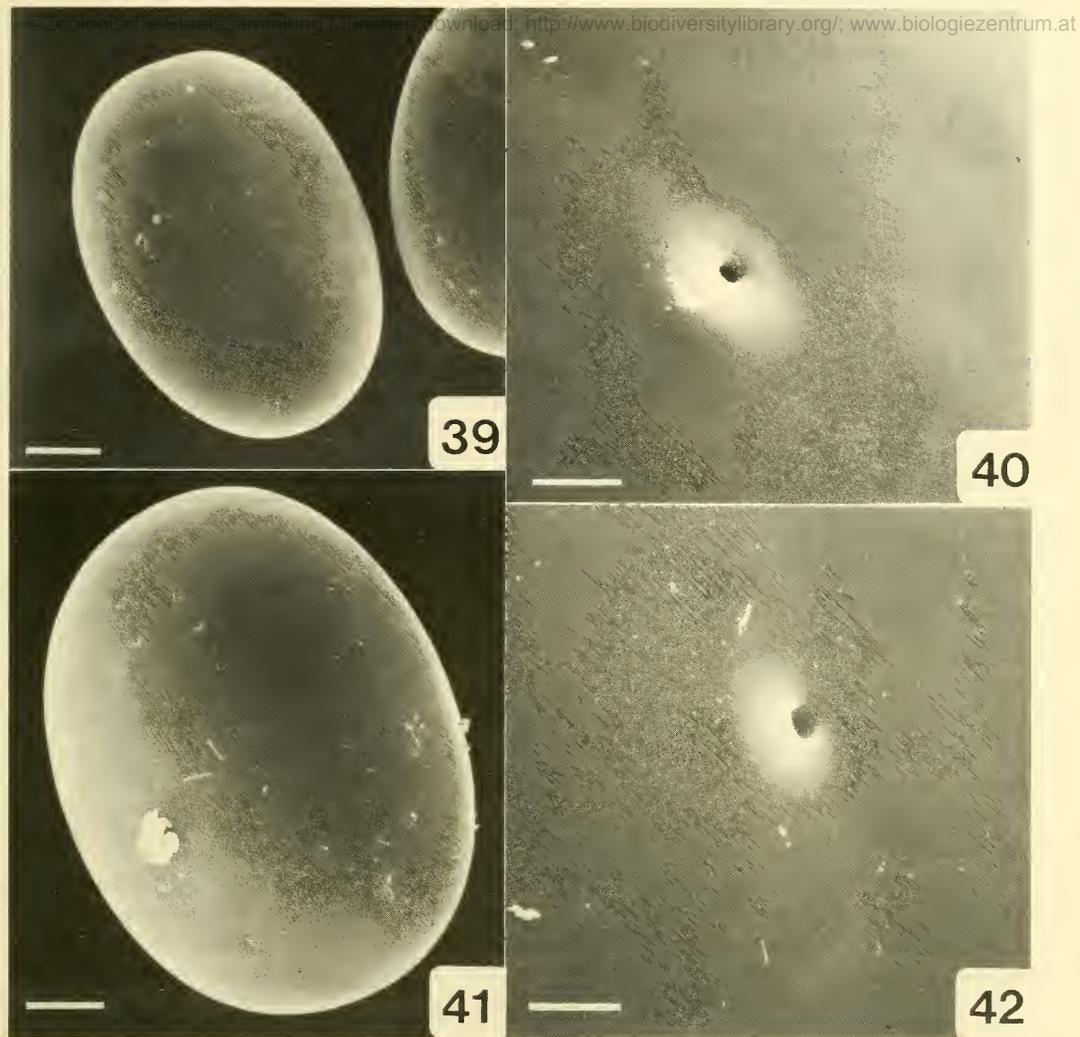


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37



38



Figs 39–42. SEM micrographs of *Cerconychia* egg. 39, 40. *C. livida*; 41, 42. *C. brunnea*. 39, 41. whole eggs; 40, 42. details of micropyles. Scales: Figs 39, 41: 50 μm ; Figs 40, 42: 5 μm .

All the syntypes of this species should be located at IPE, Germany. But a syntype is, in fact, located at NMP, Czechoslovakia. The syntypes of *C. livida* include a male of this species, which was misidentified by Klapálek.

Male

Forewing 10 mm long. General color darker than in *livida*. Wings light brown; veins brown. X-shaped sclerite of abdominal sternite 10 (Fig. 19) thicker than in *livida*. Basal shaft of cercus with a dorsal swelling posteriorly (Fig. 8, arrow); spur on the shaft constricted at the mesal side of the base

Figs 32–38. SEM micrographs of *Cerconychia livida* nymph. 32. right mola, inner view; 33. left mola, ventro-inner view; 34. apex of right lacinia, inner view; 35. chloride cells on the base of antenna; 36. trifurcate seta at the apex of tibia; 37. trifurcate setae on the distal part of tibia; 38. bud-like setae on the ventral side of third tarsus. Scales: Figs 32–34: 50 μm ; Figs 35–38: 5 μm . For the locations of the setae in Figs 36–38. see Fig. 30.

(Fig. 10, thick arrow) and curved postero-laterally with an angle (fine arrow) near the tip. Penis (Fig. 18) wider than in *livida*, ca. 0.4 mm wide at the base of ventral sclerites in retracted condition.

Female

Generally similar to the male. Forewing 15–16 mm long. Vagina (Fig. 22) wider than in *livida*, about three-fourths as wide as the length at the base. Spermatheca with eight accessory glands.

Egg (Figs. 41, 42)

Larger than *livida*, 0.34–0.35 (pinned) or 0.40–0.41 mm (in alcohol) long, otherwise indistinguishable from it.

Cerconychia livida Klapálek

(Figs 1–7, 9, 11–17, 20, 21, 23–40, 43–50, 88)

Cerconychia livida Klapálek, 1913: 125, pl. 3, fig. 5.

Material examined. Types: lectotype; ♂, here designated, CHINA: Taiwan, Kaohsiung-hsien, Kosempo, X.1911 (Sauter) (IPE): paralectotypes; 1 ex. (only mesothorax with forewings), Kosempo, X.1911; 2♂, Kaohsiung-hsien, Sokutsu, V., VI.1912; 1♀, Chiai-hsien, Suisharyo, X.1911, (Sauter) (IPE). Additional material: Taiwan, 7♂, 3♀, 6 exuviae, 5 nymphs, Taipei-hsien, Wulai, 100–200 m, 1, 2, 11, 18.IV.1982 (Uchida) (2♀, 6 exuviae, 2 nymphs, LFS; the others, SU); 51♂ 20♀, 6 exuviae, 13 nymphs, Nantou-hsien, Nanshan-chi near Puli, 700–900 m, 8, 9, 15, 16.IV.1982, nymph collected 8, 15.IV. emerged 8.–18.IV.1982 (Kawamura & Uchida) (15♂, 5♀, 3 nymphs, 6 exuviae, LFS; 1♂, 1♀, 3 nymphs, YI; the others, SU).

The adults of this species were the most abundant stoneflies at Nanshan-chi in April. They were found along the stream, especially on the blossom of evergreen Fagaceae, *Pasania*, with many species of long-horned beetles (Cerambycidae).

Male

Forewing 9–12 mm long. General color lighter than in *brunnea*. Wings hyaline; veins yellow. X-shaped sclerite of abdominal sternite 10 (Fig. 14) thinner than in *brunnea*. Basal shaft of cercus without dorsal swelling posteriorly (Fig. 7 arrow); spur on the shaft (Fig. 9) not constricted at the base and gently curved postero-laterally. Penis (Figs. 11–13, 17) more slender than in *brunnea*, ca. 0.3 mm wide at the base of ventral sclerites in retracted condition.

Female

Fore wing 9–14 mm long. Generally similar to the male. Vagina (Fig. 21) narrower than in *brunnea*, about two-thirds as wide as the length at the base. Spermatheca with five to seven accessory glands.

Last instar nymph (Figs 1, 23–38)

Body 7–10 mm long. Smaller than *C. sp.* (below), otherwise indistinguishable from it.

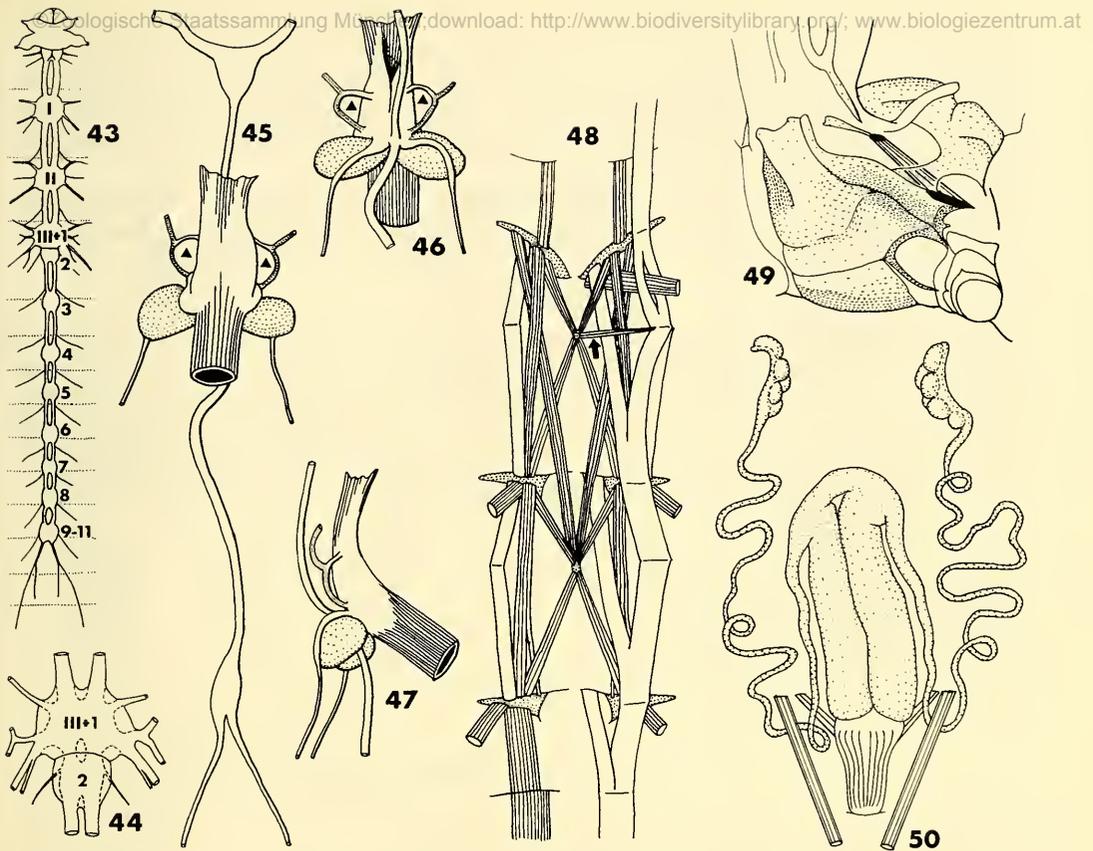
Egg (Figs 39, 40)

Smaller than *brunnea*, 0.27–0.29 (pinned) or 0.31–0.33 mm (in alcohol) long, otherwise indistinguishable from it.

Cerconychia sp.

Material examined. 1 nymph, CHINA: Taiwan, Nantou-hsien, Lushan-wenchuan, 1100 m, 7.IV.1982 (Uchida) (SU).

This nymph is not associated with the adult but is possibly *C. brunnea*.



Figs 43–50. Internal organs of *Cerconychia livida*. 43. central nervous system; 44. metathoracic and second abdominal ganglia; 45–47. retrocerebral system, dorsal (45), ventral (46) and lateral (47) views; ▲: location of musculus verticopharyngealis, dotted: corpus allatum, striped: aorta, white: nerves and innervated parts of aorta, dotted line: the main nerve from corpora cardiaca to brain; 48. female ventral muscles of thorax with atypical longitudinal muscles (white); 49. lateral view of mesothorax with the muscle *II ppm* 56; 50. male internal genitalia, dorsal view.

Nymph

Body 13 mm long. Far larger than *livida*, although it is not yet grown to the last instar. Otherwise indistinguishable from *livida*.

Genus *Styloperla* Wu

Styloperla Wu, 1935: 236.

Cerconychia Wu, 1962: 147.

Nogiperla Wu, 1973: 99.

Type Species, *Styloperla spinicercia* Wu, original design. and monotypy.

We could examine only the males of *S. inae* and *S. wui*. The following characteristics are shared by the two species. The type species, *spinicercia* Wu, 1935, was inaccessible for our examination. The holotype should be deposited in the Museum für Naturkunde, Humboldt University, Berlin, but could

not be found there (Dr. K. K. Günther, in litt.). However, Wu (1935) clearly described a longitudinally elongate brush on the middle of the male abdominal sternite 9, which is one of the following characteristics. It supports the placement of *inae* and *wui* in *Styloperla*. The descriptions of *Cerconychia flectospina* Wu, 1962 and *Nogiperla obtusispina* Wu, 1973 also represent the longitudinally elongate (though rather short in *flectospina*) brush on the middle of the sternite. The two species are therefore transferred herein.

The female diagnostic character for the distinction from *Cerconychia* is unknown. But the "chitinized plate inside the 8th abdominal segment" (Chao 1947) may be available for it; such a plate does not occur in *Cerconychia*.

Male

Abdominal sternite 8 (Figs 55, 60) with or without an inconspicuous postero-median patch of long hairs. Brush on sternite 9 longitudinally elongate and located on the anterior half of a central and posterior plateau on the sternite; U-shaped fold behind the brush absent. Tergite 10 (Figs 52, 57) without posterior hemitergal lobe. The rudiment of epiproct less sclerotized than in *Cerconychia*. Basal shaft of cercus without fringe of long hairs on the mesal side. Penis (Figs 54, 59) large; the ventral sclerite ca. 1.0 mm long; the dorsal side in part weakly sclerotized.

Species list

1. *flectospina* (Wu, 1962), comb. nov., Yunnan.
2. *inae* Chao, 1947, Fukien.
3. *obtusispina* (Wu, 1973), comb. nov., Szechwan.
4. *spinicercia* Wu, 1935, Kwangtung.
5. *wui* Chao, 1947, Fukien.

Key to the species of *Styloperla* males

(Females presently indistinguishable. Nymphs and eggs unknown.)

- | | |
|---|--------------------|
| 1. Basal shaft of cercus with a rounded knob at the dorsomesal side of the apex | <i>obtusispina</i> |
| – Basal shaft of cercus with a pointed spur at the dorsomesal side of the apex | 2 |
| 2. Spur of cercus simple | 3 |
| – Spur of cercus forked (Figs 51, 52, 56, 57) | 4 |
| 3. Basal shaft of cercus with spines at the lateral side of the apex and the mesal side of the base . . . | <i>spinicercia</i> |
| – Basal shaft of cercus without spines besides a spur | <i>flectospina</i> |
| 4. Spur of cercus with two lateral spines at one-third from the base and near the tip (Figs 51, 52) | <i>inae</i> |
| – Spur of cercus with a lateral spine at one-fourth from the tip (Figs 56, 57) | <i>wui</i> |

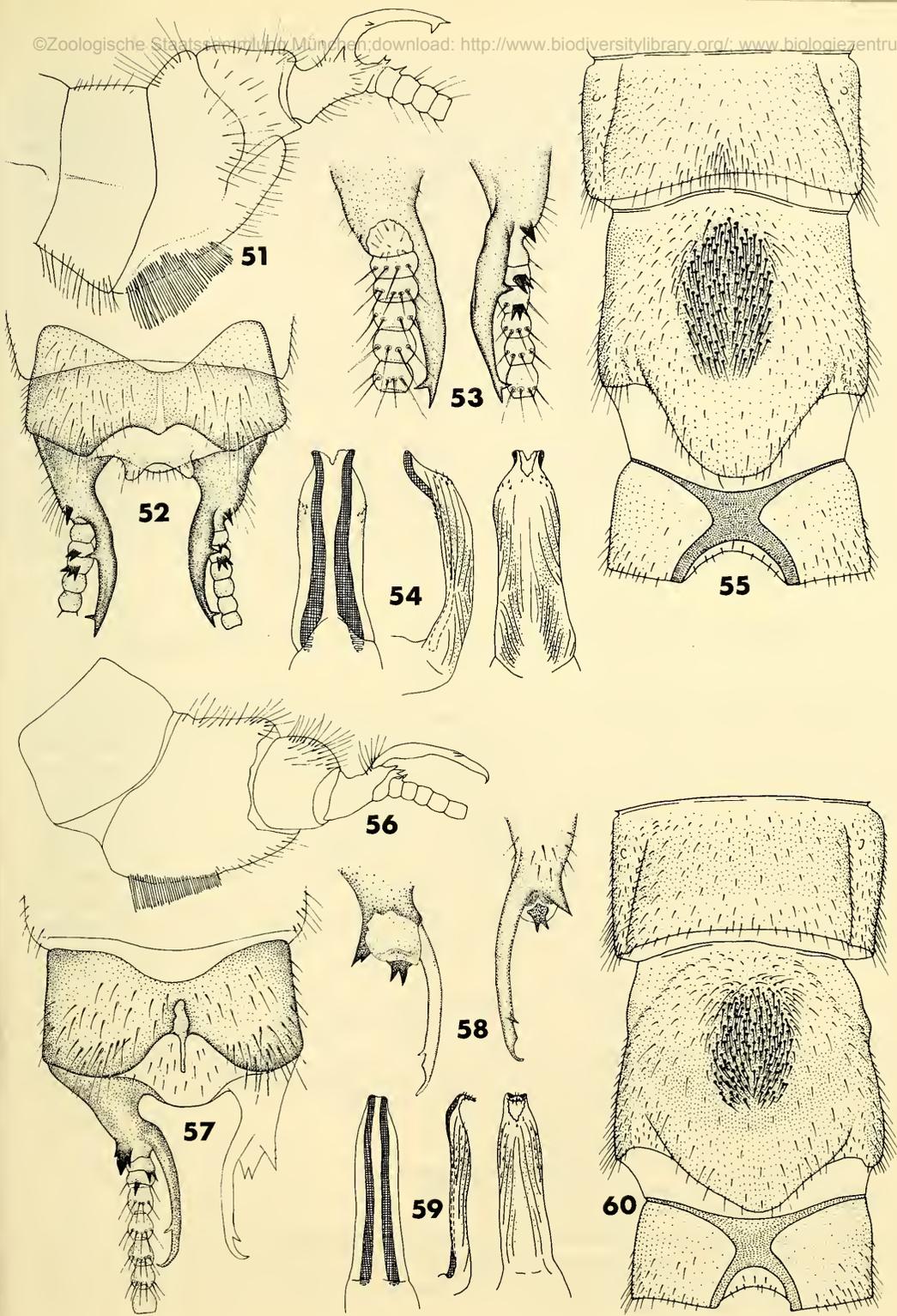
Styloperla inae Chao

(Figs 51–55)

Styloperla inae Chao, 1947: 95, figs. 3, 6, 9, 12–14.

Material examined. 7♂, CHINA: Fukien, Kuantun, 2300 m, 27°40' N, 117°40' E, 30.IV., 3, 16, 21, 27.V.1938 (Klapperich) (6♂, MKB; 1♂, LFS).

Figs 51–60. Male genitalia of *Styloperla*. 51–55. *S. inae*; 56–60. *S. wui*. 51–52, 55–57, 60. terminal segments, lateral (51, 56), dorsal (52, 57) and ventral (55, 60) views; 53, 58. details of the spurs on right cerci; 54, 59. penes, everted with KOH treatment, ventral (left), lateral (middle) and dorsal (right) views.



Forewing 14–15 mm long. Abdominal sternite 8 (Fig. 55) with an inconspicuous patch of long hairs. The concave hind margin of sternite 10 wider than in *wui*, about one-third as wide as the whole hind margin of the sternite. The spur of cercus (Figs 51–53) with two lateral spines at one-third from the base and near the tip; the lateral base of the spur bearing a spine with a pointed tip. The spinules on penis (Fig. 54) scattered dorso-laterally near the gonopore.

Styloperla wui Chao

(Figs 56–60)

Styloperla wui Chao, 1947: 94, figs. 2, 5, 8, 11.

Material examined. 2♂, CHINA: Fukien, Kuatun, 2300 m, 27°40' N, 117°40' E, 20. V., 23. VI. 1938 (Klappe-
rich) (MKB).

Male

Forewing 13–14 mm long. Abdominal sternite 8 (Fig. 60) without a patch of long hairs. The concave hind margin of sternite 10 narrower than in *inae*, about one-fourth as wide as the whole hind margin of the sternite. The spur of cercus (Figs 56–58) with a lateral spine at one-fourth from the tip; lateral base of the spur bearing a spine with three pointed tips. The spinules of penis (Fig. 59) scattered dorso-laterally near the gonopore and the apical end of the ventral sclerites.

Phylogenetic position of Styloperlidae and a revised system of Systellognatha

The history of Systellognatha systematics was well outlined by Zwick (1973, p. 7–14, figs 2–5) and the following analysis of the individual characters mostly also follows him (1973, 1980). His views on the evolution of individual organs have little been adopted, though they are excellent and informative, by recent workers on Systellognatha phylogeny (Stark & Stewart 1981, Stark & Szczytko 1982, 1984, Shepard & Stewart 1983). The proposed phylogeny of Systellognatha is shown in Fig. 61, whose numerals refer to those in the text and in Table 1. It leads to a revision of the system summarized in Table 2.

Nelson (1984) suggested other two doubts besides our changes about Zwick's system of Systellognatha; 1) the relationship among the three families in Perloidea, 2) the classification of Pteronarcyidae into genera. The former problem is also concerned with the lack of the autapomorphy of Perlodidae and is not discussed in this paper. The latter controversy was recently reviewed by Nelson (1988). We follow his classification of Pteronarcyidae into two genera, *Pteronarcella* and *Pteronarcys*.

Table 1. Synapomorphies used in Fig. 61. Numerals also refer to those in the text.

1. Paired corpora allata located closely with each other mesally.
2. Median tegumental nerves of head fused with each other mesally at the dorsal ends.
3. Arolium of pretarsus expanded laterally, with a pair of lateral sclerites.
4. Second abdominal ganglion fused with metathoracic one.
5. One of the two arches of seminal vesicles reduced.
6. Male abdominal sternite 9 with a dense tuft of long thick setae.
7. Spurs at the apex of tibia reduced, with trifurcate setae there.
8. Abdominal sternite 10 with a X-shaped sclerite.
9. Habitus of nymph cockroach-like, thorax far wider than head and abdomen.
10. Spinasternum of prothorax combined with the furcasternum.
11. Mouthparts strongly transformed; mandibles extended longitudinally, galea with a long broad band of hairs, most of long hairs on mouthparts branched.

12. Corpora allata fused with each other mesally.
13. Head strongly shortened, partly covered by prothorax, with two ocelli.
14. Basisterna of nymphal pro- and mesothorax flat, extended posteriorly and covering the furcal pits.
15. Nymphal coxa with a flap-like lobe.
16. Spurs at the apex of tibia reduced, with simple setae there.
17. Nymph carnivorous; mandible slender, without mola; maxilla sharply denticulated.
18. Gut with caecal sacs.
19. Eighth abdominal ganglion fused with the caudalmost one.

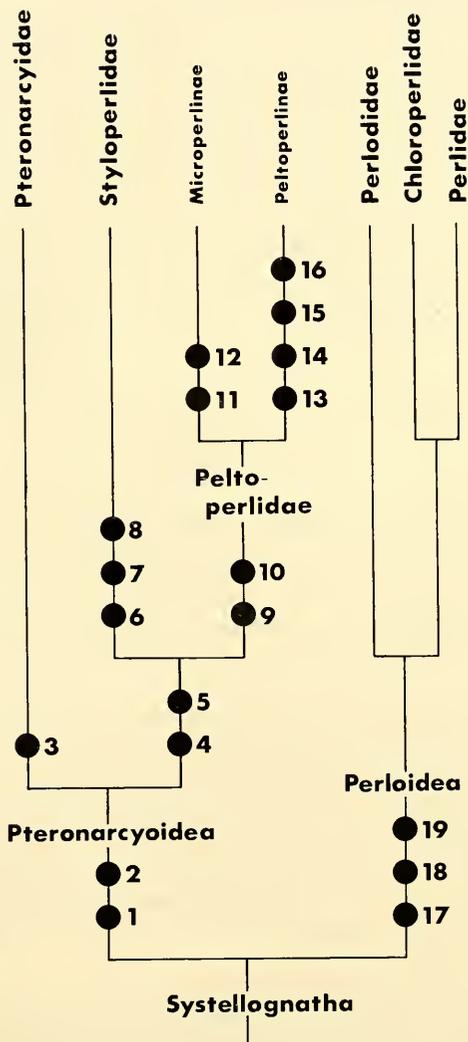


Fig. 61. Cladogram showing a proposed phylogeny of Systellognatha. Numerals refer to the synapomorphies in Table 1 and in the text. The relationship within Perloidea follows that of Zwick (1980).

Table 2. A revised system of the family group Systellognatha.

Family group Systellognatha Enderlein, 1909
Superfamily Pteronarcyzoidea Enderlein, 1909
Family Pteronarcyzoidea Enderlein, 1909
Family Styloperlidae Illies, 1966, stat. nov.
Family Peltoperlidae Claassen, 1931
Subfamily Microperlinae, nov.
Subfamily Peltoperlinae Claassen, 1931
Superfamily Perloidea Latreille, 1802
Family Perlodidae Klapálek, 1909
Family Perlidae Latreille, 1802
Family Chloroperlidae Okamoto, 1912

Table 3. Terminology of male epiprocts in Systellognatha.

This study	Nelson & Hanson (1971)	Zwick (1973)
basal anchor	inner part	Hebelarm
basal bar	ventral section	
cowl	cowl	Epiproct-Tasche
epiproct s. str.	dorsal section	Epiproct s. str.
lateral brace	lateral brace	Seitenarm
lateral stylet	fork-like structure	Seitenstylus
paragenital plate	paragenital plate	Paragenitalplatte

Material examined

Eustheniidae – *Thaumatoperla flaveola*, ♀, nymph, AUSTRALIA, Victoria, (SU); *Stenoperla* sp. ♀, AUSTRALIA, Victoria, (SU).

Austroperlidae – *Austroperla neboissi*, nymph, AUSTRALIA, Victoria, (SU); *Acruroperla atra*, nymph, AUSTRALIA, Victoria, (SU).

Gripopterygidae – *Eumotoperla kershawi*, nymph, AUSTRALIA, Victoria, (SU); *Trinotoperla nivata*, nymph, AUSTRALIA, Victoria, (SU).

Pteronarcyzoidea – *Pteronarcella badia*, ♂♀, nymph, USA, Colorado, (LFS); *Pteronarcys sachalina*, ♀, nymph, KOREA, (SU); *P. reticulata*, ♂♀, USSR, Amur, (LFS); *P. californica*; ♂♀, nymph, USA, Utah, Montana, (LFS, SU).

Peltoperlidae – *Microperla brevicauda*, ♂♀, nymph, JAPAN, (LFS, SU, YI); *Cryptoperla japonica*, ♂♀, nymph, JAPAN, (SU, YI); *Peltoperla tarteri*, ♂♀, nymph, USA, West Virginia, (SU); *Peltoperlodes bisacta*, ♀, nymph, THAILAND, (LFS); *Peltoperlopsis mindanensis*, nymph, PHILIPPINE, Mindanao, (LFS); *Sierraperla cora*, ♂♀, nymph, USA, California, (SU); *Soliperla campanula*, ♂♀, nymph, USA, Oregon, (LFS, SU); *Tallaperla anna*, ♂♀, nymph, USA, Virginia, (SU); *T. maria*, ♂♀, USA, Tennessee, (LFS); *T. sp.*, nymph, USA, Virginia, (LFS); *Yoraperla uenoi*, ♂♀, nymph, JAPAN, (SU, YI); *Viehoerperla ada*, ♂♀, nymph, USA, South Carolina, (SU).

Perlodidae – *Megarcys ochracea*, ♂♀, nymph, JAPAN, (SU); *Oroperla barbara*, nymph, USA, California, (LFS); *Perlodes microcephalus*, ♂♀, nymph, GERMANY, (SU); *Sopkalia yamadae*, ♂♀, nymph, JAPAN, (SU).

Perlidae – *Calineuria stigmatica*, ♂♀, nymph, JAPAN, (SU); *Acroneuria* (s. l.) *jouklii*, ♂, nymph, JAPAN, (SU); *Oyamia lugubris*, ♂♀, nymph, JAPAN, (SU).

Chloroperlidae – *Sweltsa* sp., ♂♀, nymph, JAPAN, (SU).

Scopuridae – *Scopura longa*, ♂♀, nymph, JAPAN, Towada-ko, (SU).

Taeniopterygidae – *Brachyptera* sp., nymph, GERMANY, (SU); *Obipteryx femoralis*, nymph, JAPAN, (SU).

Nemouridae – *Amphinemura* sp., nymph, JAPAN, (SU); *Nemoura* sp., nymph, JAPAN, (SU); *Protonemura* sp., nymph, JAPAN, (SU).

Notonemouridae – *Austrocercella?* sp., nymph, AUSTRALIA, Victoria, (SU).

Capniidae – *Capnia* sp., nymph, JAPAN, (SU).

Leuctridae – *Leuctra cercia*, nymph, JAPAN, (SU).

Family group Systellognatha Enderlein

We follow here Zwick's (1980) system of the suborders and the family groups in Plecoptera. The features of Styloperlidae on his characters 1–4 and 30–36, which are described above, firmly prove that the family belongs neither to Antarctoperlaria nor to Euholognatha but to Systellognatha. His synapomorphies 4 (cervical gills present) and 8 (egg with anchor and collar) do not typically occur in Styloperlidae. They may be secondarily reduced in the family as found in the other families of Systellognatha.

The evolution of the anchor and the collar in Systellognatha eggs is still controversial. Zwick (1973, 1980) proposed the presence of the anchor and the collar as an autapomorphy of Systellognatha; that is, as an ancestral form of the group. But Stark & Stewart (1981) considered, in Peltoperlidae, the absence of the anchor and the collar to be more primitive than their presence. The junior author (1988) accepted the view of Stark & Stewart and proposed, further in Perloidea, the same direction of evolution. The latter two views necessitate many independent developments of the collar and the anchor within Systellognatha, because the eggs without anchor and collar are scattered in many families, subfamilies and tribes of the group. Several independent developments may have occurred in Peltoperlidae, because of the diversity in the anchor forms (*Sierraperla*, *Yoraperla*, Stark & Stewart 1981; *Cryptoperla*, Uchida & Isobe 1988). But, in Perloidea, the general forms of the anchor and the collar seem to the senior author too uniform to postulate many independent developments, whereas the junior author regards the uniformity as a convergence. More detailed study is needed to determine whether the anchors and the collars are homologous. We follow here tentatively Zwick's (1973, 1980) view.

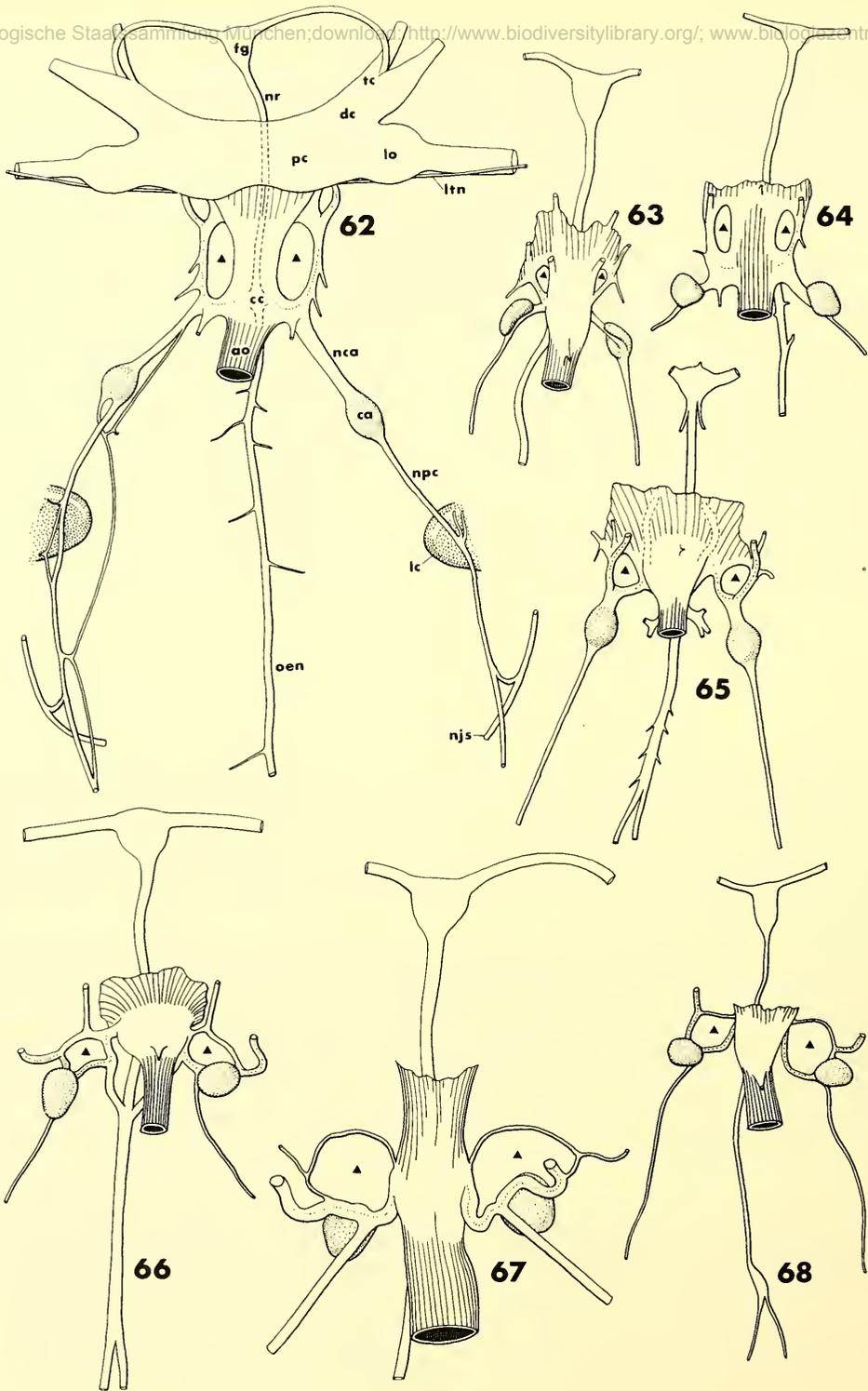
Superfamily Pteronarcyzoidea Enderlein

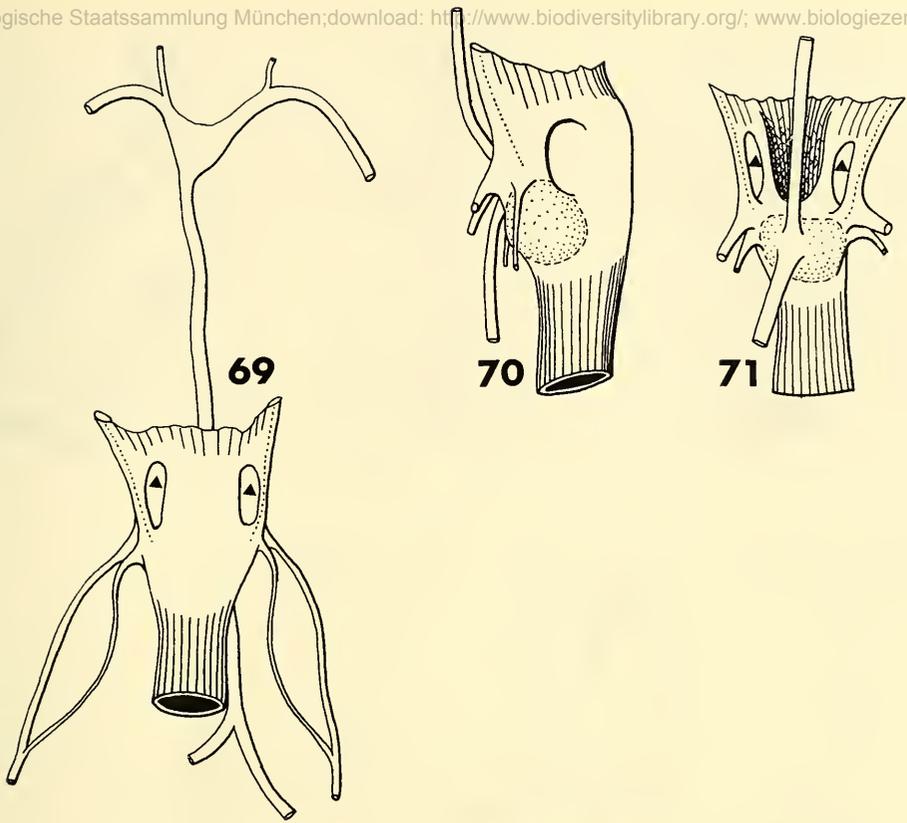
(not sensu Illies 1966)

1. Zwick (1973, p. 32, 33) confirmed that paired corpora allata in Antarctoperlaria and Systellognatha are more primitive than an unpaired corpus allatum in Euholognatha. He considered the unpaired corpus an autapomorphy of Euholognatha (Figs. 69–71: his description of the corpus allatum of *Scopura* is not exact; the corpus is already incorporated into the aorta as in the other families of Euholognatha). Further details on the arrangement of paired corpora allata have never been comparatively studied in Plecoptera.

We found a clear difference in the corpora allata of Systellognatha and classify them into two types: a) corpora allata widely separated from each other (Perlodidae, *Oroperla*, *Sopkalia*, *Megarcys*, *Perloides*; Perlidae, *Calineuria*, *Oyamia*; Chloroperlidae, *Sweltsa*: Figs 65–68); b) corpora allata in contact with each other mesally and with corpora cardiaca anteriorly (Pteronarcyzoidea, *Pteronarcella*, *Pteronarcys sachalina*, *P. californica*; Styloperlidae, see above; Peltoperlidae, *Microperla*, *Cryptoperla*, *Yoraperla*: Figs 72–80). In both types, some minor variations may be found: a') in *Sopkalia*, the corpora allata are more widely separated from each other and from the corpora cardiaca (Fig. 65); b') in Pteronarcyzoidea, the corpora allata are sometimes located only closely, not in contact medianly (Fig. 73); b'') the corpora allata of *Microperla* (Fig. 79) are fused mesally into an unpaired transversely elongate corpus.

The observation in Antarctoperlaria (Figs 62–64) suggests the type a) is plesiomorphic. The corpora allata of Eustheniidae (*Thaumatoperla*, *Stenoperla*; Fig. 62) are separated very widely from each other, located far behind the corpora cardiaca about at the middle between corpora cardiaca and the laterocervicalia on which the nervus prothoracalis collateralis innervates the musculus cervicopharyngealis. The corpora allata of Austroperlidae (*Austroheptura*, Fig. 63) and Gripopterygidae (*Eunotoperla*, *Trinotoperla*; Fig. 64) are similar to the type a). They appear to be an intermediate feature between the type of Eustheniidae and the type b). The features of the other insect orders, especially of



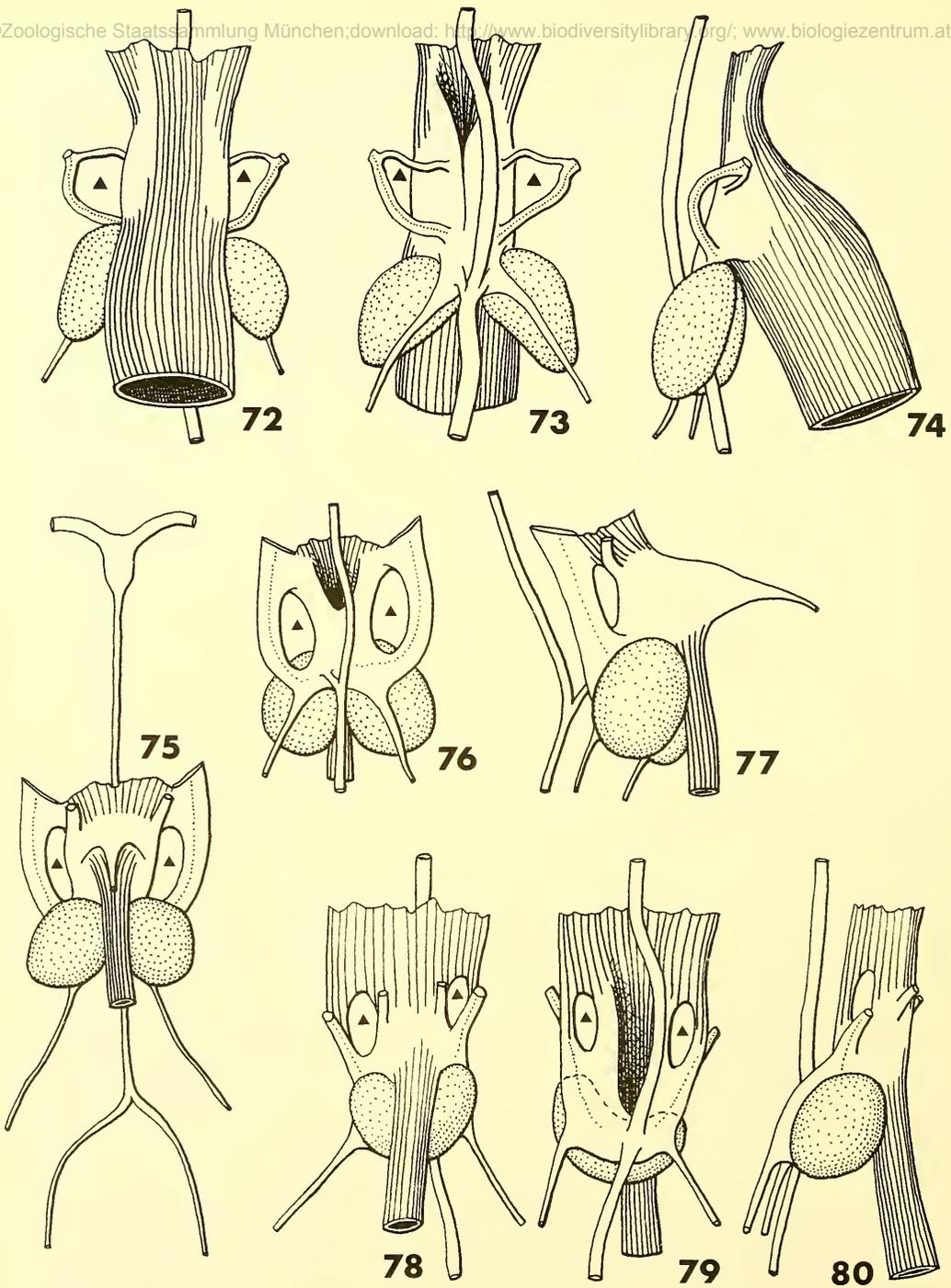


Figs 69–71. Retrocerebral system of *Scopura* (Scopuridae), dorsal (69), lateral (70) and ventral (71) views. For symbols, see the legend of Figs 62–68.

Ephemeroptera (the corpora allata located far behind the corpora cardiaca; Hanström 1941) and their ontogenetic origin (Pflugfelder 1958) support the trend from the widely separated corpora to the closely located ones. Accordingly, we consider the type b) a synapomorphy for Pteronarcyidae, Styloperlidae and Peltoperlidae. The unpaired corpus allatum of Euholognatha, which is incorporated in the aorta, has probably arisen independently of this lineage.

The nervous connection between the brain, corpora cardiaca and corpora allata also represents some variations in Plecoptera. But they are possibly affected by the feeding habits through the development of the musculus verticopharyngealis. In carnivorous stoneflies, the muscle tends to be thick and pushes caudad the main nerve from the corpora cardiaca to the brain (*Thaumatoperla*; *Stenoperla*; *Eu-*

Figs 62–68. Retrocerebral systems of Antartoperlaria and Perloidea, dorsal views. 62. *Thaumatoperla* (Eustheniidae); 63. *Austroheptura* (Austroperlidae); 64. *Eumotoperla*, (Gripopterygidae); 65. *Sopkalia* (Perlodidae); 66. *Perlodes* (Perlodidae); 67. *Calineuria* (Perlidae); 68. *Sweltsa* (Chloroperlidae). Abbreviations: ao: aorta; ca: corpus allatum; cc: corpus cardiacum; dc: deutocerebrum; fg: frontal ganglion; lc: laterocervicalia; lo: lobus opticus; ltn: lateral tegumental nerve of head; nca: nervus corporis allati; njs: nervus jugularis secundus; npc: nervus prothoracalis collateralis; nr: nervus recurrens; oen: oesophageal nerve; pc: protocerebrum; tc: tritocerebrum. Symbols: ▲: location of musculus verticopharyngealis; striped: aorta; dotted: corpus allatum; white: nerves and innervated parts of aorta; dotted line: the main nerve from corpora cardiaca to brain.



Figs 72–80. Retrocerebral systems of Pteronarcyzoidea. 72–74. *Pteronarcys californica* (Pteronarcyidae); 75–77. *Yoraperla* (Peltoperlidae); 78–80. *Microperla* (Peltoperlidae). 72, 75, 78. dorsal views; 73, 76, 79. ventral views; 74, 77, 80. lateral views. For symbols, see the legend of Figs 62–68.

nōtoperla; *Trinotoperla*, though phytophagous; Perloidea: dotted line in Figs 62, 64–68). The nerve runs, at first, postero-laterally or laterally behind the muscle, branches off the nervus corporis allati (Eustheniidae, Gripopterygidae, *Sopkalia*) or bears the corpus allatum (Perloidea except *Sopkalia*) and then curves anteriorly lateral to the muscle and runs dorsally to the brain. In phytophagous stoneflies, on the other hand, the muscle is thin and does not push the nerve caudad (Austroperlidae, Scopuridae, Pteronarcyioidea, dotted line in Figs 63, 69–80). The nervus corporis allati originates directly from the corpora cardiaca and the nerve to the brain is directed antero-laterally. Accordingly, these features may have often changed by the thickness of the muscle and are insufficient for a discussion on the higher phylogenetic relationships.

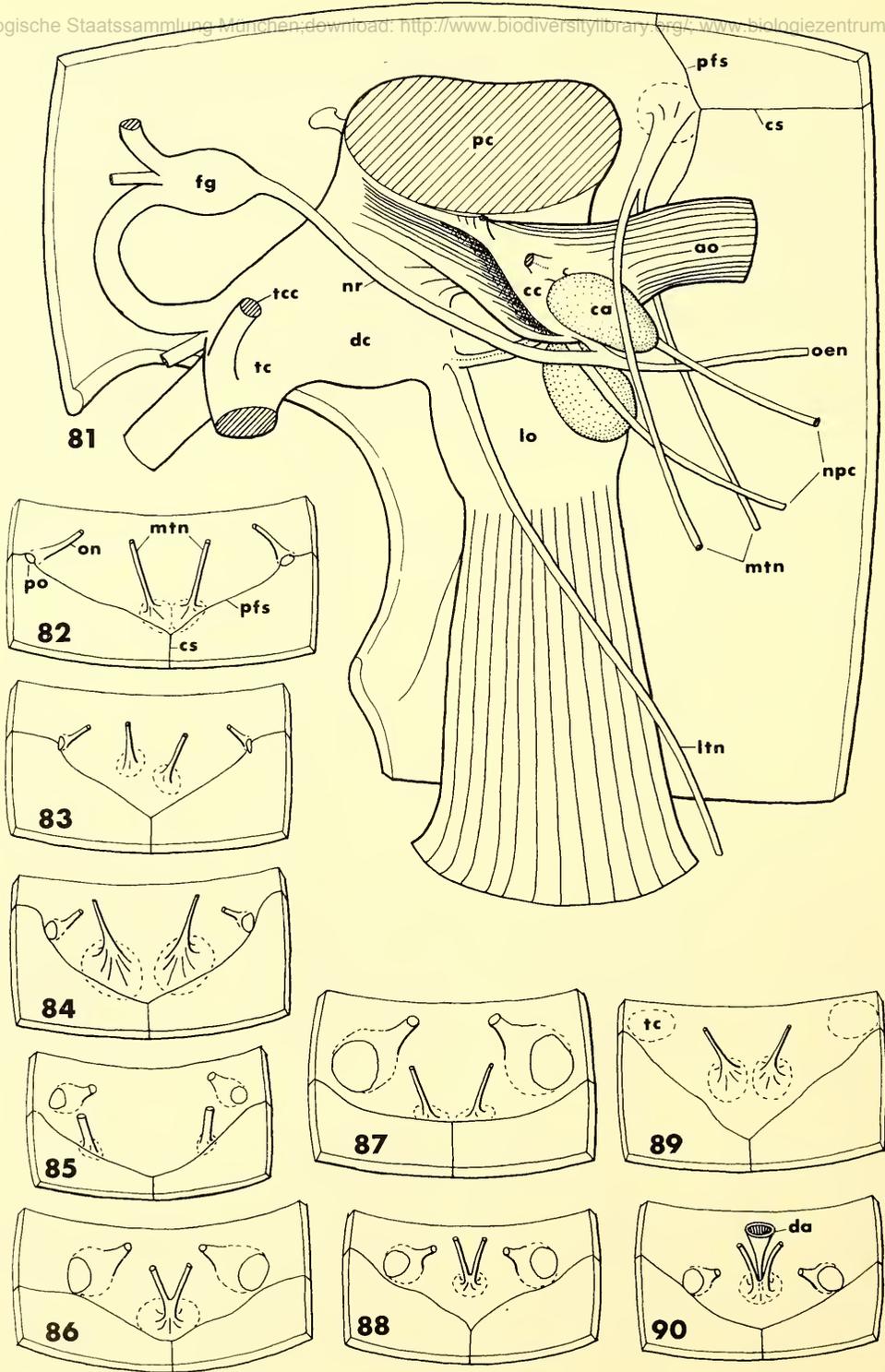
The dorsal wall of aorta above corpora cardiaca is peculiarly produced dorsally in *Cryptoperla* and *Yoraperla* (Peltoperlidae, Fig. 77, but not in *Microperla*, Fig. 80). The projection is tapered apically and prolonged and attached to the dorsal sclerite of head (vertex) just before the fused end of the median pair of tegumental nerves (Fig. 90, see also the character 2). Similar projections are also found in Perlodidae (*Perlodes*, *Sopkalia*, Figs 65, 66), Chloroperlidae (Sweltsa, Fig. 68) and Austroperlidae (*Austroheptura*, Fig. 63) but they are attached to the brains. In Pteronarcyidae (*Pteronarcys*), the projection occurs far behind on the aorta in prothorax and is attached to the antecosta of pronotum. The occurrence of the projection is occasional even within a single species (i. e., *Perlodes microcephalus*; three with it, three without it, in six examined nymphs) and sometimes very small and inconspicuous, although it occurs always conspicuously in *Cryptoperla* and *Yoraperla*. We believe the projection is only a structure to fix the aorta to the dorsal sclerite or brain, which may be developed and reduced independently along many phylogenetic lineages. The conspicuous development in Peltoperlidae may be attributed to the peculiar form of head, which is strongly shortened and bent ventrad.

2. Two pairs of tegumental nerves (Figs 81–90, ltn, mtn) occur in the occiputs of all the representatives of Plecoptera we examined, except *Sweltsa* (Chloroperlidae, without the median pair). The lateral pair (ltn), which runs from the brain to the postero-mesal sides of compound eyes, was described by Chisholm (1962) and is uniform through all representatives of Plecoptera examined here. The median pair (mtn) runs from the lateral sides of tentorium above to the dorsal integument postero-mesal to the posterior ocelli. Its origin is not yet clear, but it may possibly be from the nervus jugularis primus. The tegumental nerve runs near the retrocerebral system but is never connected with it.

The dorsal ends of the median nerves represent two types in Plecoptera: a) the ends separated from each other (Eustheniidae, *Thaumatoperla*; Austroperlidae, *Austroheptura*; Gripopterygidae, *Eunotoperla*, *Trinotoperla*; Scopuridae, *Scopura*; Perlodidae, *Sopkalia*, *Perlodes*; Perlidae, *Calineuria*, *Oyamia*: Figs 82–85, 87, 89); b) the nerves fused into each other mesally above aorta, then terminating together on the integument (Eustheniidae, *Stenoperla*; Pteronarcyidae, *Pteronarcys californica*; Styloperlidae, *Cerconychia*; Peltoperlidae, *Cryptoperla*, *Microperla*, *Yoraperla*: Figs 81, 86, 88, 90). This distribution in the system suggests that the type a is primitive, because it occurs in most families of Plecoptera including primitive ones. Accordingly, the feature b is adopted as a synapomorphy for Pteronarcyidae, Styloperlidae and Peltoperlidae; the further occurrence in *Stenoperla* may have arisen independently.

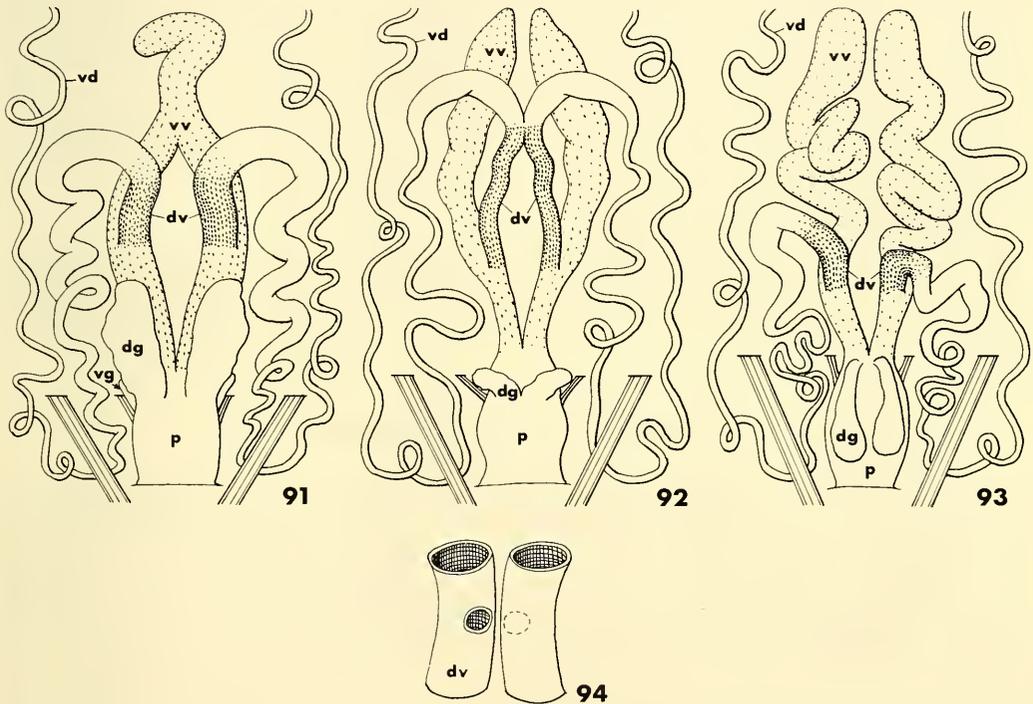
Family Pteronarcyidae Enderlein

3. Nelson & Hanson (1971, p. 149, fig. 21) proposed a pair of lateral sclerites on laterally expanded arolium of pretarsus as an autapomorphy of Pteronarcyidae. The sclerites are mostly hidden under claws and no stonefly systematist except them has given attention to the character. We reconfirmed that the autapomorphy occurs only in Pteronarcyidae within Plecoptera.



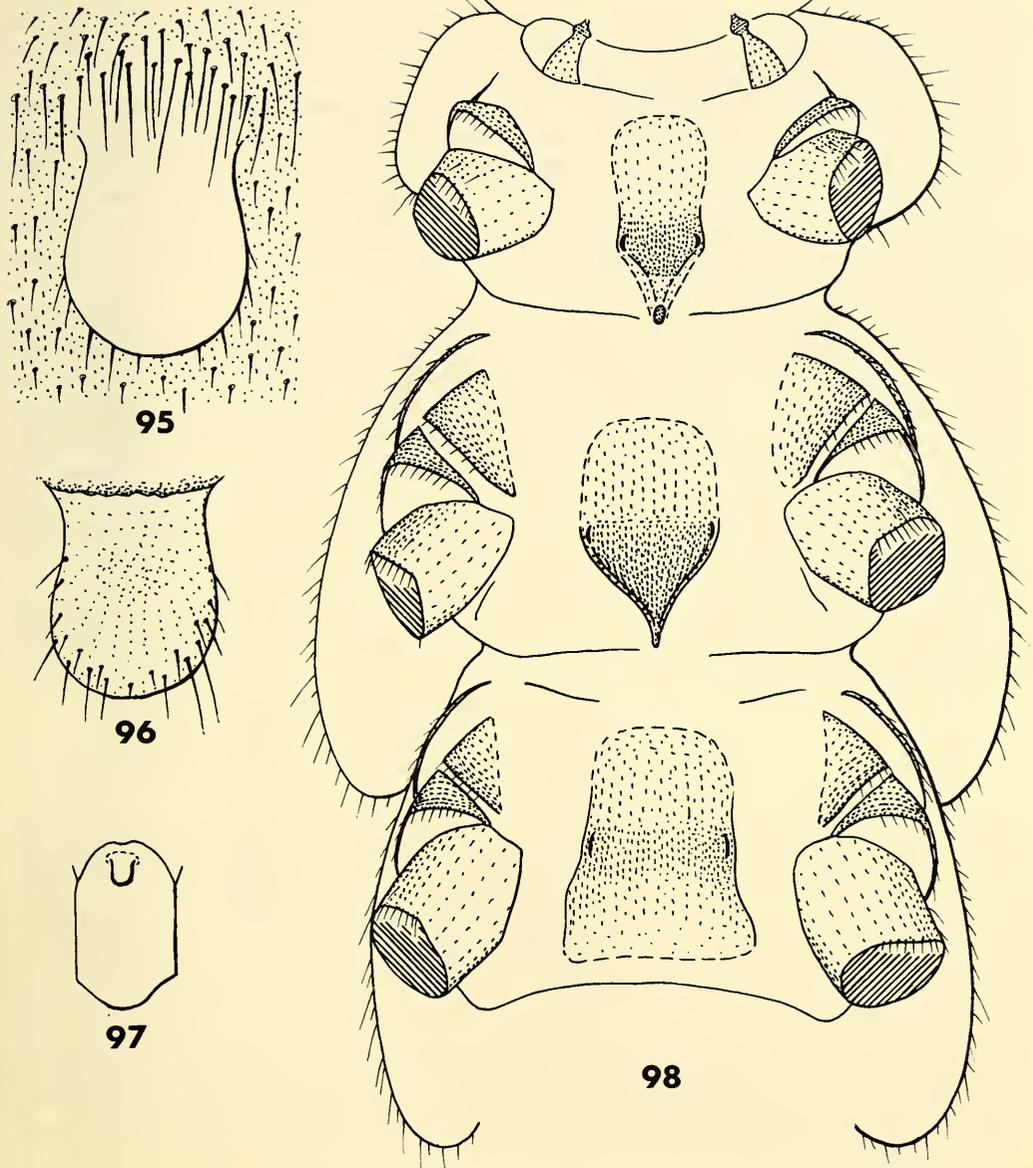
4. Zwick (1980) regarded a feature of abdominal ganglia as a synapomorphy (No. 40) for Peltoperlidae and Perloidea; that is, less than eight individual abdominal ganglia, at least an additional fusion of ganglia occurring at the caudal end of the central nervous system. But the feature occurs only in Perloidea (reconfirmed in *Oroperla*, *Sopkalia*, *Calineuria* and *Oyamia*) and therefore his argumentation necessitates an improbable reversal in Peltoperlidae (the eighth ganglion again separated from the caudalmost one). Accordingly, we restrict the synapomorphy to Perloidea (No. 19).

On the other hand, the second abdominal ganglion is fused into metathoracic one (already including the first abdominal one) in Styloperlidae (Fig 43, 44), Peltoperlidae and Perlidae. The fusion has reduced the number of ganglia also less than eight. But the reduction has followed different manner



Figs 91–94. Posterior parts of internal genitalia of Perloidea. 91. *Sopkalia* (Perlodidae); 92, 94. *Acroneuria* (s. lat.) *jouklii* (Perlidae); 93. *Oyamia* (Perlidae). 91–93, dorsal views; 94. dorso-lateral view of anterior end of dorsal seminal vesicle, the connection of the vesicles is cleaved off. Abbreviations: dg: dorsal accessory gland; dv: dorsal seminal vesicle; p: penis; vd: vas deferens; vg: ventral accessory gland; vv: ventral seminal vesicle.

Figs 81–90. Nervous system in dorso-median and right dorsolateral part of *Pteronarcys californica* (Pteronarcyidae) head (81. ventro-lateral view) and dorsal ends of median tegumental nerves in Plecoptera heads (82–90. postero-ventral views). 82. *Thaumatoperla* (Eustheniidae); 83. *Austrobeptura* (Austroperlidae); 84. *Eunotoperla* (Gripopterygidae); 85. *Perlodes* (Perlodidae); 86. *Pteronarcys californica* (Pteronarcyidae); 87. *Calineuria* (Perlidae); 88. *Cerconychia* (Styloperlidae); 89. *Scopura* (Scopuridae); 90. *Yoraperla* (Peltoperlidae). Abbreviations: cs: coronal suture; da: dorsal projection of aorta; mn: median tegumental nerve of head; on: ocellar nerve; pfs: post-frontal suture; po: posterior ocellus; tcc: tritocerebral commissure; for the other abbreviations, see the legend of Figs 62–68.



Figs 95–98. Vesicle on abdominal sternite 9 (95–97) and nymphal thoracic sternite (98) of *Microperla*. 95, 96. details of the vesicle (95. ventral; 96. dorsal views); 97. the whole sternite.

We prefer the earlier view of Zwick to Rupprecht's on the development of hammers in Systellognatha. Zwick considered the vesicle-like hammer in Peltoperlidae an intermediate form from the vesicle to the hammer, whereas Rupprecht assumed a secondary convergence from the hammer. The vesicle of *Microperla* (Figs 95–97), which both Rupprecht and Zwick did not examine, supports Zwick's view. The vesicle is located near the front margin of sternite 9, free from the sternite and movable. The hairs on and around the vesicle are directed caudad. These features agree well even with Rupprecht's

definition of the vesicle in Euholognatha. Such a strict correspondence could not easily be regarded as a result of convergence. Accordingly, we homologize them again; that is, we accept the latter part of the synapomorphy 3 of Zwick (1980) for Arctoperlaria.

The “hammers” or “brushes” on the abdominal sternites except the ninth, however, might have developed independently (e. g., that of *Isoperla* on the sternite 8). They could be homodynamous to the proper hammer or vesicle (Zwick 1973; Rupperecht 1976). But the homonomous “hammers” on two or three sternites occur only in apparently derived representatives of Systellognatha (*Cultus*, *Isogenoides*) and never in a primitive stonefly together with the proper hammer or vesicle. This fact is inconsistent with the homodynamy. The “hammer” of Pteronarcyidae (Stark & Szczytko 1982) also appears to be a secondary structure.

7. A pair of spurs on the apex of tibia (Fig. 111) occurs in most families of Plecoptera and represents a primitive state (Zwick 1980). The spurs do not occur in Styloperlidae and most Peltoperlidae (*Cryptoperla*, *Peltoperla*, *Peltoperlodes*, *Peltoperlopsis*, *Sierraperla*, *Soliperla*, *Tallaperla*, *Viehooperla*, *Yoraperla*) within Systellognatha (though in Chloroperlinae nymphs also inconspicuous). The reduction could be a synapomorphy for Styloperlidae and Peltoperlidae. But the shapes of fine setae at the apices of tibiae are different from each other (Styloperlidae, trifurcate, Fig. 36; Peltoperlidae, simple) and *Microperla* (Peltoperlidae) normally represents the spurs. These facts suggest that they were reduced independently in the two lineages. Accordingly, the reduction of the spurs and presence of the trifurcate setae are proposed as an autapomorphy of Styloperlidae and the reduction and presence of the simple setae are considered that of most peltoperlids (the synapomorphy 16).

8. The median part of abdominal sternite 10 is sclerotized to a unique X-shaped structure (Figs 14, 19, 55, 60) in Styloperlidae. The feature appears to have been derived from the normal segmental sternite as found in the other Plecoptera.

Family Peltoperlidae Claassen

9, 10. Zwick (1980) proposed three autapomorphies (No. 52–54) of Peltoperlidae, detailing his earlier one (Zwick 1973, No. 49, cockroach-like nymph): a) head strongly shortened, partly covered by prothorax, with two ocelli; b) basisterna of the nymphal pro- and mesosterna flat, extended posteriorly and covering the furcal pits (also proposed by Stark & Stewart 1981); c) spinasternum of the prothorax combined with the furcasternum. Our observation also confirmed that most Peltoperlidae (*Cryptoperla*, *Peltoperla*, *Peltoperlodes*, *Peltoperlopsis*, *Sierraperla*, *Soliperla*, *Tallaperla*, *Viehooperla*, *Yoraperla*) share all the apomorphies. But *Microperla* represents only the feature c) (Fig. 98), although the habitus of the nymph is typical for Peltoperlidae (cockroach-like, Kawai & Isobe 1985, fig. 4/2). Accordingly, we propose the habitus again as an autapomorphy for the family (9). One (c) of Zwick’s (1980) is accepted for the second autapomorphy (10). The other two autapomorphies (a, b) of Zwick (1980) are transferred to those of Peltoperlinae (13, 14) below.

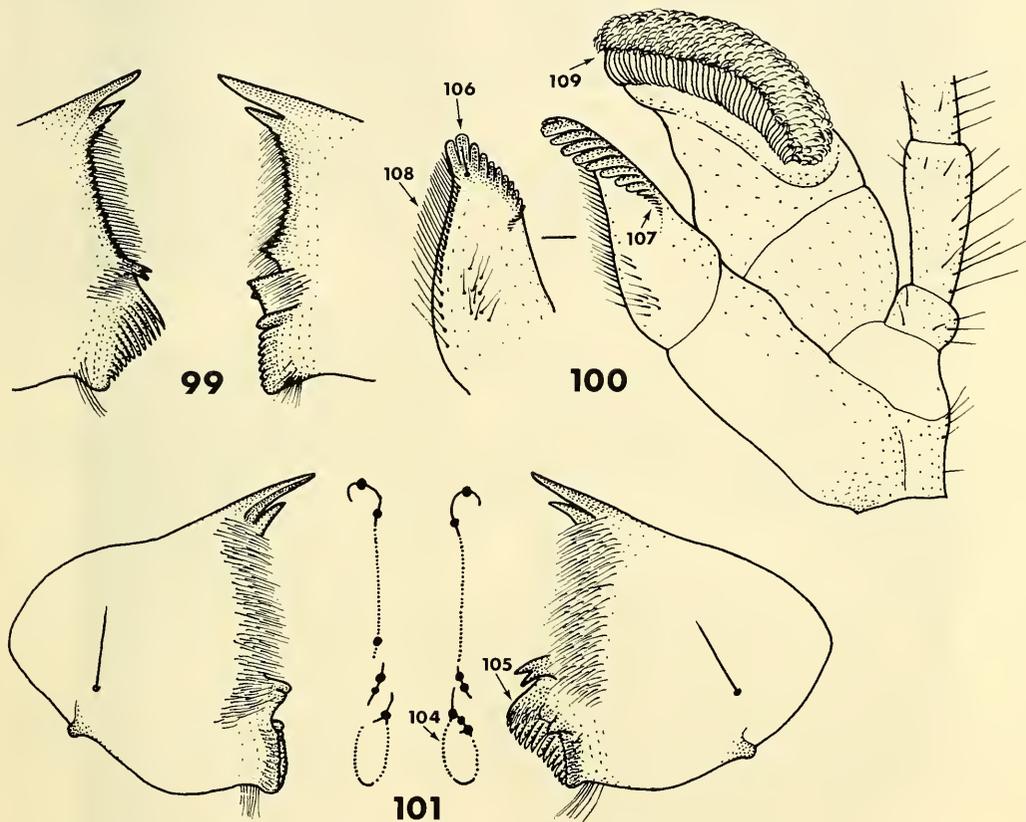
Subfamily Microperlinae, nov.

Type genus: *Microperla* Chu, 1928.

Chu (1928) and Kawai (1958) clearly described the presence of three ocelli in *Microperla geei* from China and *M. brevicauda* from Japan respectively, whereas only two ocelli occur in the other genera of Peltoperlidae. But subsequent workers have never paid attention to this characteristic of *Microperla*. Zwick (1980) proposed, accordingly, the reduction of the anterior ocellus as a part of an autapomorphy (No. 52) of Peltoperlidae. Recently, the junior author discovered the nymph of *M. brevicauda*. The nymph is distinguished by many features from the other genera of Peltoperlidae. This dis-

covery results in the change of the autapomorphies of the family proposed by Zwick (1980) and Stark & Stewart (1981) and leads to the establishment of a new subfamily.

The egg of *M. brevicauda* (Isobe 1988) is superficially similar to that of *Yoraperla* (Pelotoperlinae) in shape (flat, wafer-like) and fine chorion structure (with hexagonal meshes). Dr. B. P. Stark (in litt.) pointed out the similarity between *Microperla* and *Sierraperla* (Peltoperlinae) in their lack of membranous processes on meso- and metascutella. But we regard these similarities as convergences. It necessitates still more convergences (in the characters 13–16) to postulate the monophyly by these similarities.



Figs 99–101. Nymphal mouthparts of *Microperla*. 99, 101. mandibles, dorsal (99) and ventral (101) views with schematic inner views of tooth arrangement (101. middle); 100. maxilla, ventral view with inner view of lacinia. Arrows refer to the locations of Figs 104–109.

11. The mouthparts of *Microperla* nymph are strongly transformed from the general feature of phytophagous stoneflies: mandible (Figs 99, 101) extended longitudinally and strongly sclerotized only at the anterior end and the posterior third which contains a mola, a tooth row between the sclerotizations with a dense band of long hairs ventrally, ventral base of mandible with a long hair near the condyle; molae (Figs 102, 103) with thorn carpet surfaces (“comb-like surface” of Stark & Stewart 1981), the left one with finely branched flagella (Fig. 105) at the anterior end and with long comb-like teeth on the dorsal edge, the teeth flattened and extended dorso-ventrally at the bases and with postero-dorsal and antero-ventral rows of spines (Fig. 104); lacinia (Fig. 100) with a ventro-apical row of 11 flat

teeth, the row prolonged to a short row of hairs ventrally, inner base of the second apical tooth with an unbranched sensillum (Fig. 106), the dorsal edge with a fine tooth and a long row of hairs; galea (Fig. 100) with a large band of long hairs which are recurved and bearing comb-like apices (Fig. 109); some or many flagella (Fig. 108) branching off apically from each thread of hairs on the mandible and the dorsal edge and the mesal side of lacinia; each hair at the ventral side of lacinia (Fig. 107) also with a row of offshoots. From these features, we selected the autapomorphy 11 in Table 1, which is unique in Plecoptera.

The mouthparts must be adapted to the feeding of epilithic algae. According to Arens (in press), the feature may function as follows. 1) The hair band on galea (Figs 100, 109) scrapes algae off a stone and holds them in the mouthparts. 2) The hairs with flagella on mandible and lacinia (Fig. 108) capture the algae and lead them to the molae. 3) The thorn carpet surfaces of molae (Figs 102, 103) concentrate the suspension of algae as a filter, before they shred the algae. Some of these features are also found in other stoneflies (Stark & Stewart 1981, Arens, in press), but *Microperla* has far better adapted its mouthparts to the feeding of epilithic algae than the others. It is a good example of convergence with the other scrapers, especially with some Ephemeroptera, as shown by Arens (in press).

12. The corpus allatum of *Microperla* (Figs 78–79) is unpaired, transversely elongate and located directly behind the corpora cardiaca. This feature is found neither in Peltoperlinae nor in any of the other families of Plecoptera and must have been derived from the closely located paired corpora allata as in Pteronarcyidae, Styloperlidae and Peltoperlinae (Figs 45–47, 72–77). See also the character 1.

Subfamily Peltoperlinae Claassen

We restrict to here the three features (14–16) that have been proposed as the autapomorphies of Peltoperlidae. *Microperla* still retains primitive states in these characters.

13, 14. See the character 9, 10.

15. See Stark & Stewart (1981, p. 309).

16. See the character 7.

Superfamily Perloidea Latreille

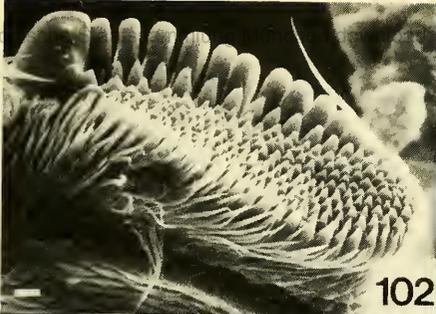
17, 18. We reconfirmed and follow two of the three autapomorphies of Perloidea proposed by Zwick (1980, No. 55, 57).

19. This autapomorphy is adopted from the character 40 of Zwick (1980). See the character 4.

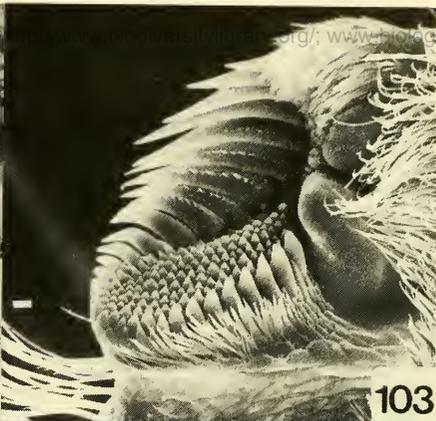
Inadequate characteristics

Reduction of frontoclypeal suture occurs only in Peltoperlidae and Perloidea within Plecoptera and was considered a synapomorphy for the group (Zwick 1980, No. 44). But the head capsules of most Peltoperlidae (Peltoperlinae) are peculiarly shortened and are bent downward and accordingly differ greatly from Perloidea. This difference suggests that the reduction in Peltoperlidae may

Figs 102–109. SEM micrographs of nymphal mouthparts of *Microperla*. 102, 103. right (102) and left (103) molae, ventro-inner views; 104. comb-like teeth on left mola, inner view; 105. anterior end of left mola, ventro-inner view; 106. apex of left lacinia, inner view; 107, 108. hairs on ventral (107) and dorsal (108) edges of lacinia, ventral (107) and inner (108) views; 109. hairs on galea, ventral view. Scales: 5 μm . For the locations of Figs 104–109, see Figs 100, 101.



102



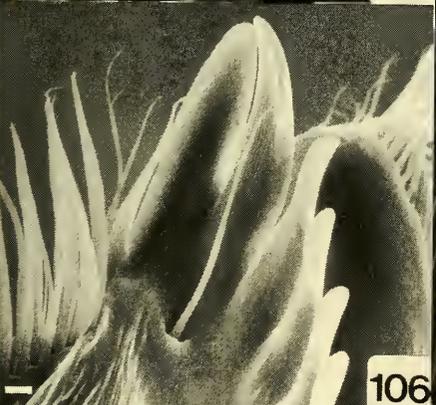
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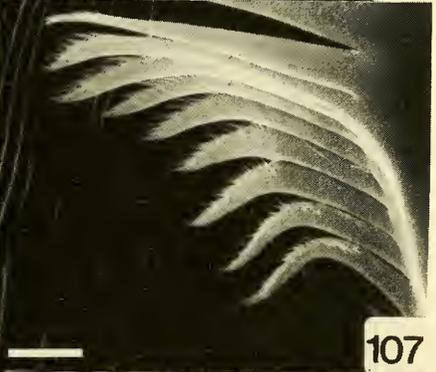
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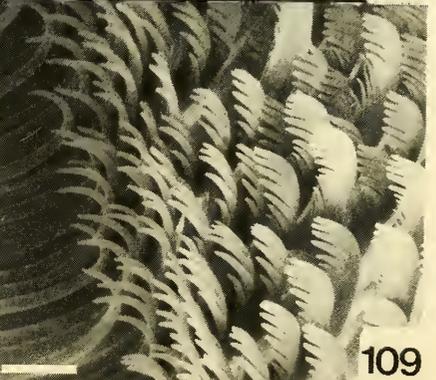
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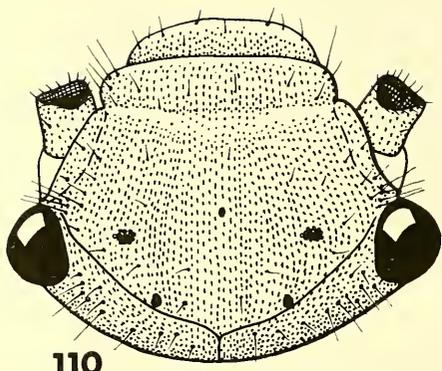
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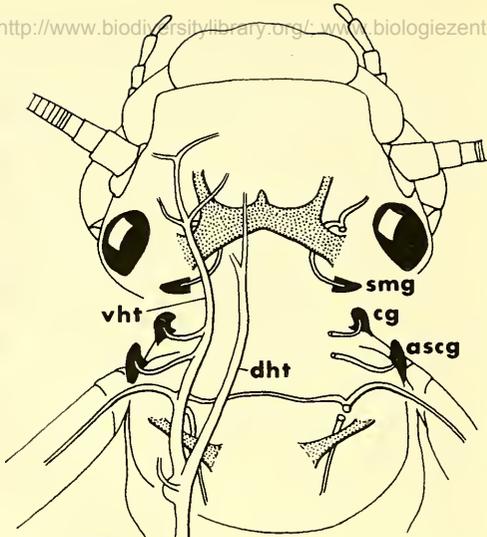
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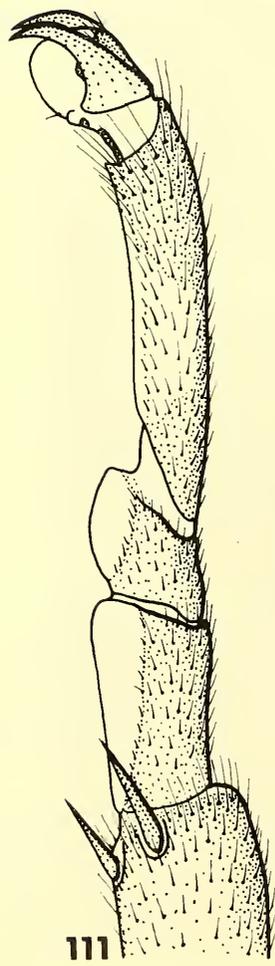
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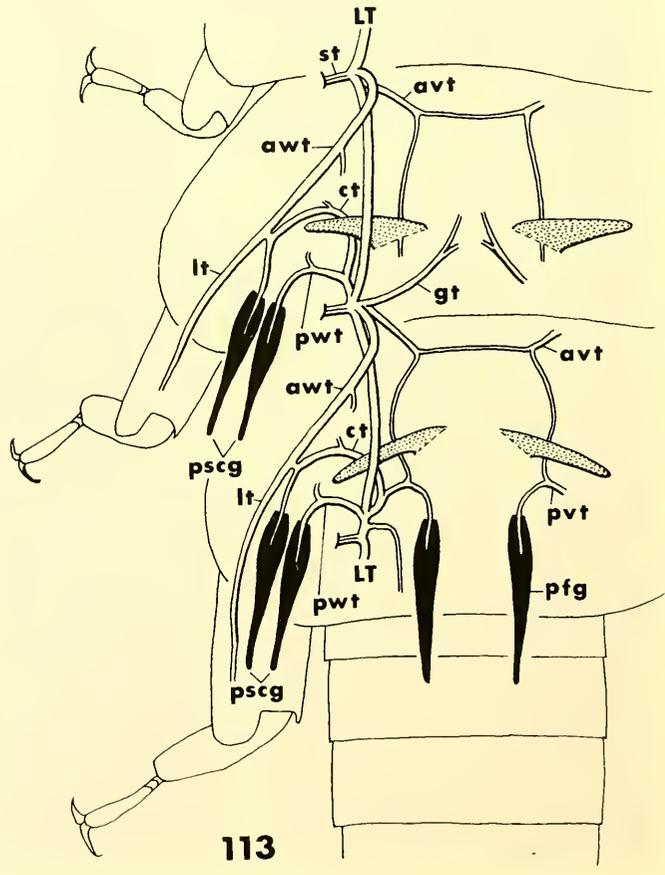
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112 LT



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113

be affected by the peculiar form of head and has occurred independently of that in Perloidea. This assumption is supported by the remnant of the suture in *Microperla* (Peltoperlidae) nymph (Fig. 110, as a pair of light bands), whose head is rather normal.

Thorn carpet surface of nymphal mola. Stark & Stewart (1981 as “comb-like surface”) proposed the feature as an autapomorphy of Peltoperlidae. But the feature was further found in *Brachyptera* (Taeniopterygidae) and *Trinotoperla* (Gripopterygidae) by Arens (in press). According to him, the feature may have arisen in many lineages as a convergence; it was also found in *Baetis* (Ephemeroptera).

Tridentate lacinia of nymph is considered a feature which suggests the affinity between Pteronarcyidae and Peltoperlidae (Stark & Stewart 1981). But the feature is apparently plesiomorphic or even the ancestral form of Plecoptera, because it occurs in almost all phytophagous families of Plecoptera including primitive ones (Austroperlidae, *Austroheptura*, *Acruroperla*; Styloperlidae, *Cerconychia*, Fig. 28; Scopuridae, *Scopura*; Taeniopterygidae, *Obipteryx*; Nemouridae, *Amphinemura*, *Nemoura*, *Protonemura*; Notonemouridae, *Austrocercella*; Capniidae, *Capnia*; Leuctridae, *Leuctra*).

The trachea leading from head to cervical gills was regarded as an autapomorphic feature of Pteronarcyidae (Zwick, 1973, No. 37; 1980, No. 38). But it tracheates only the median two of three pairs of the gills, which occur only in Pteronarcyidae within Systellognatha. The character is therefore unassessable in the other families and inadequate as an autapomorphy. Moreover, the presence of similar tracheae leading to submental gills in Perlodidae (*Oroperla*, *Sopkalia*, *Megaracys*; Fig. 112) suggests that the trachea may be plesiomorphic in Systellognatha and subsequently reduced in most representatives in the group.

Short basal segments of tarsus was considered an autapomorphy of Perloidea (Zwick 1973, No. 54) or a synapomorphy for Peltoperlidae and Perloidea (Zwick 1980, No. 43). But some genera of Perlodidae (*Sopkalia*, *Megaracys*) still retain long basal segments of tarsus (Fig. 111) like Pteronarcyidae and the other primitive families of Plecoptera. Accordingly, the short segments must have been independently derived at least in two lineages (Perloidea and Pteronarcyidae) within Systellognatha.

Postfurcal gills were regarded as an autapomorphic feature of Pteronarcyidae (Zwick 1973, No. 38; 1980, No. 39). But he could not surely homologize the thoracic gills of Peltoperlidae to those of the other families in Systellognatha. The gills are here homologized by observing the tracheation (Fig. 113). The postfurcal gills (pfg) occur also in Peltoperlidae. The tracheation from the posterior ventral trachea is the same as in Pteronarcyidae (Zwick 1973, p. 111, fig. 30). It is not clear when the postfurcal gills developed in the evolution of Systellognatha, because they do not occur in most extant representatives of the group.

Less than eight individual abdominal ganglia. See the character 5 above.

The reduction of segmental abdominal gills was considered a synapomorphy for Peltoperlidae and Perloidea (Zwick 1973, No. 40, 1980, No. 41). Only one species (*Oroperla barbara*) within the group represents the gills (seven pairs) against the synapomorphy. Accordingly, Zwick (1973) considered the occurrence an atavism. However, we prefer to consider it the retention of the plesiomorphic segmental gills. The reasons are as follows. 1) Some genera of Perlodidae including *Oroperla* may represent many primitive features; e. g., many crossveins on wings, long basal segments of tarsus, cervical gills, complex structure of epiproct which is similar to the ground plan of Systellognatha. 2)

Figs 110–113. Nymphal head of *Microperla* (110. Peltoperlidae), apex of tibia and tarsal segments of *Sopkalia* (111. Perlodidae) and nymphal tracheation in head and prothorax of *Oroperla* (112. Perlodidae) and in meso- and metathorax of *Tallaperla* (113. Peltoperlidae). Abbreviations: ascg: anterior supracoxal gill; avt: anterior ventral trachea, awt: anterior wing trachea; cg: cervical gill; ct: coxal trachea; dht: dorsal head trachea; gt: gut trachea leading to proventriculus; LT: lateral trunk; lt: leg trachea; pfg: postfurcal gill; pscg: posterior supracoxal gill; pvt: posterior ventral trachea; pwt: posterior wing trachea; smg: submental gill; st: spiracular trachea (closed in nymph); vht: ventral head trachea.

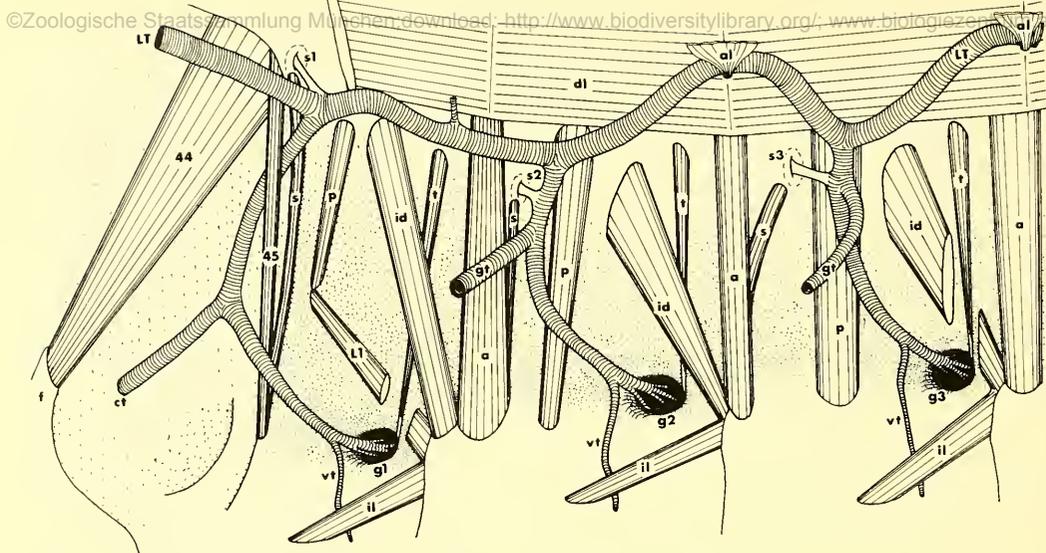


Fig. 114. Tracheation and musculature in the pleural region of basal (1–3) abdominal segments of *Oroperla*. Ventral longitudinal muscles are removed. Abbreviations: a: anterior dorsoventral muscle; al: alary muscle of heart; ct: coxal trachea; dl: dorsal longitudinal muscle; f: metafurca; gt: gut trachea; g1, g2, g3: gills of abdominal segments 1, 2, 3; id: intersegmental dorsoventral muscle; il: intersegmental longitudinal muscle; LT: lateral trunk; L1: longitudinal muscle of sternite 1, the origin on metasternum is shifted laterad with that of postspiracular dorsoventral muscle; p: postspiracular dorsoventral muscle; s: spiracular muscle; s1, s2, s3: spiracles of abdominal segments 1, 2, 3; t: tergal muscle of gill; vt: ventral trachea.

The musculature of the gills (Zwick 1973, p. 115; reconfirmed, Fig. 114) is the same as that of Pteronarcyidae and the tracheation (Fig. 114) is also the same as that of the other families with abdominal gills (both the musculature and tracheation of the segments 4–7 of *Oroperla* are the same as those of the segments 2 and 3 in Fig. 114). 3) The tergal muscle of gill (Fig. 114, t) is also found in *Sopkalia* in the basal two abdominal segments. Their pleural regions represent no gill but are expanded to membranous swellings. It suggests that the gills of *Oroperla* are not an only exception.

Accordingly, the abdominal gills must have been reduced in at least two lineages within Systellognatha (Perlodidae except *Oroperla* + Chloroperlidae, Styloperlidae + Peltoperlidae) or incorporated into the thorax in Perlidae (Zwick 1973, p. 113). Zwick (1973) further suggested that a pair of metasternal gills of Peltoperlidae may have originated from abdominal gills, or derived independently. But we homologize it to the postfurcal gill of Pteronarcyidae. See also postfurcal gills above.

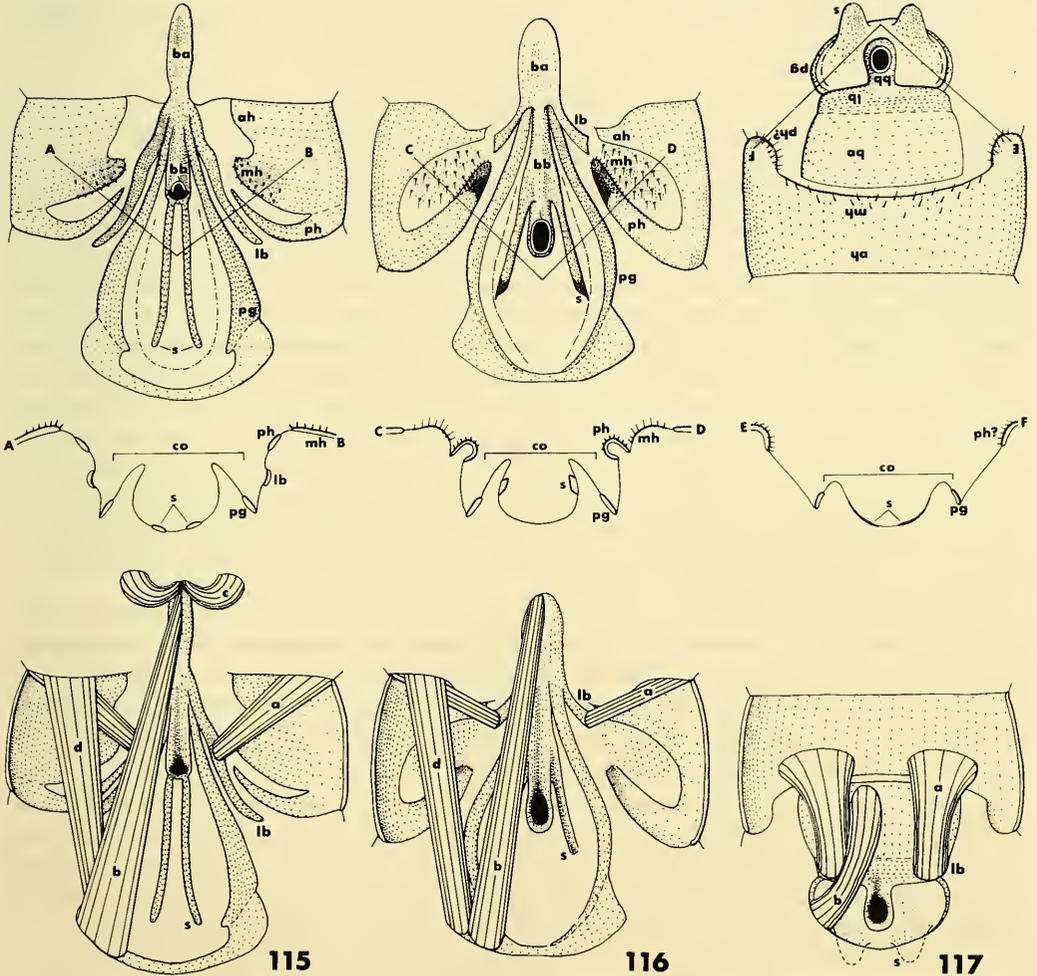
Reduction of the hammer on male abdominal sternite 9 was proposed as an autapomorphy of Pteronarcyidae (Zwick 1973, No. 36; 1980, No. 37). But he admitted, at the same time, the inadequacy of the characteristic to the reconstruction of phylogeny within Systellognatha (Zwick 1973, p. 185). We follow his latter attitude and hesitate to adopt it as an autapomorphy. See also the character 6 above.

Spine-like process on the hind margin of nymphal abdominal tergite 10 is considered a feature which suggests the affinity between Pteronarcyidae and Peltoperlidae (Stark & Stewart 1981). But the feature is scattered in some genera of distantly related families (Zwick 1980, p. 29, fig. 15) and has probably developed as a convergence in many phylogenetic lineages.

Presence of posterior hemitergal lobe on male abdominal tergite 10. Nelson & Hanson (1971) described three pairs of hemitergal lobes on the male abdominal tergite 10 of Pteronarcyidae.

dae. We found a pair of the lobes (posterior) also in Styloperlidae (only in *Cerconychia*). The lobe is similar to that in Pteronarcyidae but the similarity must be attributed to a symplesiomorphy. Nelson & Hanson further discussed the homology of the hemitergal lobes between Pteronarcyidae and Perloidea. They doubted the homology. We tentatively homologize the lobes of Pteronarcyidae to those of Peltoperlidae and Perlodidae. But no support by the musculature is available (Figs 115–117).

Male epiproct with lateral stylets. Nelson & Hanson (1971, p. 154) suggested the homology between the “fork-like structure” of epiproct in Pteronarcyidae (*Pteronarcys*) and the lateral stylets in Perlodidae and Chloroperlidae. Zwick (1973 p. 23, 148) found the lateral stylets further in Peltoperlidae (*Soliperla*, we found them additionally in *Viehoperla*) and considered it a synapomorphy (1973,



Figs 115–117. Abdominal terga 10 and epiprocts of Systelognatha, schematic, epiprocts s. str. are removed. Top: dorsal (external) views; middle: cross sections, capital letters refer to the positions of sections in the top; bottom: ventral (internal) views with musculature. 115. *Pteronarcys reticulata* (Pteronarcyidae); 116. *Sopkalia* (Perlodidae); 117. *Soliperla* (Peltoperlidae). Abbreviations and symbols: ah: anterior hemitergal lobe; ba: basal anchor; bb: basal bar; co: cowl; lb: lateral brace; mh: median hemitergal lobe; pg: paragenital plate; ph: posterior hemitergal lobe; s: lateral stylet; - - - : ridge of the convex fold on cowl.

No. 41; 1980, No. 42) for Peltoperlidae and Perlodea. He regarded Pteronarcyidae as lacking the stylets but did not mention the fork-like structure. Our observation, however, supports the homology of these sclerites between Pteronarcyidae, Peltoperlidae and Perlodidae (Figs 115–117). The fork-like structure (Fig. 115, s) is located very similarly to the lateral stylets of *Sopkalia* (Fig 116, s), in the sac of epiproct (cowl). The lateral stylets of *Soliperla* (Fig. 117, s) are less similar to those of *Sopkalia* than the fork-like structure, but we consider them also homologous. We further assume that the lateral stylets are homologous to the lateral external sclerites of the triplicate epiproct s. str. of *Pteronarcella* and to a pair of the dorso-lateral buttresses on the epiproct s. str. of *Pteronarcys californica* etc., although they are strongly transformed. In any case, the lateral stylets or similar structures were very possibly present already in the epiproct of the Systellognatha ancestor and their presence is regarded as an autapomorphy of Systellognatha.

We redefine here the ground plan of the Systellognatha epiproct with the terminology (Table 3, mainly according to Brinck 1956). Two features are added to that of Zwick (1973, 1980); a) lateral stylets, b) muscle *d*. The three parts of the mesal lever-like sclerite are more clearly defined.

A mesal sclerite of the epiproct is divided into three parts. 1) An apical free epiproct s. str. may contain a sperm cup which is eversible by the pressure of coelomic fluid. 2) A basal bar is located anterior to the epiproct s. str. and deep in a membranous cowl or a sac of epiproct. The boundary between the epiproct s. str. and the basal bar is marked by an opening for pouring coelomic fluid into the hollow in epiproct s. str. 3) A basal anchor is attached to the anterior end of basal bar, which is marked by the branching of lateral braces and paragenital plates. It is prolonged anteriorly over the front margin of tergite 10. From this mesal sclerite complex, three pairs of lateral sclerites branch laterally. 1) Lateral braces branch dorso-laterally at the boundary between the basal anchor and the basal bar and bear the muscles *a* which arise on the lateral sides of the antecosta on tergite 10. 2) Paragenital plates also branch at the same location with the lateral braces but are directed, at first, ventro-laterally and posteriorly, then are prolonged along the lateral margins of the cowl and meet each other behind the cowl. The posterior parts of the plates are weakly sclerotized and bear the muscles *c* and *d* which draw the basal anchor and the lateral side of the antecosta on tergite 10 respectively. 3) Lateral stylets branch from the posterior part of the basal bar, are prolonged postero-laterally on the inside of cowl and are produced postero-dorsally free from the cowl at the apices. The muscle *c*, which arises on tergite 9 and inserts on the basal anchor, has been secondarily derived in *Pteronarcys* and is absent in the ground plan.

Fusion of the basal segments of male cercus into a shaft. This characteristic was considered an autapomorphy of Peltoperlidae. It was the only ground for the placement of Styloperlinae into Peltoperlidae (Zwick 1973, No. 50), although later deleted (Zwick 1980). It is shared by only a part of Peltoperlidae and otherwise by Perlidae (*Caroperla*) and Chloroperlidae (*Neaviperla*). This distribution in the system suggests that the shaft has been developed independently in four families: Styloperlidae, Peltoperlidae, Perlidae and Chloroperlidae.

Dense band of anteriorly directed setae along the posterior margin of female abdominal sternite 9. Nelson & Hanson (1971) and Stark & Szczytko (1982) proposed the feature as an autapomorphy of Pteronarcyidae. It occurs also in Styloperlidae (Fig. 20). But the band is further found in many primitive representatives of Plecoptera (Eustheniidae, *Thaumatoperla*; Peltoperlidae, *Soliperla*; Perlodidae, *Sopkalia*, *Perlodes*). Accordingly, the feature is probably plesiomorphic.

Hemispherical, dorsally flattened eggs were considered an apomorphic feature which suggests the affinity between Pteronarcyidae and Peltoperlidae (Stark & Stewart, 1981). If the feature is a synapomorphy for the two families, the ancestor of Pteronarcyidae must have represented the hemispherical egg. But Stark & Szczytko (1982) regarded oval eggs more primitive than the hemispherical egg within Pteronarcyidae. We follow Stark & Szczytko and do not adopt the feature as a synapomorphy for the two families. The hemispherical egg may have been derived independently in Pteronarcyidae, Peltoperlidae and Perlodidae (*Perlodes*).

Micropyles at the pole opposite to collar on egg. This feature is proposed as an autapomorphy of Perloidea (Zwick 1973, No. 52; 1980, No. 56), whereas the feature in Pteronarcyidae and Peltoperlidae was regarded as representing the arrangement near collar. However, recent works on Systellognatha eggs (Stark & Stewart 1981, Stark & Szczytko 1982, 1984) obscured the difference between the two features. They reported many equatorial arrangements between the two poles.

The position of embryo in the egg could depend upon the arrangement of micropyles (Zwick 1973, 1980). But the embryo of *Kamimuria* (Perlidae; Kishimoto & Ando 1985) is initially placed like in *Pteronarcys* (Pteronarcyidae; Miller 1939), despite the difference in micropyle arrangement. The difference in the position of hatching embryo originates in the katarrepsis at a later stage of embryonic development, which may be influenced by the shape of the egg (Kishimoto & Ando 1985).

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