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Ignac SIVEC, Bill P. STARK and Shigekazu UCHIDA:

Synopsis of the World Genera of Perlinae (Plecoptera: Perlidae)

Pregled rodov poddružine Perlinae (Plecoptera: Perlidae) sveta

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Synopsis of the World Genera of Perlinae (Plecoptera: Perlidae)

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ABSTRACT – The taxonomic status and phylogenetic relationships among world genera of Perlinae are presented. Nineteen genera, including *Tyloperla* SIVEC & STARK, gen. nov., and *Furcaperla* SIVEC, gen. nov., are recognized. Perlini consists of the *Perla (Perla, Eoperla, Dinocras), Etrocorema (Etrocorema, Kamimuria, Neoperlops, Tetropina)* and *Paragnetina (Paragnetina, Togoperla, Tyloperla, Oyamia, Agnetina, Marthamea)* complexes, and is a presumptive sister group of Neoperlini (*Neoperla, Chinoperla, Phanoperla, Furcaperla*). *Claassenia* is thought to be a sister group of all other Perlinae whereas *Miniperla* could not be placed due to inadequate data. All available Perlini types were examined and keys and generic diagnoses are presented for adults and larvae. *Caucasoperla* and *Simpliperla* are placed as synonyms of *Paragnetina* and *Neoperla* respectively.

IZVLEČEK – PREGLED RODOV PODDRUŽINE PERLINAE (PLECOPTERA: PERLIDAE) SVETA – Podan je prikaz taksonomskega statusa in filogenetskih odnosov rodov poddružine Perlinae sveta. Poddružino tvori 19 rodov, med katerimi sta na novo opisana *Tyloperla* SIVEC & STARK in *Furcaperla* SIVEC. Skupine rodov tribusa Perlini *Perla (Perla, Eoperla, Dinocras), Etrocorema, (Etrocorema, Kamimuria, Neoperlops, Tetropina)* in *Paragnetina (Paragnetina, Togoperla, Tyloperla, Oyamia, Agnetina, Marthamea)* so verjetno sestrska skupina tribusa Neoperlini (*Neoperla, Chinoperla, Phanoperla, Furcaperla*). Rod *Claassenia* imamo za sestrsko skupino vseh ostalih perlin, medtem ko ostaja zaradi pomanjkljivih podatkov nejasen položaj rodu *Miniperla*. Preučili smo ves dostopen tipski material predstavnikov poddružine Perlinae. Za odrasle in larvalne stadije predstavljamo diagnoze rodov in določevalne ključe. *Caucasoperla* je nov sinonim rodu *Paragnetina*, *Simpliperla* pa je nov sinonim rodu *Neoperla*.

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1. Introduction

At the time of the ILLIES (1966) catalogue, thirteen genera were placed in the subfamily Perlinae, but few of these were well known. Much confusion existed about generic limits and similar species were described first in one genus and then in another, so that »well-known« groups like *Perla*, *Paragnetina*, *Kamimuria* and *Togoperla* became almost inextricably tangled. *Agnetina* was at that time an obscure synonym of *Dinocras* while *Marthamea* and *Phasganophora* (= *Agnetina*) could not be reliably separated and *Etrocorema* was so poorly known that a generic synonym, *Neoeuryplax* was listed in a separate subfamily, Acroneuriinae. From this abysmal state, gradual progress has been made in perline systematics, particularly in the past decade.

STARK & GAUFIN's (1976) study indicated many characters of potential taxonomic and phylogenetic significance occur on eggs, internal genitalia and in nymphal proventriculi and setation patterns. Although this study emphasized Nearctic Perlidae, a tribal classification for the world fauna was proposed, and *Claassenia* was transferred to Perlinae. ZWICK (1980 a, b, 1981, 1982 a, b, d, 1983, 1984, 1986, 1988) has made major contributions to our knowledge of the Oriental Neoperlini and in another series of papers (ZWICK, 1982 c, e, 1984 a, b, c, 1985, 1988) he clarified the status of *Etrocorema*, *Tetropina*, *Neoperlops*, *Oyamia*, and *Tylopyge*, which were formerly essentially unknown. Other studies including data on Oriental Neoperlini during this period are STARK & BAUMANN, 1978, STARK, 1983, 1987, STARK & SZCZYTKO, 1979, SIVEC, 1984, SIVEC & ZWICK, 1987 and ZWICK & SIVEC, 1980. STARK, 1986 and STARK & SZCZYTKO, 1981, include limited data on Oriental *Agnetina* and *Paragnetina* in their treatment of the Nearctic members of these genera. HARPER (1976, 1977) included descriptions of *Kamimuria*, *Neoperla* and *Phanoperla* in his studies of Himalayan stoneflies.

Despite all these studies the »Gordian knot« remained intact, particularly in reference to *Kamimuria*, *Tylopyge*, *Paragnetina*, and *Togoperla* systematics for the Oriental region. The only clear solution to this problem lay in a massive study of museum typic material in which we have been involved for the past decade. All available types of named Perlini species have now been examined by us, but it has not been possible to check for perline species which may have been described in other families (e. g. Perlodidae). On a visit to China one of us (IS) found all existing Wu and Chu types are now in Peking (Zoological Institute, Academica Sinica); types named prior to 1962 are all destroyed and the »neotypes« named or labelled as such by WU (1962) have no status under the code. In this paper, we attempt to »unravel the knot« at least at the generic level, and present our current understanding of relationships among these genera. Our overview of this fauna is necessarily based largely on dried museum specimens collected by non-Plecopteran specialists, supplemented with fresh, alcohol preserved specimens from Japan and a few scattered mainland localities. Hopefully this report will stimulate and facilitate a continued collecting and research so badly needed on these animals, many of which are doubtlessly endangered, or extinct through habitat degradation.

2. Material and Methods

An attempt has been made to study all available type material within subfamily Perlinae including valid and uncertain species recorded in the catalogues ILLIES, 1966, ZWICK, 1973. Specimens of all primary types and several additional ones were borrowed from the museums listed below. The most abundant material came from the authors' collections from North America, Japan and Europe. Most Oriental specimens borrowed from museums were collected during light trapping for other insect groups and there is very little additional label in-

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formation about the circumstances under which the specimens were collected. Most museum specimens were dry and pinned and had to be relaxed in a moist chamber for about an hour. Male abdomens were detached and treated with a cold maceration technique (ZWICK, 1983) or briefly treated with hot KOH so the penis could be removed. For a detailed study artificial eversion of the internal sac is needed. The best way to achieve this is by gently squeezing the abdominal tip of live males to evert the penis from its resting position. If necessary, they were temporarily mounted in glycerol for the study of armature. Female abdominal tips were first soaked in water so that the eggs could be removed, then they were usually cleared in hot KOH. Genitalia have been stored in glycerol in microvials or mounted in Canada balsam on transparent celluloid and as a rule attached to the specimen pin.

Eggs were placed in 80 % ethanol, hand cleaned with forceps and agitated in an ultrasonic cleaner for several minutes. Specimens were transferred to acetone, air dried, and fixed on specimen stubs with a double stick tape. Specimens were gold coated in a Hummer II sputter coater before examination with an AMR 1000 SEM. Adults and larvae were studied with a Wild M5-A stereo dissecting microscope, and line drawings have been prepared with the aid of Wild, or Leitz-Dialux drawing equipment. Throughout the text we use the abbreviations T(Terga), S(Sterna) and FCI (Follicle cell impression). Penis structures were described by using the following words for the three parts: 1) basal everted »envelope«, 2) intermediate uneverted »tube«, and 3) apical everted »sac«. The terminology of eggs follows that of STARK & SZCZYTKO (1988). In the list of »valid species« for each genus, we have indicated with an asterisk those species we have studied.

A number of museums and individuals made the material available for this study. Included among these are:

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4. Phylogeny

Perlinae, as presently defined, include two major groups, Neoperlini and Perlini. Monophyly for this assemblage is asserted on the basis of a common type of male genitalia, the specialized type of hemitergal lobes found throughout this group (1), the presence of an evenly spaced row peg sensilla set on a low, relatively straight nymphal occipital ridge (2), and the occurence of 3 basal sclerites on the remnant of AT2, 3 gills (3), rather than the usual 2 found in other Perlidae (UCHIDA, unpublished).

Among male systellognathan Plecoptera, a cleft T10 occurs in all Pteronarcyidae, and in some members of Perlodidae, Peltoperlidae, and Chloroperlidae. Less commonly, but among all Acroneuriinae, Isoperlinae and scattered among other groups, the 10th tergum is entire and paraprocts are modified as external genitalia. Although the situation is far from certain, we feel the cleft T10 is a synapomorphy for Systellognatha; whether all Acroneuriinae (and other groups) display a secondary loss of the cleft, or the plesiomorphic condition is unclear.

Species with a cleft T10 have the remaining structure developed into a lateral pair of lobes, or hemitergites. These structures typically contain areas of sensilla basiconica, and possibly function during copulation either as hooks or probes to depress the female subgenital plate, or as »guides« for the penis. The location of sensilla basiconica on the inner basal margins of perline hemitergites suggests, in many cases, that these provide males with information about the everted penis position rather than details of the female. Other sensilla in more exposed positions are assumed to provide information on the mate. The basic hemitergite form in Peltoperlidae, Perlodidae, and Chloroperlidae is a broad, thin unspecialized sheet, while Pteronarcyidae and Perlinae each display distinctively different modifications from this basic plan. We suggest the narrow, more finger-like hemitergites of Perlinae represent a synapomorphy for the entire subfamily.

The distribution and arrangement of peg sensilla on the occiput of perlid larvae has been discussed by STARK & GAUFIN (1976). Variable, irregular arrangements of these structures occur among Acroneuriinae and Perlodidae species, while the orderly association of sensilla along a more or less straight ridge is peculiar to Perlinae. Most Neoperlini have the sensilla reduced, and exhibit a bare straight ridge; a few Perlini also have et least some mesal reduction of sensilla.

Several generic clusters have been identified within Perlini on the basis of our limited data (Table 1, Fig. 1). Three principally European genera, *Perla*, *Eoperla* and *Dinocras* are apparently descended from an early *Kamimuria* or *Etrocorema*-like ancestor with relatively small hemitergites and simple abdominal terga; these genera are allied by a divided anterior margin of T9 (27). In other Perlinae and Acroneuriinae, the sclerotized anterior margin of T9 is entire, but in these genera, the sclerite is interrupted in the mesal third by membrane.

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Table 1. Apomorphic characters (plesiomorphy)

1. Specialized hemitergites (simple *Dictyogenus – Cultus* type)
2. Larval occipital sensilla row and ridge regular and complete (interrupted, irregular)
3. Three basal sclerites on the remnant of AT2, 3 gills (two)
4. Secondary loss of abdominal pleural brushes (presence)
5. Female intersternal 9–10 setal-like microtrichia (small triangular microtrichia)
6. Hammer loss (presence)
7. Sensilla basiconica cluster on hemitergite apex (absence)
8. *Paragnetina* type basal penial sclerite (no basal sclerite)
9. Upturned, swollen, basal callus on hemitergite (no basal callus)
10. T9 sclerotized anterolaterally, membranous mesally (T9 without anterolateral sclerite)
11. Penis sac strongly recurved, complexly lobed (penis sac straighter, simply lobed)
12. T5 modified with lobe or sensilla patch (T5 unmodified)
13. Tongue-like, long subgenital plate (subgenital plate short or unspecialized)
14. Basal lobe on penis tube (penis tube without basal lobe)
15. Small, mesocaudal lobe on T8 (T8 without mesocaudal lobe)
16. Complexly lobed anterior process of hemitergites (simple anterior hemitergite process)
17. Anterior chorionic fold (no anterior chorionic fold)
18. Hemitergites with basolateral knob (no basolateral knob)
19. Slender, mesal sclerite on T9 (T9 sclerite absent or of other type)
20. Hemitergite anterior process with slender ventral and enlarged dorsal lobe (hemitergite anterior process unlobed)
21. Two ocelli (three ocelli)
22. Sclerotized mesocaudal process on T9 (T9 without such a process)
23. Elongate, posteriorly located tentorial callosities (oval callosities, forward of ocelli)
24. Massive subgenital plate (unspecialized subgenital plate)
25. Anterior T9 sclerite prolonged mesally (T9 anterior sclerite normal)
26. Egg anchor multifibrous with lateral projections (egg anchor simple)
27. T9 anterior sclerite interrupted mesally (T9 anterior sclerite complete)
28. Larval submentum with basolateral sutures (submentum without basolateral sutures)
29. T9 mesal field with chitinous spines (T9 mesal field simple)
30. Penial sac armature long and seta-like (penial sac armature short and triangular)
31. Egg collar rim thick with few thick ribs (collar rim thin with multiple ribs)
32. Male abdominal S8-9 with sensilla basiconica (abdominal sterna without sensilla basiconica)
33. Penial tube basal sclerite with constricted opening (basal sclerite opening wide)
34. Hemitergite basal piece flattened beyond origin of anterior process (hemitergite without flattened basal piece)
35. Egg chorion striate (egg chorion non-striate)
36. Secondary loss of anterior ocellus (three ocelli)
37. Bifurcate anterior hemitergal process (simple anterior process)
38. Long basal cercal segment (short basal cercal segment)
39. Large black penial sac armature (brown variable sac armature)
40. Modified T7 (unmodified T7)
41. Slender, cleft mesal sclerite on T8 (T8 without such a sclerite)
42. Short Sc vein (normal Sc vein)
43. Basally curved Cu2 vein (straight Cu2 vein)
44. Nymphal thoracic sterna with setal fringes (thoracic sterna without setal fringes)

Within this cluster, *Eoperla* and *Dinocras* larvae exhibit a basal suture (28) on the lateral submental lobes. This character is incompletely expressed in *Phanoperla* and probably represents a convergence in this group. This presumed apomorphy unites these two genera, while the *Perla* species all exhibit unique, chitinous plates in the mesal field of T9 (29). *Dinocras*

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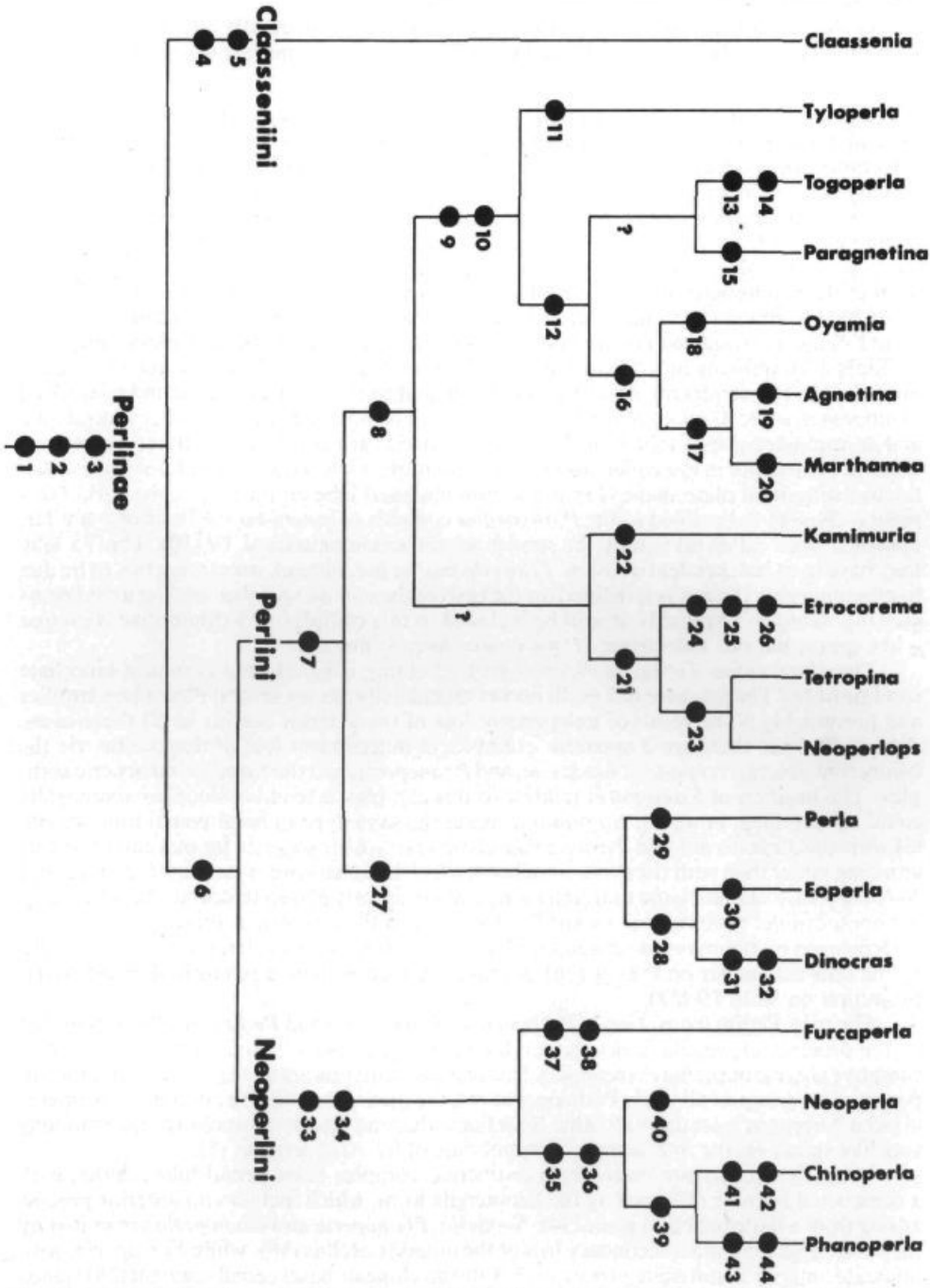

Fig. 1. Proposed phylogeny of Perlinae genera. (*Miniperla* not included). The numbers (1–44) refer to table 1.

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species share a similar, unusual collar form (31), and scattered sensilla basiconica on male abdominal sterna (32), while *Eoperla* is distinguished by penial armature which includes long seta-like spines on the sac (30).

Togoperla, *Paragnetina*, *Marthamea*, *Agnetina*, and *Oyamia* all have a highly modified male abdominal T5 (12). Typically this modification takes the form of a prolonged and sometimes cleft lobe, but lobe reduction to small knobs or sensilla basiconica patches has apparenty occured independently in three *Paragnetina* and an *Agnetina* species. *Marthamea*, *Agnetina* and *Oyamia* appear to be allied by their unusually massive and complexly lobed hemitergites (16), but the *Togoperla-Paragnetina* grouping rests entirely on an intuitive, probably plesiomorphic, similarity. *Oyamia* species are distinctive in the peculiarly massive form of the hemitergites which have a low lateral knob (18). *Marthamea* and *Agnetina* are allied by a common chorionic fold, collar type and anchor (17), but an alternative arrangement linking *Agnetina* and *Oyamia* on the basis of reduced penis armature (plesiomorphic?) or bilobed T6 (missing in some species of both genera) is less satisfactory. *Agnetina* species are united by the slender mesal sclerite on T9 (19) and by the much elongated and sclerotized hemitergites, while *Marthamea* species share bilobed hemitergites with a slender ventral lobe and an expanded dorsal lobe (20). *Paragnetina* species are allied by the shared process on T8 (15), similarities in egg collar, and vaginal armature, while *Togoperla* species share a distinctive subgenital plate shape (13) and a common basal lobe on the penis tube (14). *Tyloperla* is thought to be allied to the *Paragnetina* complex of genera on the basis of a similar, upturned basal callus (9) and by the similar sclerotization pattern of T9 (10). The T5 lobe may have been independently lost in *Tyloperla* but we are, instead, presuming this to be due to plesiomorphy; the genus is defined on the basis of the complexly lobed and recurved penis sac (11). *Miniperla* probably should be included in this complex as a diminutive *Agnetina* – like genus, but our knowledge of this unique form is limited.

The *Etrocorema-Tetropina-Neoperlops* trichotomy is based on a common biocellate condition (21). The presence of 2 ocelli occurs sporadically among several Plecoptera families and presumably is the result of independent loss of the anterior ocellus in all these cases. Among Perlinae there are 2 apparent examples of independent loss of this ocellus viz the Neoperlini genera, *Neoperla*, *Chinoperla*, and *Phanoperla*, and the *Etrocorema* generic complex. The position of *Kamimuria* relative to this complex is tenuous since no apomorphy could be identified, however, *Kamimuria* shares the same type of basal penial tube sclerite (8) with the *Etrocorema* and *Paragnetina* complexes which suggests its placement in this grouping rather than with the *Perla* complex in which this character is lacking. *Tetropina* and *Neoperlops* are united by the unusually long and posteriorly placed tentorial callosities (23), but apomorphies have not been identified for either of these genera at present. *Etrocorema* is recognized by the massive subgenital plate (24), distinctive T9 sclerite in males (25) and by the unusual anchor on the egg (26). *Kamimuria* species share a sclerotized, mesocaudal projection on male T9 (22).

The tribe Perlini (consisting of *Paragnetina*, *Etrocorema* and *Perla* complexes) is united by the presence of sensilla basiconica on the hemitergite apex (7), and Neoperlini, the presumptive sister group, shares secondary hammer loss with this group (6). *Claassenia*, the apparent sister group of all other Perlinae, has lost the pleural brushes on abdominal segments (4) which occur in essentially all other Systellognatha, and has an unusual expression of long seta-like spines on the intersegmental membrane of S9-10 in females (5).

Neoperlini genera are united by a distinctive, complex basal penial tube sclerite, with a constricted opening (33), and by the hemitergite form, which includes an anterior process arising from a flattened basal piece (34). *Neoperla*, *Phanoperla* and *Chinoperla* are united by the striate eggs (35) and a secondary loss of the anterior ocellus (36), while *Furcaperla*, with bifurcate anterior hemitergite processes (37) and an elongate basal cercal segment (38) stands as the sister group of this complex. *Chinoperla* and *Phanoperla* are united on the basis of

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similar large, shining black penial sac armature (39). *Neoperla* is a large, complex genus but the great majority of species share a similarly modified T7 (40). *Chinoperla* species are united by the long, slender, cleft sclerite on T8 (41) and by the very short Sc vein in the forewing (42), while *Phanoperla* species share synapomorphies in the basally curved Cu2 vein (43) and the nymphal posterior thoracic sternal fringes (44), otherwise known only among a few peltoperlid genera.

5. Key to Perlinae Males

1. Lobes or sensilla basiconica patches on T5 2
– T5 without lobes or sensilla basiconica 6
2. Hemitergites with 2 or 3 lobes in lateral aspect, or extending forward to at least T8 3
– Hemitergites with only a basal callus, unlobed in lateral aspect, and reaching only T9 5
3. T7 with dense mesal sensilla basiconica patch; hemitergal lobes bilobed in lateral aspect, and bearing a basal callus ..... *Marthamea*
– T7 with at most a few scattered sensilla basiconica, not forming a dense mesal patch; hemitergal lobes simple, bilobed or trilobed in lateral aspect, but without a basal callus 4
4. T9 completely membranous mesally ..... *Oyamia*
– T9 co with a sclerotized mesal band ..... *Agnetina*
5. Mesal field of T8 usually sclerotized and produced posteriorly into a small lobe ..... *Paragnetina*
– Mesal field of T8 membranous and without a posterior lobe ..... *Togoperla*
6. Biocellate 7
– Triocellate 11
7. Hemitergites simple, finger-like, without basal callus or anterior process extending from basal piece 8
– Hemitergites bifurcate, with anterior finger-like process extending from mesally directed basal piece 9
8. Anterior sclerotized margin of T9 projects into mesal membranous field, partially dividing tergum; hemitergites extend forward over T9 ..... *Etrocorema*
– Anterior margin T9 straight, not projecting caudally; hemitergites short, scarcely reaching posterior margin T9 ..... *Tetropina*
9. T9 with strongly sclerotized, usually Y-shaped medial sclerite ..... *Chinoperla*
– T9 without sclerotized, Y-shaped sclerite 10
10. Cu2 of forewing curved basally, arising from Cu1 at an almost right angle; T7 without lobe ..... *Phanoperla* (in part)
– Cu2 of forewing straight basally, arising from Cu1 at an acute angle; T7 typically with a lobe ..... *Neoperla*
11. T4–5 with anterior sclerotized band and membranous posterior field; mesal field of T9 without spiny projections ..... *Miniperla*
– T4–5 uniformly sclerotized or mesal field of T9 with spiny projections 12
12. Hemitergites bifurcate, apex of anteriorly projecting portion without sensilla basiconica 13
– Hemitergites simple, with at most a basal callus 14
13. Projecting portion of hemitergites forked ..... *Furcaperla*
– Projecting portion of hemitergites simple ..... *Phanoperla* (in part)
14. T9 with mesal field of spiny projections ..... *Perla*
– T9 without spiny projections in mesal field 15
15. T8 with mesal lobe and T9 with mesal membranous field; hemitergites with well developed basal callus ..... *Tyloperla*
– T8 without lobe, T9 mesal field sclerotized and usually covered with sensilla basiconica 16
16. Sclerotized anterior margin projecting deeply into mesal field of T9, European and North African species 17
– Sclerotized anterior margin of T9 straight; Asian species ..... *Kamimuria*
17. Projecting portion of hemitergites about as long as wide ..... *Eoperla*
– Projecting portion of hemitergites longer than wide ..... *Dinocras*

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6. Key to Perlinae Females

1. Biocellate 2
– Triocellate 7
2. Sc not extending beyond basal third of forewing ..... *Chinoperla*
– Sc extending to distal half of forewing 3
3. Subgenital plate narrowly notched and massive, covering most of ventral abdominal apex ..... *Etrocorema*
– Subgenital plate small or unproduced, with or without notch 4
4. Cu2 of forewing curved basally, arising from Cu1 at an almost right angle... *Phanoperla* (in part)
– Cu2 of forewing straight basally, arising from Cu1 at an acute angle 5
5. Tentorial callosities adjacent to ocelli, linear and approximating ocelli in width 6
– Tentorial callosities forward of ocelli, oval and smaller than ocelli ..... *Neoperla*
6. Occiput with a small mesal knob; egg with a distinct eclosion line below micropylar line ..... *Tetropina*
– Occiput without mesal knob; egg without eclosion line ..... *Neoperlops*
7. Cu2 of forewing curved basally, arising from Cu1 at an almost right angle... *Phanoperla* (in part)
– Cu2 of forewing straight, arising from Cu1 at an acute angle 8
8. Body length less than 10 mm; endemic to Japan ..... *Miniperla*
– Body length greater than 10 mm 9
9. Intersegmental membrane of S9–10 with a dense band of long setae; egg spindle shaped with button collar ..... *Claassenia*
– Intersegmental membrane of S9–10 without dense band of long setae; egg shape and collar variable 10
10. European, or/and circum-Mediterranean species 11
– Asian and Nearctic species 15
11. Subgenital plate unproduced 12
– Subgenital plate distinctly produced 13
12. Egg with wide collar; vagina without anterior accessory glands ..... *Eoperla*
– Egg with button-like attachment of anchor; vagina with anterior accessory glands ..... *Marthamea* (in part)
13. Subgenital plate distinctly notched; chorion granular to ornate ..... *Perla*
– Subgenital plate without notch; chorion smooth 14
14. Anterior vaginal accessory glands present; egg with button-like attachment of anchor; rare or extinct potamon species, recent records of *Agnetina* only from Poland, Anatolia and the Caucasus ..... *Marthamea* (in part), *Agnetina*
– Anterior vaginal accessory glands absent; egg with wide, sessile collar; common species in small and large streams throughout much of Europe ..... *Dinocras*
15. Anterior vaginal accessory glands present 16
– Anterior vaginal accessory glands absent 18
16. Subgenital plate long, tongue shaped, usually without notch; egg chorion smooth; collar sessile or absent ..... *Togoperla*
– Subgenital plate length variable, usually short and triangular, often notched; egg chorion variable, collar stalked or button-like 17
17. Subgenital plate entire or truncate; vaginal sclerites present; egg collar button-like ..... *Agnetina*
– Subgenital plate notched, vaginal sclerites usually absent; egg collar stalked ..... *Paragnetina*
18. Spermatheca an irregular, large, inflated sac 19
– Spermatheca a slender sausage-like sac. 20
19. Subgenital plate reaches posterior third of S8 ..... *Tyloperla*
– Subgenital plate not reaching posterior third of S8 ..... *Kamimuria*
20. Subgenital plate short, broadly rounded and shallowly notched; basal cercal segment about 2 times long as wide; known from South China ..... *Furcaperla*
– Subgenital plate entire or truncate; basal cercal segment wider than long; known from Japan, Korea, northeastern China and Soviet Far East ..... *Oyamia*

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7. Key to Perlinae Larvae

(*Furcaperla*, *Miniperla*, *Neoperlops* and *Chinoperla* unknown)

1. European and circum-Mediterranean species 2
– Asian and Nearctic species 6
2. Posterior setal fringe complete on S7 3
– Posterior setal fringe incomplete on S7 5
3. Abdominal terga with black clothing hairs; lateral submental lobes without basal suture ..... *Agnetina* (in part)
– Abdominal terga without black clothing hairs; lateral submental lobes with basal sutures 4
4. Head between ecdysial suture and occipital setal row mostly pale; abdominal terga with white clothing hairs; abdomen with 2 more or less complete pale longitudinal bands ..... *Eoperla*
– Head between ecdysial suture and occipital setal row mostly dark; abdominal terga with short, thick intercalary setae; abdomen without pale longitudinal bands ..... *Dinocras*
5. Area between posterior ocelli with at least a small area of pale pigmentation; cerci typically with dorsal swimming hairs along basal segments; posterior tergal fringes with only short thick setae ..... *Perla*
– Area between posterior ocelli entirely dark; cerci without swimming hairs; posterior tergal fringes typically with a few long setae mixed with short thick ones ..... *Marthamea*
6. Biocellate 7
– Triocellate 10
7. Anterolateral submental lobes offset by basal suture; one pair PSC3 gills; posterior margin of mesosternum with setal fringe ..... *Phanoperla* (in part)
– Anterolateral submental lobes without basal suture; two pairs PSC3 gills; posterior margin of mesosternum without setal fringe 8
8. Occipital ridge with close-set, complete row of short, thick setae; body densely covered with black clothing hairs ..... *Tetropina*
– Occipital ridge with at most a few short, thick setae laterally; clothing hairs sparse and typically brown 9
9. Lateral margins of pronotum completely fringed with thick setae; anal gills absent ..... *Etrocorema*
– Lateral margins of pronotum with fringe incomplete; anal gills typically present ..... *Neoperla*
10. Anterolateral submental lobes offset by basal suture; one pair PSC3 gills; posterior margin of mesosternum with setal fringe ..... *Phanoperla* (in part)
– Anterolateral submental lobes without basal suture; two pairs PSC3 gills; posterior margin of mesosternum without setal fringe 11
11. Anal gills present 12
– Anal gills absent 15
12. Posterior setal fringe of S7 incomplete ..... *Paragnetina*
– Posterior setal fringe of S7 complete 13
13. Posterior fringe of T2–4 with at least a few conspicuously long setae intermixed with short, thick ones; less than 10 thick intercalary setae on T9 14
– Posterior fringe of T2–4 consists of relatively uniform setae; typically more than 10 thick intercalary setae on T9 ..... *Claassenia*
14. Posterior fringe of metanotum and most abdominal terga with multiple long setae intermixed with short thick ones ..... *Agnetina*
– Posterior fringe of metanotum and most abdominal terga with only 1 or 2 long setae intermixed with short thick ones ..... *Oyamia*
15. Thorax and abdomen with a median row of long silky setae; proventriculus armed with two well developed groups of sclerotized bands 16
– Thorax and abdomen without a median row of long silky setae; proventriculus with anterior group of sclerotized bands reduced and posterior group well developed ..... *Togoperla*
16. PSC2, 3 gills single ..... *Tyloperla*
– PSC2, 3 gills double ..... *Paragnetina*, *Kamimuria*

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8. Tribus CLAASSENIINI, new tribe

8.1. *Claassenia* WU

Adelungia KLAPÁLEK (1914). Type species *Adelungia caudata* KLAPÁLEK, orig. desig. Preoccupied (MELICHAR, 1902).
Claassenia WU (1934). Replacement for *Adelungia* KLAPÁLEK.

Adult habitus. – Triocellate, large and generally dark brown. Wings greyish, veins dark brown. Females and males macropterous or brachypterous. Mesal occipital knob absent.

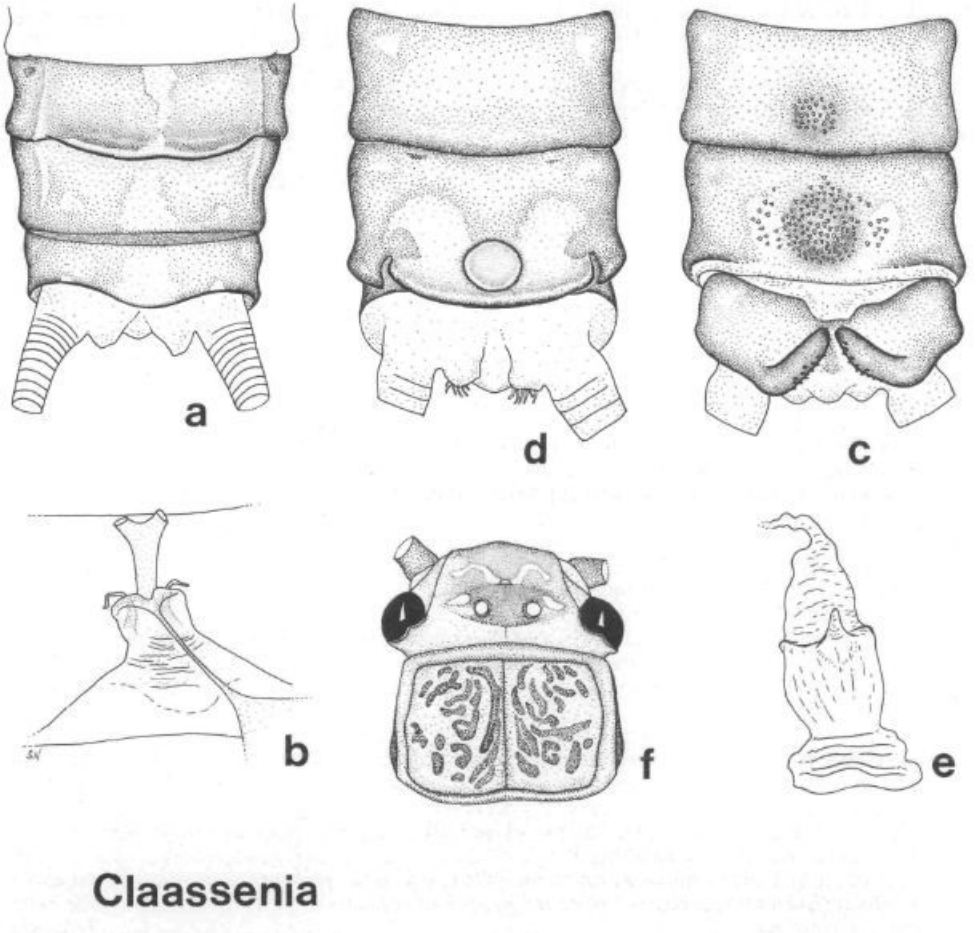

Fig. 2. *Claassenia sabulosa* (BANKS) [USA]: Abdominal tip of female (a), vagina (b), head and prothorax (f); *Claassenia radiata* (KLAPÁLEK) [China]: Abdominal tip of male, ventral (d), dorsal (c), and everted penis (e).

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Claassenia

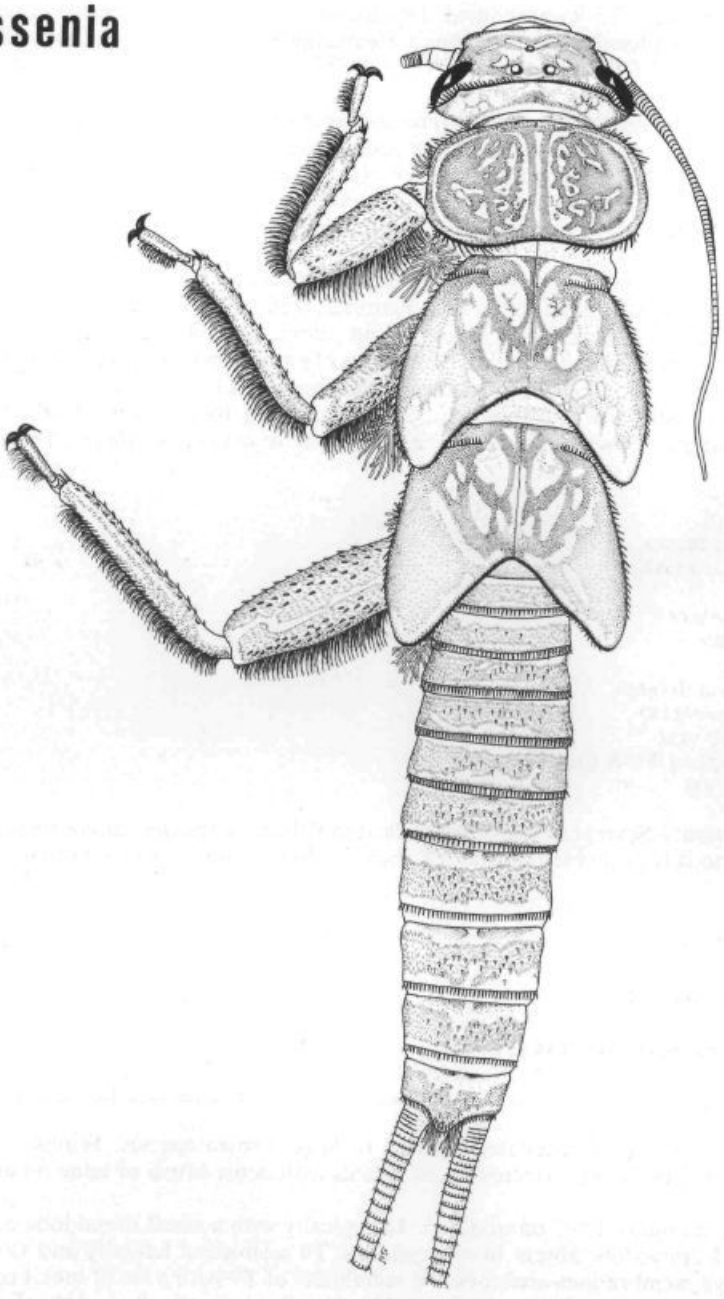

Fig. 3. *Claassenia* sp. [China]: Nymph habitus.

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Male genitalia. – T5-9 unmodified; T9 with large mesal patch of sensilla basiconica; T8 sometimes with scattered sensilla basiconica. Hemitergites simple, finger-like, typically reaching posterior margin of T9, at most anterior third of T9; a few sensilla basiconica scattered along inner, dorsal surface of hemitergite. S9 with circular hammer; abdominal sterna without brushes. Penis envelope membranous, tube and sac membranous, unarmed or weakly armed with minute triangular spines and slender seta-like spines.

Female genitalia. – Subgenital plate weakly produced or unproduced. Intersegmental membrane of S9–10 with dense band of long setae. Vagina membranous, accessory glands present or absent. Spermathecal stalk short; spermatheca large, bulbous, with an irregular shape.

Egg. – Spindle shaped with or without button-like collar. Chorion smooth or with weak FCIs on posterior pole. Micropyles subequatorial; orifices sessile; canals slanted.

Larva. – Distinctly patterned in brown and yellow. Occipital setal row with a few setae missing from ridge behind ocelli. Lateral margins of pronotum fringed with short thick setae; fringe sometimes incomplete. Abdominal tergal fringes uniform. Black clothing hairs present. S7 with posterior fringe complete. Cercal swimming hairs absent. Anal gills present.

Distribution.– Nearctic, Soviet Far East, Korea, mainland Southeast Asia.

Valid species.–
bishoffi (WU)
brachyptera BRINCK
caudata (KLAPÁLEK)
fulva WU
* *gigas* (KLAPÁLEK)
longistyla WU
magna WU
* *manchuriana* (BANKS)
* *radiata* (KLAPÁLEK)
* *sabulosa* (BANKS)
* *semibrachyptera* WU & CLAASSEN
tincta (NAVÁS)

Discussion. – Several of the Oriental-eastern Palearctic species cannot be distinguished presently and it is probable that the list above includes a number of synonyms.

9. Tribus PERLINI

9.1. *Tyloperla* SIVEC & STARK, n. gen.

Type species. – *Tylopyge attenuata* WU & CLAASSEN = *Tyloperla attenuata,* here designated.

Adult habitus. – Triocellate, medium to large, brown species. Wings suffused with brown, veins dark brown. Macropterous. Males with dense brush of setae on anterior metasternum.

Male genitalia. – T5–7 unmodified. T8 typically with a small mesal lobe covered with sensilla basiconica; lobe absent in some species. T9 sclerotized laterally and along anterior margin, large membranous area mesally; membrane of T9 with a small mesal patch of sensilla basiconica. Hemitergite simple, finger-like, usually acute apically and usually with a well developed basal callus covered with sensilla basiconica. S4–7 with hair brushes; brushes longest on S6. Penis envelope sparsely covered with minute, triangular spines; tube membranous

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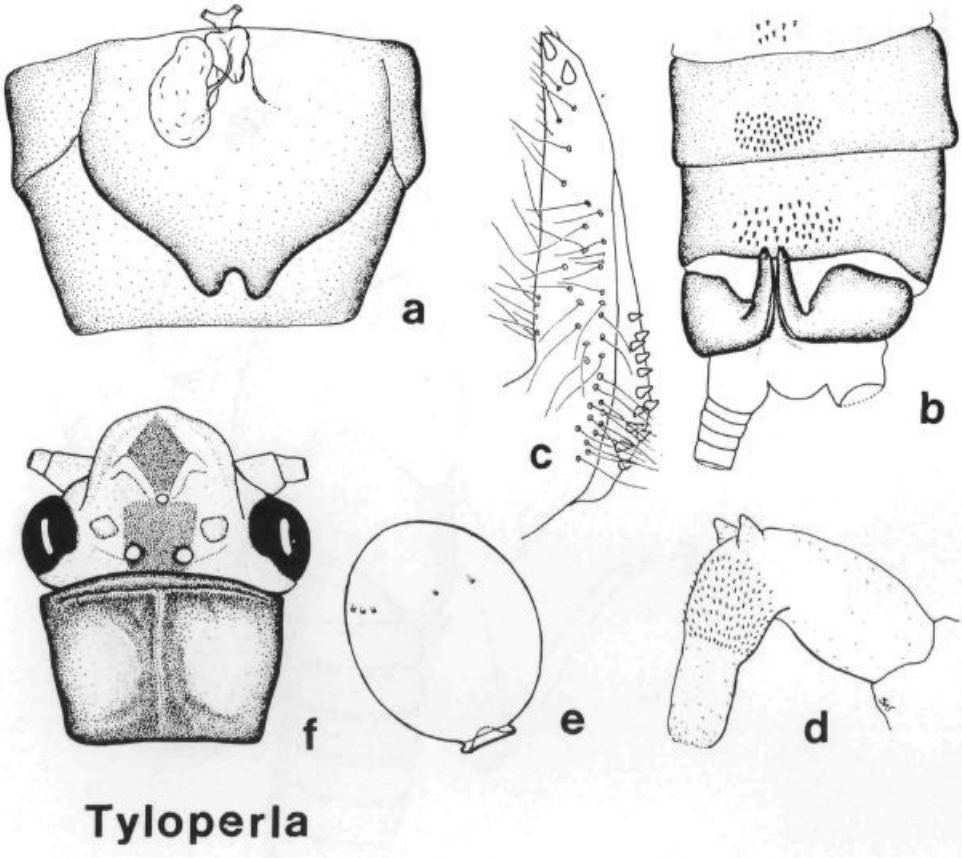

Fig. 4. *Tyloperla formosana* (OKAMOTO) [Taiwan]: Abdominal tip of female (a), abdominal tip of male (b), hemitergite (c), everted penis (d), head and prothorax (f), and egg (e).

unarmed, with apical pair of lobes; basal sclerites well developed; sac apically recurved, with pair of basal lobes; sac armature of variable size spines covering lobes, and usually apex.

Female genitalia. – Subgenital plate large, subtriangular covering most of S9, and notched apically. Vagina membranous, accessory glands absent. Spermathecal stalk slender, subequal to vaginal lenght; spermatheca inflated, of somewhat irregular elongate shape.

Egg. – Elongate oval with short wide collar. Rim smooth, unflanged. Chorion smooth. Micropyles in posterior third; orifices sessile.

Larva. – Brown without distinctive pattern. Occipital setal row complete. Pronotum completely fringed with short, thick setae. Abdominal tergal fringes with few long setae. S7 posterior fringe incomplete. Anal gills absent. Cercal swimming hairs present; silky hairs on dorsum of head, thorax and abdomen.

Distribution. – Taiwan and mainland Southeast Asia.

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Tyloperla

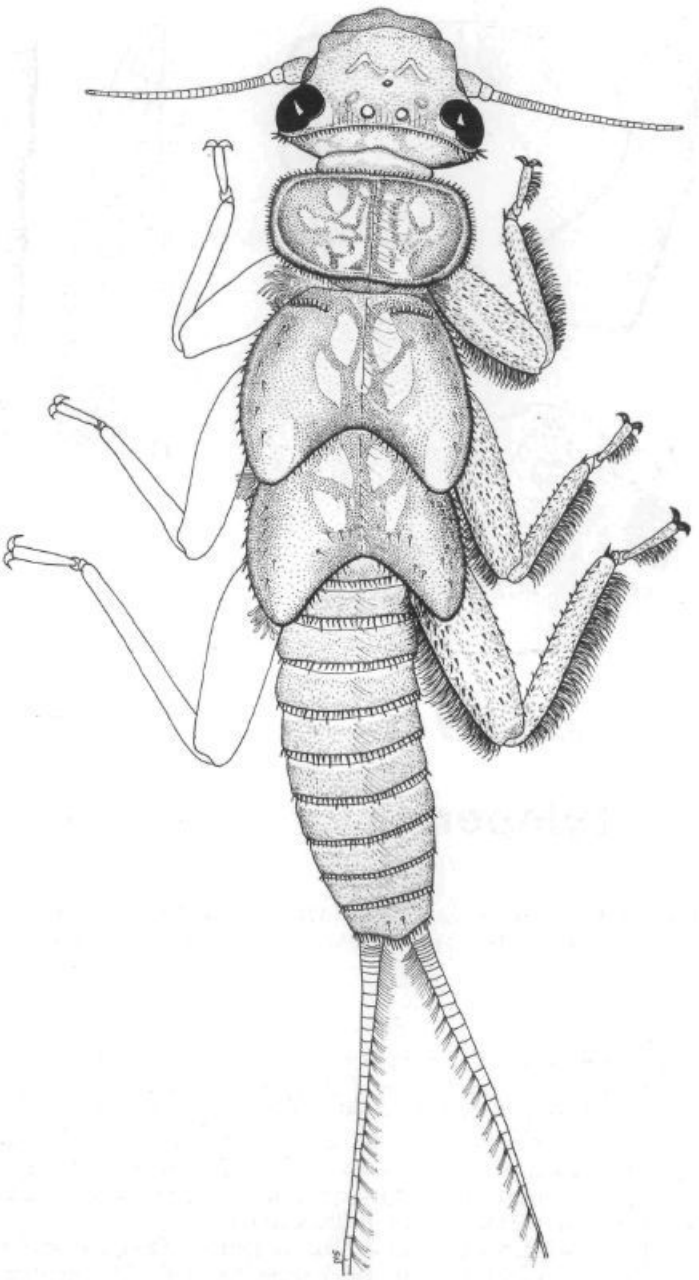

Fig. 5. *Tyloperla formosana* (OKAMOTO) [Taiwan]: Nymph habitus.

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Valid species.–
* *attenuata* (WU & CLAASSEN), n. comb.
* *formosana* (OKAMOTO), n. com. = *minor* (KLAPÁLEK), *signata* (BANKS), n. syn.
* *sauteri* (NAVÁS), n. comb.

Discussion. – This genus includes the distinctive remnants of *Tylopyge* which was based on *T. planidorsa*, a species of *Paragnetina* (ZWICK, 1988). *T. attenuata* types are lost, but two males from China, collected by D. C. Graham in July and August, are in the United States National Museum and these specimens agree closely with WU & CLAASSEN's (1934) description and figures, particularly in hemitergal shape and tergal modifications.

9.2. *Togoperla* KLAPÁLEK

Perla (*Togoperla*) KLAPÁLEK (1907). Type species *Perla limbata* PICTET, desig. KLAPÁLEK (1923).

Adult habitus. – Triocellate, large, brown to dark brown species. Wings suffused, veins brown. Macropterous. Mesal occipital knob absent.

Male genitalia. – T5 produced into a slightly excavated or bilobed process. T6-9 sclerotized laterally and along anterior margin; membranous posteromesally; membrane of T6–9 typically setose. Hemitergites with short, broad to slender anterior process, and well developed basal callus; apex of anterior process and basal callus with sensilla basiconica. S4–8 and metasternum with hair brush. Penis envelope membranous; tube membranous with basal, and usually a pair of small lateral lobes; distally tube is armed with small triangular spines; sac subequal to tube and armed basally with small spines, apically with patch of long slender seta-like spines.

Female genitalia. – Subgenital plate long, produced over most of S9, subtriangular to tongue-shaped and sometimes excavated or slightly notched apically. Vagina long, membranous with accessory glands on anterior margin. Spermathecal stalk shorter than vagina; spermatheca sausage-like, often wrinkled, pointed apically and bearing a few accessory glands.

Egg. – Elongate oval to elliptical, with or without collar. Chorion smooth. Collar, when present, sessile, wide with smooth, unflanged rim; row of pits around collar base. Micropyles in posterior third; orifices sessile; canals slanted. Anchor, when present, mushroom-like with small flat cap and short pedicel.

Larva. – Mostly brown with subtle pattern of yellow on head and thorax. Occipital setal row complete. Pronotum with complete fringe of short thick setae. Abdominal tergal fringes of mixed long and short setae; often with mesal pair of prominent tergal intercalary setae. S7 posterior fringe incomplete. Black clothing hairs present. Cercal swimming hairs present. Anal gills absent.

Distribution. – Mainland Southeast Asia and Japan.

Valid specis.–
* *fortunati* (NAVÁS), n. comb. = *canilimbata* (ENDERLEIN), *grahami* BANKS, n. syn.
* *limbata* (PICTET) = *kawamurae* (OKAMOTO), *matsumurae* (OKAMOTO), n. syn.
* *perpicta* KLAPÁLEK = *bifoveolata* KLAPÁLEK, *elongata* (WU & CLAASSEN), *pichoni* (NAVÁS), n. syn.
* *sinensis* BANKS = *chekiangensis* (CHU), *klapaleki* BANKS, *tricolor* KLAPÁLEK, *valvulata* WU, n. syn.

Discussion. – The new synonymies listed above result from the study of all available types; the types of *elongata*, *bifoveolata*, *chekiangensis*, *valvulata* and *kawamurae* are lost.

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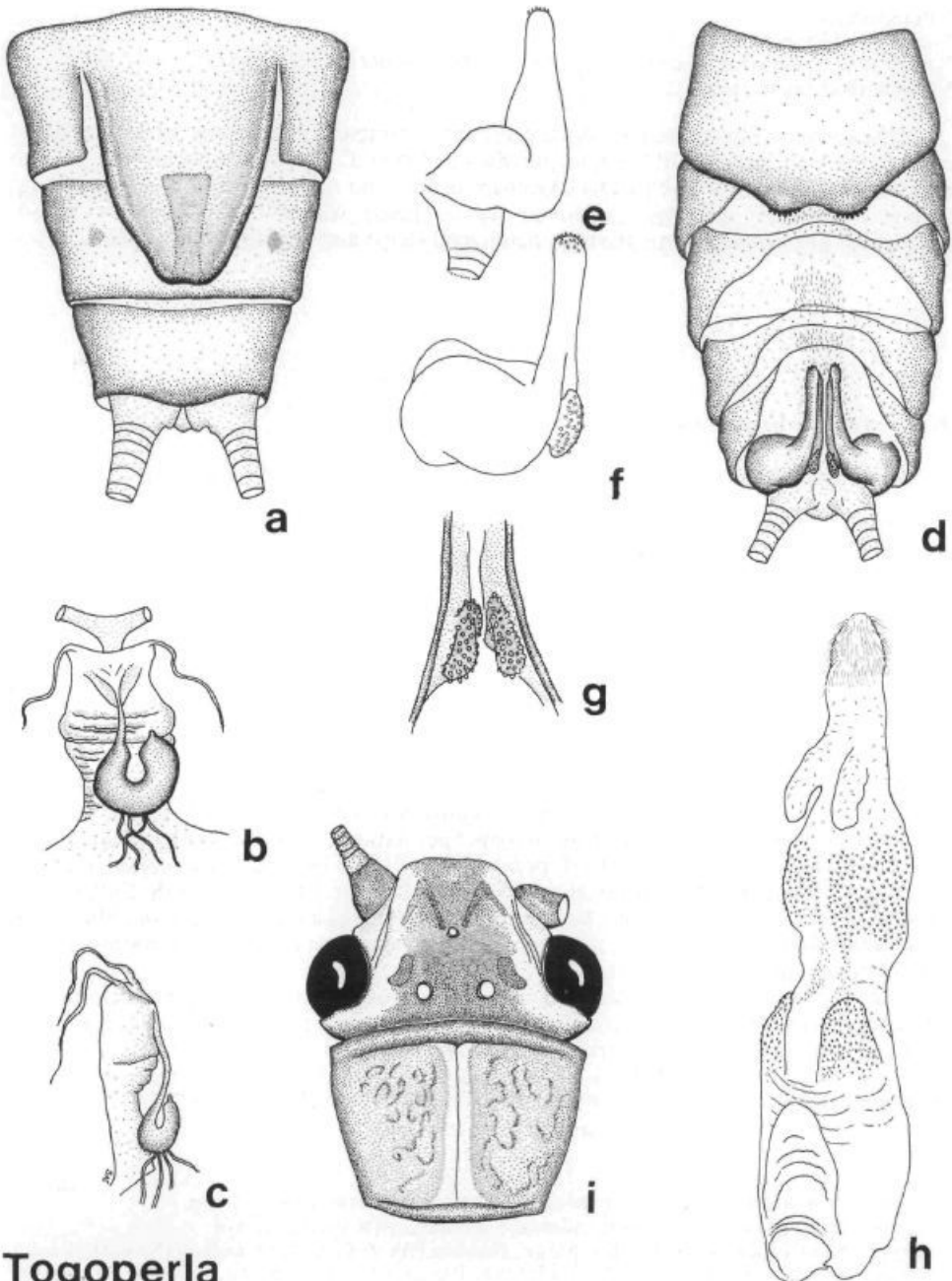

Fig. 6. *Togoperla perpicta* (KLAPÁLEK) [China]: Abdominal tip of female (a), vagina (b,c), abdominal tip of male (d), hemitergite (e,f), basal callus of hemitergites (g) everted penis (h), and head and prothorax (i).

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Togoperla

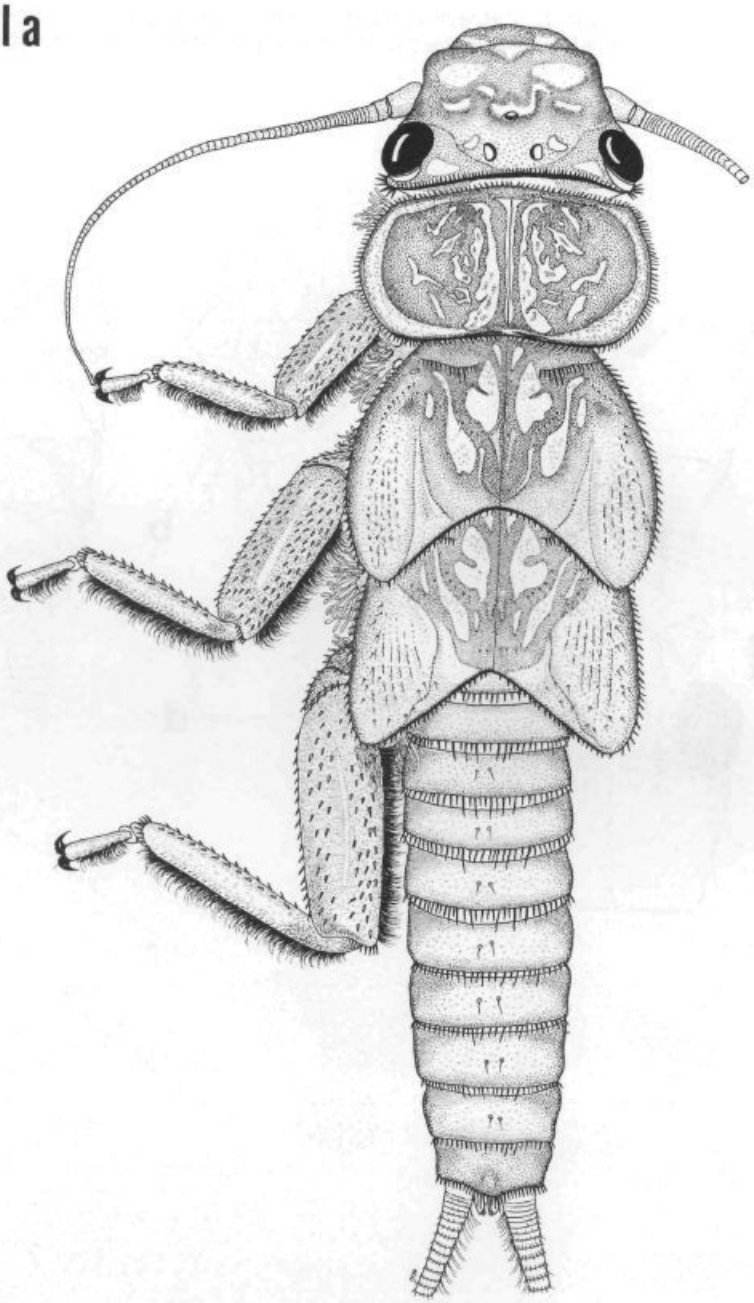

Fig. 7. *Togoperla limbata* (PICTET) [Japan]: Nymph habitus.

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The genitalia of the *T. tonkinensis* (NAVÁS) type is missing, since no figure of the genitalia exists in the literature, this species is unrecognizable. *Perla tennina* NEEDHAM has been included in *Togoperla* since KLAPÁLEK's (1907) study but it is a member of *Stavsolus* (Perlodidae).

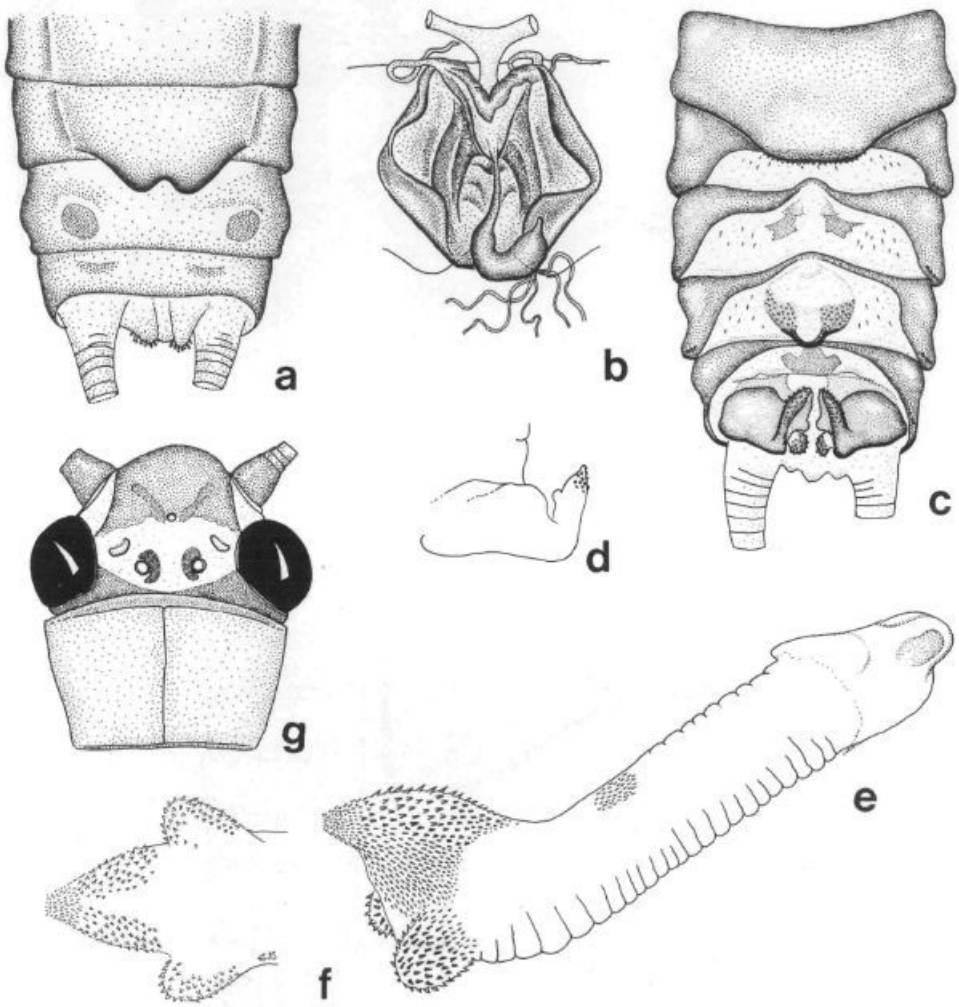

Fig. 8. *Paragnetina lacrimosa* (KLAPÁLEK) [China]: Abdominal tip of female (a), vagina (b), abdominal tip of male (c), hemitergite (d), everted penis (e), and ventral view of everted sac (f).

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9.3. *Paragnetina* KLAPÁLEK

Perla (Paragnetina) KLAPÁLEK (1907). Type species *Perla tinctipennis* MCLACHLAN, monotypy.
Banksiella KLAPÁLEK (1921). Type species *Sialis immarginata* SAY (misidentified as *Perla kansensis* BANKS), orig. desig., preoccupied (MUIR, 1917).
Banksiana CLAASSEN (1936). Replacement for *Banksiella* KLAPÁLEK.
Caucasoperla ZHILTZOVA (1967). Type species *Caucasoperla spinulifera* ZHILTZOVA, monotypy, n. syn.
Tylopyge KLAPÁLEK (1913). Type species *Tylopyge planidorsa* KLAPÁLEK, orig. desig.

Adult habitus. – Triocellate, medium to large, pale yellow to black species. Wings pale to black, veins brown to black. Macropterous. Mesal occipital knob absent.

Male genitalia. – T5 typically produced into a rounded, excavated or cleft lobe; lobe absent in *kansensis*, *spinulifera*, and *planidorsa*; lobe or membrane of T5 with sensilla basiconica. T6–8 typically sclerotized laterally and anteriorly, membranous mesally; T7–8 with at least some manifestation of mesal sclerite covered with sensilla basiconica; T8 mesal sclerite prolonged into a small posterior lobe. T9 typically membranous mesally with mesal sensilla basiconica patch. Hemitergites with short, broad to slender, pointed anterior process, and well developed basal callus; apex of anterior process and basal callus with sensilla basiconica. S3–7 with hair brushes. Penis envelope membranous; tube membranous with annulations, weakly to strongly sclerotized, or with distinct sclerites. Tube sometimes bearing small spiny lobes; sac lobed or simple, variously armed with triangular spines or rounded, scale-like spines.

Female genitalia. – Subgenital plate slightly to strongly produced, usually subtriangular and excavated, or notched apically. Vagina membranous, typically lined with fine golden seta-like spines; accessory glands present. Spermathecal stalk shorter than vagina. Spermatheca usually sausage-shaped, curled and bearing a few accessory glands.

Egg. – Elongate oval, typically with stalked, flanged collar. Collar typically short and wide, but long and narrow in media; rim typically irregularly incised. Chorionic surface smooth, granular or with shallow to deeply impressed FCIs. Micropyles usually large and numerous, set in posterior third; orifices sessile; canals usually not evident on surface. Anchor mushroom-like with short pedicel and globular cap.

Larva. – Brown to dark brown with or without distinctive pattern. Occipital setal row complete. Pronotum completely fringed laterally with stout spines. Abdominal tergal fringes of mixed long and short setae; terga with few stout intercalary setae; black clothing hairs present. Dorsum of body typically with mesal, longitudinal row of long, silky setae. S7 posterior fringe incomplete. Cercal swimming hairs present. Anal gills present or absent.

Distribution. – Mainland Southeast Asia, Japan, Taiwan, Soviet Far East, the Caucasus, Central Asia, eastern Nearctic.

Valid species.–
acutistyla WU
* *chinensis* (KLAPÁLEK), n. comb.
* *flavotincta* (MCLACHLAN)
* *fumosa* (BANKS)
* *hummelina* (NAVÁS), n. comb. = *pronotalis* (NAVÁS), *radialis* (NAVÁS), n. syn.
* *ichusa* STARK & SZCZYTKO
* *immarginata* (SAY)
indentata WU & CLAASSEN
* *japonica* (OKAMOTO)

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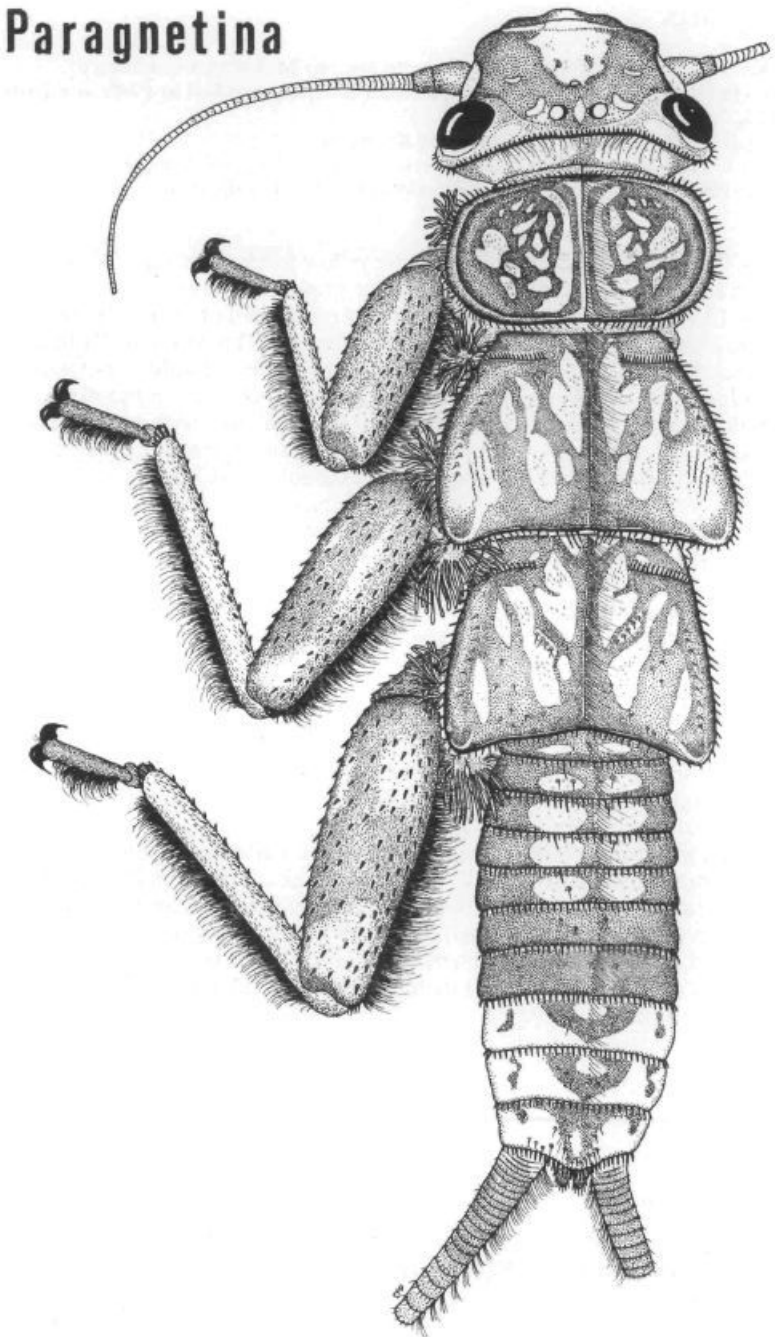

Fig. 9. *Paragnetina tinctipennis* (McLachlan) [Japan]: Nymph habitus.

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* *kansensis* (BANKS)
* *lacrimosa* (KLAPÁLEK)
* *ledoensis* STARK & SZCZYTKO
* *media* (WALKER)
* *ochrocephala* KLAPÁLEK= *burmana* NAVÁS, *esquiroli* NAVÁS, *oliveri* NAVÁS, *rubriceps* NAVÁS, n. syn.
* *pieli* (NAVÁS)
* *planidorsa* (KLAPÁLEK)
* *spinulifera* (ZHILTZOVA), n. comb.
* *suzukii* (OKAMOTO)
* *tinctipennis* (MCLACHLAN)

Discussion. – Types of *P. acutistyla*, *P. indentata*, *P. pieli*, *P. lutescens* NAVÁS, and *P. schenklingi* KLAPÁLEK are lost or unavailable. *P. pieli* is associated with our specimens on the basis of a distinctive color pattern and figures of external genitalia in WU (1938). *P. indentata* may be synonymous with *P. hummelina* but until better material is available, this association cannot be formalized. *P. acutistyla* was recently described by WU (1973) and the type should still exist, but has not been studied by us. The remaining names, *P. lutescens* and *P. schenklingi*, are regarded as nomina dubia. *P. bolivari* (KLAPÁLEK) is a member of the »*Acroneuria*« *jouklii* complex, and eight additional nominal *Paragnetina* have been removed to *Togoperla* or *Kamimuria* in this study. They are: *chekiangensis* CHU, *elongata* WU & CLAASSEN, *formosana* KLAPÁLEK, *fortunati* NAVÁS, *infumata* NAVÁS, *integra* KLAPÁLEK, *excavata* KLAPÁLEK, *tonkinensis* NAVÁS. The matter of fixing a type for *Banksiana* has been referred to the International Commission on Zoological Nomenclature by STARK & ZWICK, and the *Tylopyge* synonymy resulted from a recent study by ZWICK (1988).

9.4. *Oyamia* KLAPÁLEK

Perla (Oyamia) KLAPÁLEK (1907). Type species *Perla gibba* KLAPÁLEK= *Oyamia lugubris* (MCLACHLAN), orig. desig.

Adult habitus. – Triocellate, large, dark brown (Korean species with brightly banded legs, Japanese species with brown legs). Wings suffused, veins brown. Macropterous. Mesal occipital knob absent.

Male genitalia. – T5 with a massive, bilobed, heavily sclerotized process. T6 with or without a broadly bilobed process. T6–8 with mesal membranous field, anterior and lateral margins sclerotized. Hemitergites massive, complexly bilobed and heavily sclerotized; apex of lower lobe and inner basal margins of upper lobe with sensilla basiconica; lateral base of hemitergite with a sclerotized knob. S4–8 with hair brushes. Penis envelope with mesolateral patches of fine seta-like spines; tube armed with fine transparent spines; sac membranous, without armature; entire penis simple, without complex lobes or sclerites.

Female genitalia. – Subgenital plate short, extending over about a third of S9; apical margin rounded or slightly excavated. Vagina membranous with paired basal sclerites, accessory glands present. Spermathecal stalk slender, shorter than vagina; spermatheca about equal to stalk in length, sausage-shaped, and attenuated apically; multiple accessory glands present.

Egg. – Elongate oval with short wide collar. Rim slightly flanged, smooth and irregularly scalloped; ribs on collar numerous. Chorion mostly smooth or with irregular punctations and irregular FCIs around collar. Micropyles subequatorial; orifices sessile, round and well defined; canals straight. Anchor mushroom-like; pedicel short; cap flat, unspecialized.

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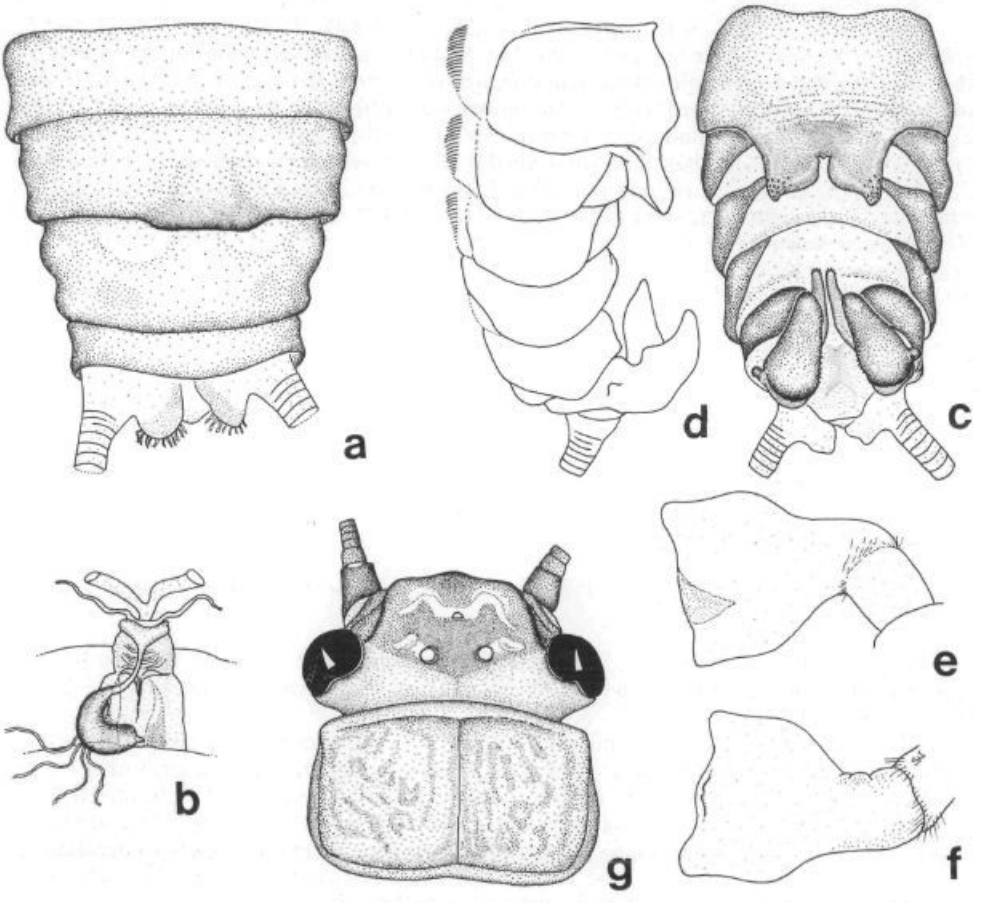
Larva. – Distinctly patterned in yellow and brown; most abdominal terga with pale spots or transverse bars. Occipital setal row complete. Pronotal fringe of short thick setae, complete laterally. Abdominal tergal fringes primarily with short thick setae interspersed with a few long ones. Black clothing hairs present. S7 posterior fringe complete. Cercal swimming hairs absent. Anal gills present.

Distribution. – Japan, Korea, northeastern China and Soviet Far East.



Oyamia

Fig. 10. *Oyamia lugubris* (McLachlan) [Japan]: Abdominal tip of female (a), vagina (b), abdominal tip of male (c, in lateral view d), everted penis (e,f), and head and prothorax (g).

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Oyamia

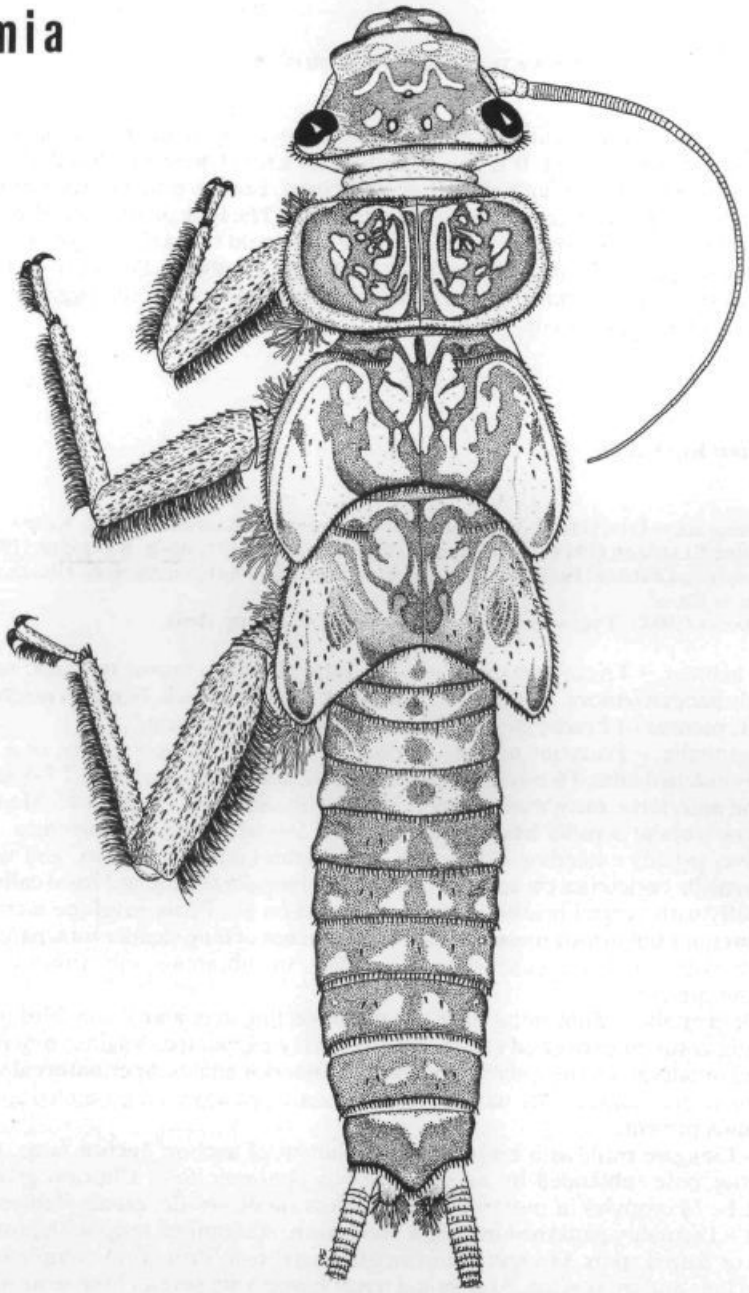

Fig. 11. *Oyamia lugubris* (McLachlan) [Japan]: Nymphs habitus.

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Valid species.–
* *lugubris* McLachlan
* *nigribasis* Banks = *coreana* (Okamoto), *amurica* Klapálek, n. syn.
* *seminigra* (Klapálek) = *lezeyi* (Navás), n. syn.

Discussion. – *O. coreana* and *O. amurica* are synonymized with *O. nigribasis*. The type of *coreana* is very possibly lost. It is not located at Hokkaido University, Sapporo, where all survived specimens of Okamoto's stoneflies are housed. But his original description agrees well with *nigribasis* in color patterns and male genitalia. The type of *amurica* also could not be examined by us. The synonymy is based on the agreement between the type of *nigribasis* and the redescription of *amurica* by Zhiltzova & Zapekina-Dulkeit (1986). The synonymy of *lezeyi* with *seminigra* was proved by characteristics of the eggs (Isobe, 1988) from the *lezeyi* holotype female.

9.5. *Agnetina* Klapálek

Perla (Agnetina) Klapálek (1907). Type species *Perla elegantula* Klapálek, desig. Klapálek (1923).
Phasganophora Klapálek (1914). Type species *Perla capitata* Pictet, desig. Klapálek (1921).
Neophasganophora Lestage (1921). Unnecessary replacement for *Phasganophora* Klapálek, not *Phasgonophora* Gray.
Harrisiola Banks (1948). Type species *Perla flavescens* Walsh, orig. desig.

Adult habitus. – Triocellate, medium size, generally dark brown to black; sometimes with brightly banded femora. Wings dark, veins dark brown to black. Females macropterous, males macropterous or brachypterous. Mesal occipital knob absent.

Male genitalia. – Posterior margin T5 produced into paired low knobs, or a rounded, or shallowly notched lobe. T6 usually with broadly bilobed anterior sclerite; T7–8 sclerotized laterally and anteriorly, membranous mesally; T9 with slender mesal sclerite. Membrane of T7–9 with or without sensilla basiconica; lobes of T5–6 with sensilla basiconica. Hemitergites massive, usually extending beyond T9, sometimes complexly lobed, and with large, spine-like sensilla basiconica on apex, and scattered along dorsal margin; basal callus absent. S5–7 typically with ventral brushes, usually strongest on S6. Penis envelope membranous; tube membranous but armed mesally with paired patches of long slender transparent spines, and apically with small triangular spines; sac short, membranous and without armature. Basal sclerite present.

Female genitalia. – Subgenital plate usually projecting over about one third to one half of S9; margin entire or excavated and frequently darkly pigmented. Vagina sometimes with paired basal or lateral sclerites; accessory glands at anterior angles. Spermathecal stalk slender and shorter than vagina; spermatheca slender basally, enlarged and rounded apically; accessory glands present.

Egg. – Elongate oval, with button-like attachment of anchor; anchor large, umbrella-like. Anterior pole subtended by an inconspicous chorionic fold. Chorion granular and without FCIs. Micropyles in posterior third; orifices small, sessile; canals slanted.

Larva. – Distinctly patterned in yellow and brown. Abdominal terga with posterior yellow bands or paired spots. Occiput with complete setal row. Pronotum completely fringed with mixed long and short setae. Abdominal tergal fringes with several long setae mixed with short thick ones. Black clothing hairs present. S7 posterior fringe complete. Cercal swimming hairs absent. Anal gills present.

Distribution. – Nearctic, Palearctic, mainland Southeast Asia, Taiwan.

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Valid species.–
acutipennis KLAPÁLEK
* *aequalis* (BANKS), n. comb.
* *annulipes* (HAGEN)
* *armata* (BANKS)
* *brevipennis* (NAVÁS)
* *capitata* (PICTET)
chrysodes (NAVÁS)
* *circumscripta* (KLAPÁLEK), n. comb.
dubia ZWICK
duplistyla (WU)
* *elegantula* (KLAPÁLEK)
* *extrema* (NAVÁS) = *senilis* (KLAPÁLEK), *costulata* (NAVÁS), *undata* (KLAPÁLEK), *pedata* (KOPONEN), ? n. syn.

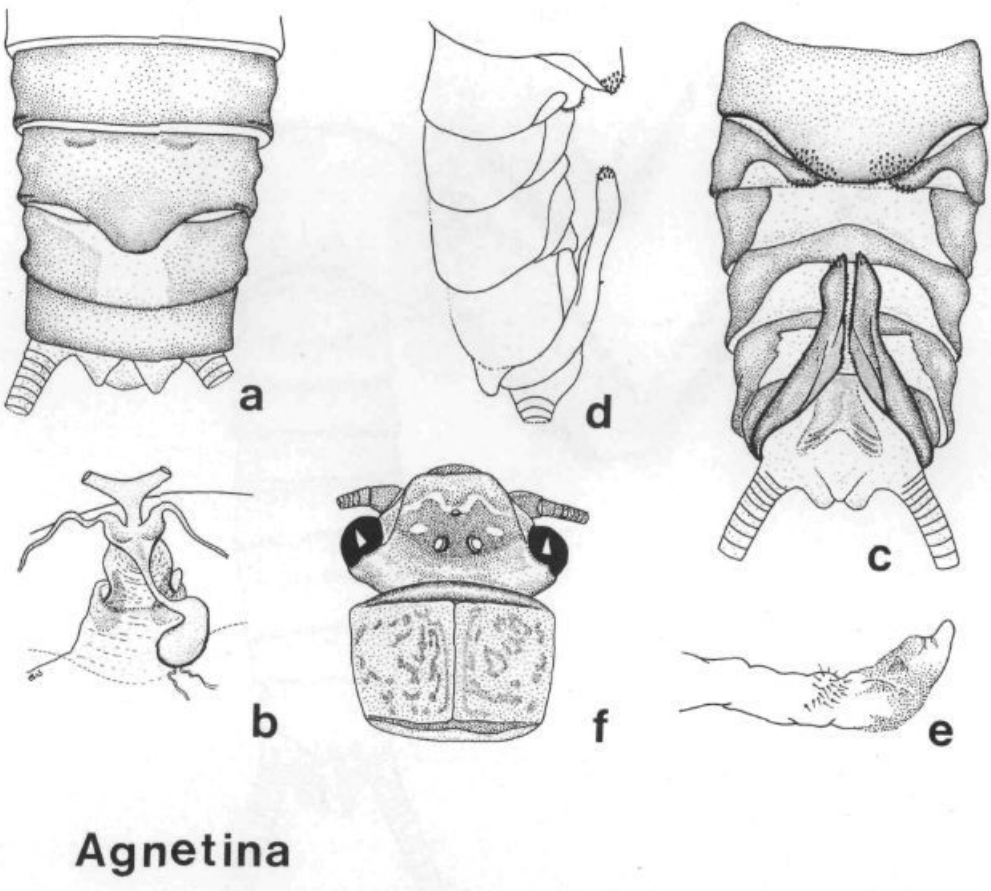

Fig. 12. *Agnetina capitata* (PICTET) [Canada]: Abdominal tip of female (a), vagina (b), head and prothorax (f), abdominal tip of male (c, in lateral view d); *Agnetina brevipennis* (NAVÁS) [Mongolia]: everted penis (e).

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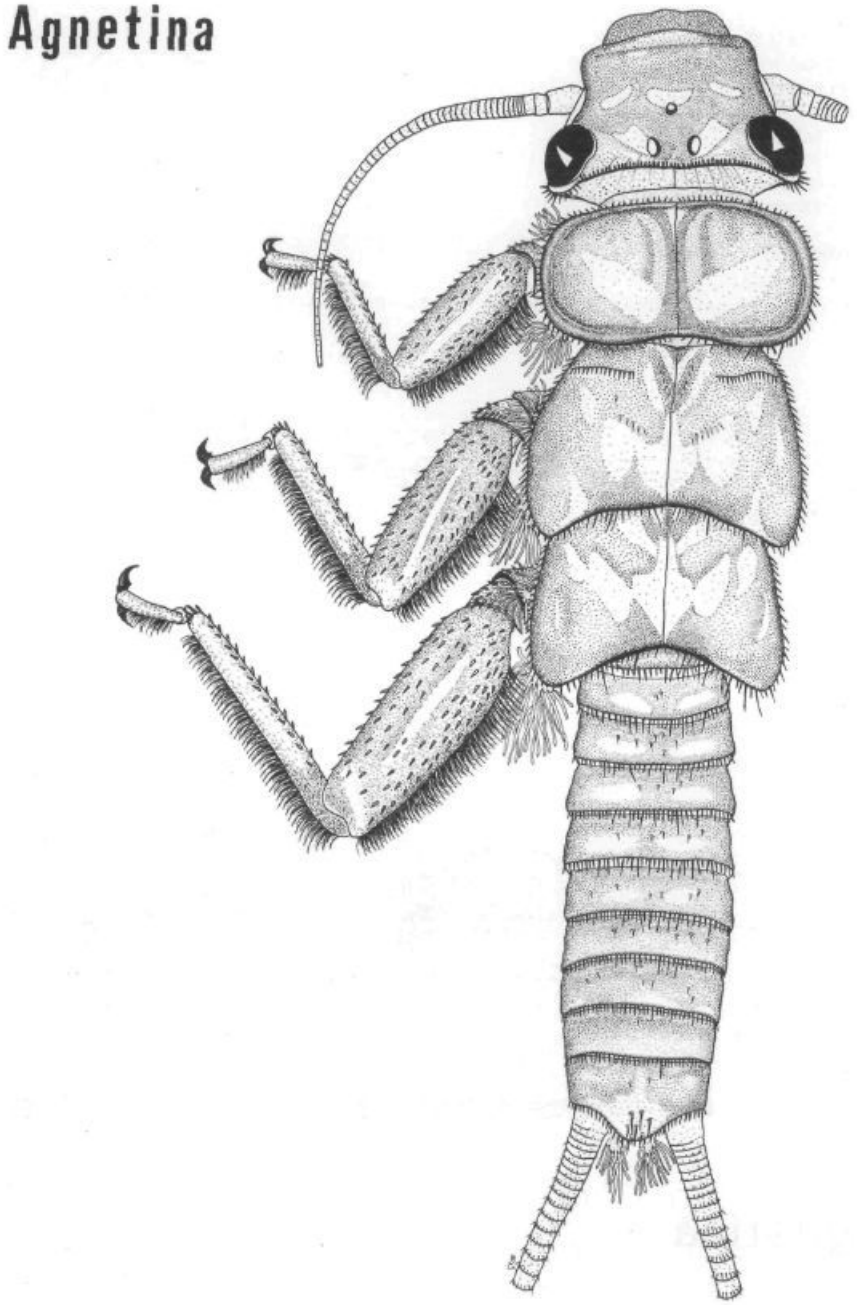

Fig. 13. *Agnetina flavescens* (WALSH) [USA]: Nymph habitus.

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* *flavescens* (WALSH)
gladiata (WU)
multispinosa (WU)
navasi (WU), n. comb.
* *praeusta* (KLAPÁLEK), n. comb.
* *quadrituberculata* (WU) n. comb.
spinata (WU)
* *werneri* (KEMPNY)

Discussion. – STARK (1986) noted the Nearctic species of *Agnetina* are apparently the sister group of *A. elegantula* from Europe. Earlier, STARK & GAUFIN (1976) suggested this might be due to a trans-Atlantic dispersal, but it now seems more probable that an Oriental, *elegantula*-like ancestor dispersed westward into eastern Europe and eastward across the Bering Bridge as part of the Pliocene faunal exchange between Asia and eastern North America. ZWICK (1984) and STARK (1986) have recently reviewed European and Nearctic *Agnetina*.

9.6. *Marthamea* KLAPÁLEK

Perla (Marthamea) KLAPÁLEK (1907). Type species *Perla vitripennis* BURMEISTER, desig. KLAPÁLEK (1923).
Perla (Lerpa) NAVÁS (1909). Type species *Lerpa beraudi* NAVÁS.

Adult habitus. – Triocellate, medium size and generally dark brown to black. Wings transparent, veins dark, costal field pale. Usually macropterous, some males brachypterous. Mesal occipital knob absent.

Male genitalia. – Posterior margin T5 produced into a rounded or shallowly notched lobe covered posteriorly with sensilla basiconica. T6–8 sclerotized laterally and anteriorly, membranous mesally; dense mesal patch of sensilla basiconica present on at least T7. T9 completely sclerotized around anterior margin. Hemitergites bilobed in lateral aspect; ventral lobe slender, dorsal lobe broad; both lobes with apical sensilla basiconica. Dorsal aspect of hemitergites with inner basal callus covered with sensilla basiconica. S6–7 with mesal hair brushes but less well developed on S7. Penis envelope membranous, tube weakly sclerotized, transversely annulate and unlobed; sac larger than tube and armed with variable size, thick triangular spines; basal sclerite present.

Female genitalia. – Subgenital plate slightly projecting over anterior margin S9. Vagina membranous, slender accessory glands at anterior angles. Spermathecal stalk slender; spermatheca small, apex rounded, accessory glands present.

Egg. – Elongate oval, with button-like attachment of anchor; anchor large, umbrella-like. Anterior pole subtended by chorionic fold. Chorion granular without FCIs. Micropyles in posterior third; orifices small with slightly raised lip; canals slanted.

Larva. – Distinctly patterned in yellow and brown. Head mostly yellow, but dark between posterior ocelli. Abdominal terga with posterior yellow bands or paired spots. Occiput with complete setal row. Pronotum completely fringed with mixed long and short setae. Abdominal tergal fringes of long and short setae. Black clothing hairs scattered over dorsal body surface. S7 with posterior fringe interrupted. Cercal swimming hairs absent. Anal gills present or absent.

Distribution. – Europe and Middle East.

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Valid species.–
* *beraudi* (NAVÁS)
* *selysii* (PICTET)
* *vitripennis* (BURMEISTER)

Discussion. – *Marthamea* was redefined and the Palearctic species revised by ZWICK (1984), who also noted the great similarity in egg and larval characters with *Agnetina*, the apparent sister group. Our study of the types of Asian perlids sometimes included in *Marthamea*, indicates that all Oriental species belong to other genera and that *Marthamea* is a European-Middle Eastern genus. *Marthamea* is a potamophilic group, and according to ZWICK (1984) many European populations are endangered, or already extinct.

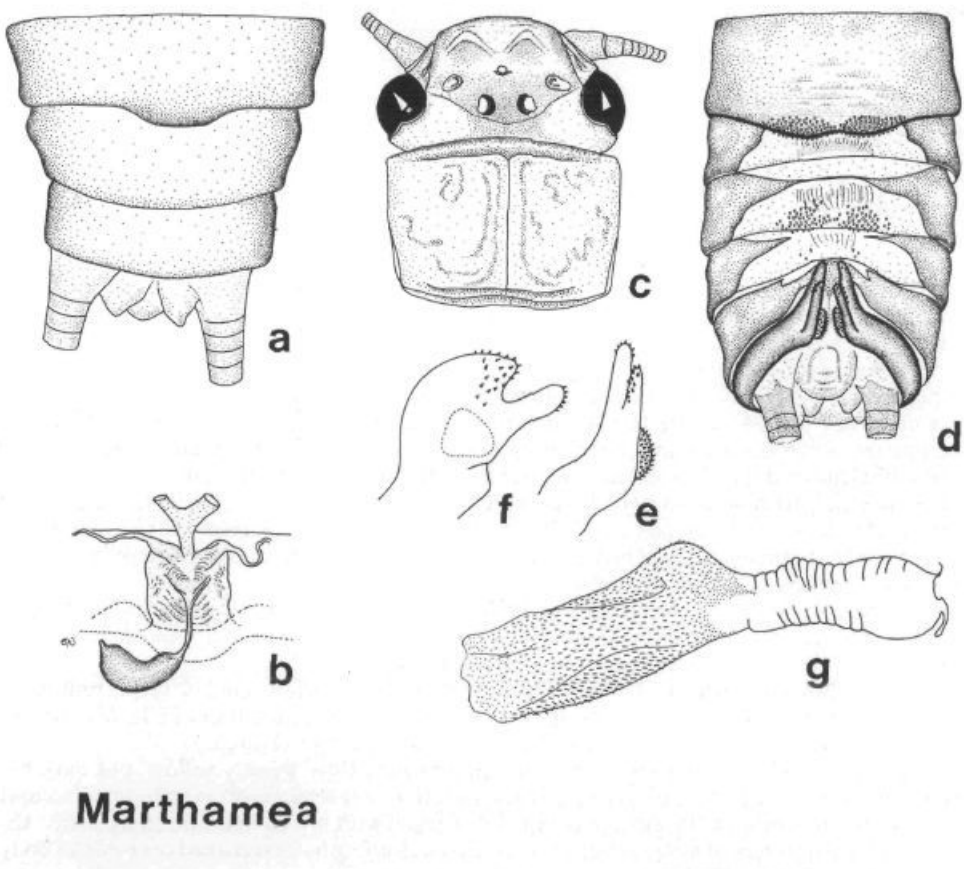

Fig. 14. *Marthamea selysii* (PICTET) [Spain]: Abdominal tip of female (a), vagina (b), head and prothorax (c), abdominal tip of male (d), hemitergite in dorsal (e), and lateral view (f), and everted penis (g).

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Marthamea

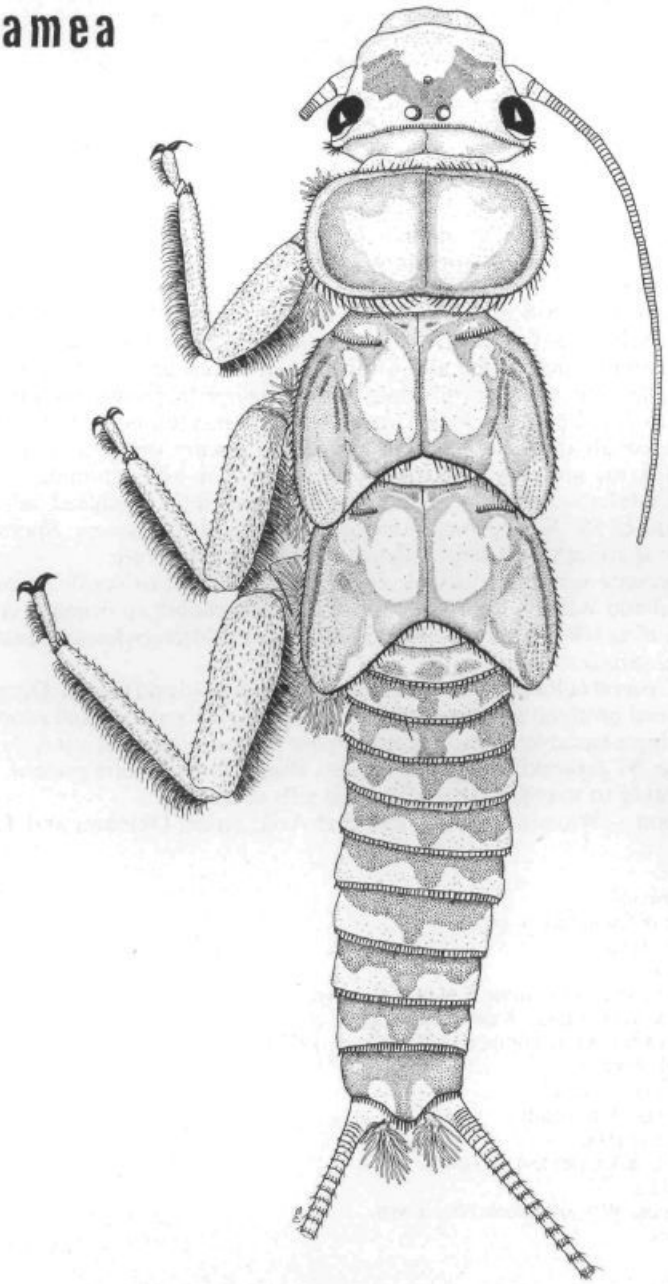

Fig. 15. *Marthamea selysii* (PICTET) [Spain]: Nymph habitus.

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9.7. *Kamimuria* KLAPÁLEK

Perla (Kamimuria) KLAPÁLEK (1907). Type species *Perla tibialis* PICTET, desig. KLAPÁLEK (1923).

Adult habitus. – Triocellate, medium to large, pale brown to brown. Wings pale or suffused, veins brown. Females macropterous, males brachypterous or macropterous. Mesal occipital knob absent.

Male genitalia. – T5–8 unmodified; T7–8 sometimes with sensilla basiconica. T9 frequently with small mesal lobe and median sclerite covered with sensilla basiconica. Hemitergites short, simple, finger-like, and without basal callus; apex with sensilla basiconica. S4–7 and metasternum with hair brushes. Penis envelope frequently with fine spines; tube sometimes with small paired sclerites, more typically membranous; tube typically armed with stout and small spines; sac shorter than tube, usually with a few simple lobes and variously armed; sac armature in some species massive, in others minute.

Female genitalia. – Subgenital plate weakly to moderately produced, seldom extending over basal third of S9. Vagina membranous, accessory glands absent. Spermathecal stalk small, slender; spermatheca a large inflated, balloon-like structure.

Egg. – Elongate oval with variable collar. Collar stalked or sessile, usually wide; rim usually flanged and weakly incised. Chorionic surface smooth to ornately sculptured; frequently sculpturing takes the form of large, shallow pits. Micropyles subequatorial; orifices usually sessile, canals straight.

Larva. – General color brown with subtle pattern on head and thorax. Occipital setal row complete. Lateral pronotal fringe complete, consisting of mixed long and short setae. Abdominal tergal fringes variable; a few long setae on more basal segments; intercalary setae abundant, or sparse. S7 posterior fringe incomplete. Black clothing hairs present. Cercal swimming hairs weakly to strongly expressed. Anal gills absent.

Distribution. – Widespread over mainland Asia, Japan, Okinawa and Taiwan.

Valid species.–
* *amoena* KLAPÁLEK
* *brunneicornis* (KLAPÁLEK), n. comb.
* *coarctata* KLAPÁLEK
  crocea HARPER
* *exilis* (MCLACHLAN) = *luteicauda* KLAPÁLEK, n. syn.
* *fulvescens* KLAPÁLEK = *latior* KLAPÁLEK, n. syn.
* *formosana* (KLAPÁLEK), n. comb. (not OKAMOTO, 1912)
  himalayana HARPER
* *infumata* (NAVÁS), n. comb.
* *integra* (KLAPÁLEK), n. comb.
* *kelantonica* KLAPÁLEK
* *klapalekia* (WU & CLAASSEN), n. comb.
* *lepida* KLAPÁLEK
  liui WU = *brevata* WU, *spinulata* WU, n. syn.
* *lutulenta* ZWICK
  nigrita WU
  orthogonia WU
* *quadrata* KLAPÁLEK
  sahlbergi KOPONEN
  senticosa HARPER

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* *sikkimensis* (ENDERLEIN), n. comb.
* *similis* KLAPÁLEK
* *tibialis* (PICTET)
trapezoidea WU
tuberosa WU

Discussion. – The species list above excludes 14 *Kamimuria* names proposed by WU prior to 1962, for which type material is lost, and 2 NAVÁS and 2 KLAPÁLEK *Kamimuria* under similar circumstances. We have also excluded 14 Asian species described by various authors

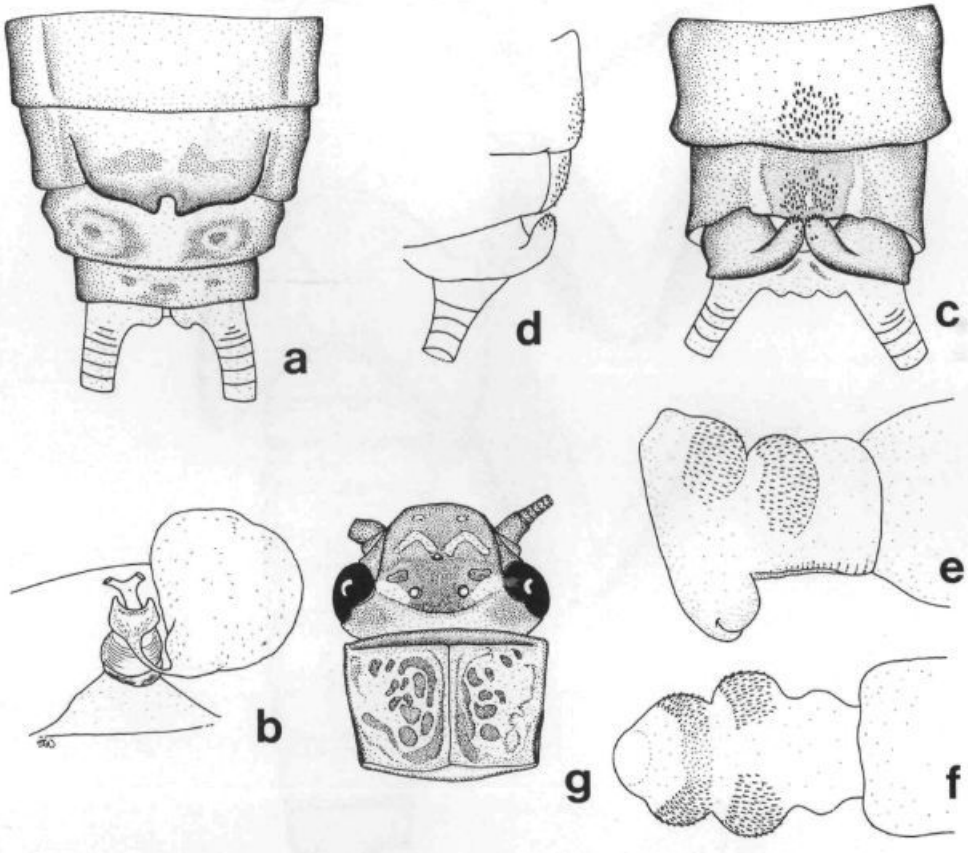

Fig. 16. *Kamimuria tibialis* PICTET [Japan]: Abdominal tip of female (a), vagina (b), head and prothorax (g), abdominal tip of male (c), in lateral view (d), and everted penis (e,f).

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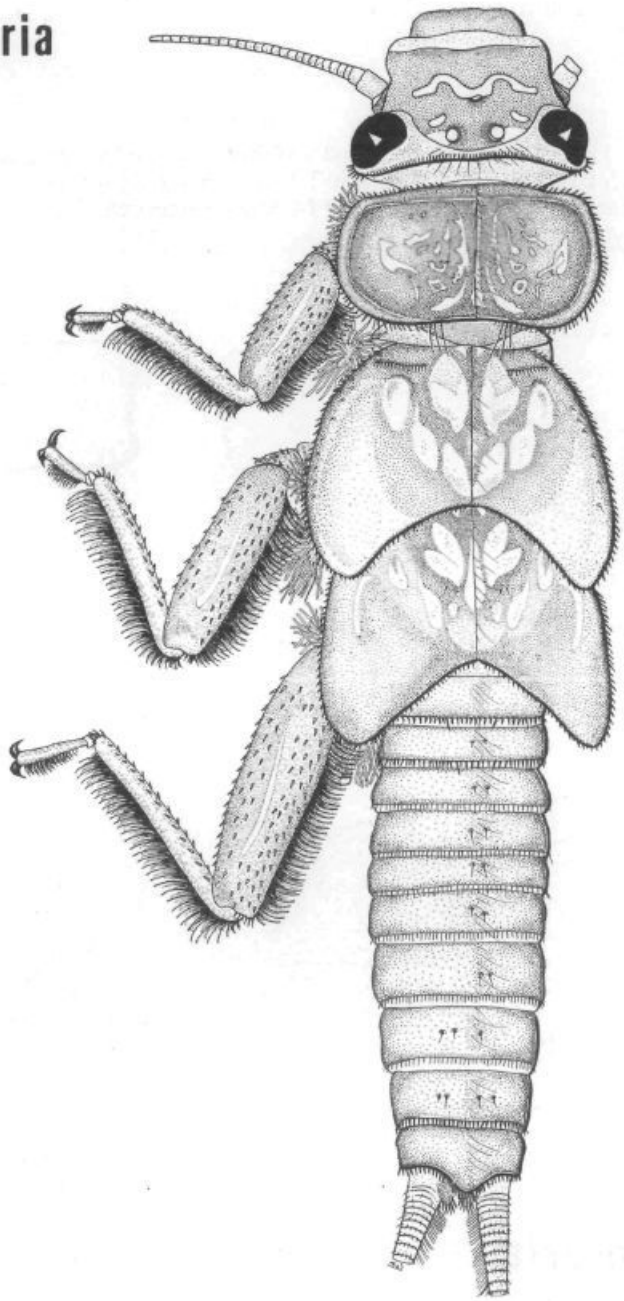

Fig. 17. *Kamimuria tibialis* PICTET [Japan]: Nymph habitus.

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in the late 19th or early 20th century in the genus *Perla*. Lost type material and inadequate descriptions preclude their inclusion in *Kamimuria* or other perline genera at present. *Perla nirvana* BANKS, *P. melanophtalma* NAVÁS, and *Kamimuria flavata* NAVÁS, 1933 (not *Perla (Kamimuria) flavata* NAVÁS, 1923) are also excluded from Perlinae and are considered as undetermined Acroneuriinae. Six other species (*Perla anamensis* BANKS, *P. shestoperowi* NAVÁS, *P. stictica* NAVÁS, *Paragnetina excavata* KLAPÁLEK, *Kamimuria polainina* NAVÁS, *K. ramosa* NAVÁS) are known from female types which could not be associated with any generic name.

Our preliminary study of types, and other *Kamimuria* specimens, indicate several, rather distinctive, species groups are included. We presently recognize 7 groups; the largest group *(lutulenta)* includes 4 named species from the Himalayas. UCHIDA & ISOBE are revising the *tibialis* group from Japan.

9.8. *Etrocorema* KLAPÁLEK

Etrocorema KLAPÁLEK (1909). Type species *Etrocorema ahenobarba* KLAPÁLEK= *Ochthopetina nigrogeniculata* ENDERLEIN, Monotypy.
Euryplax KLAPÁLEK (1909). Type species *Euryplax ochrostoma* KLAPÁLEK, Preoccupied (STIMPSON, 1859).
Neoeuryplax CLAASSEN (1936). Replacement for *Euryplax* KLAPÁLEK.

Adult habitus. – Biocellate, medium to large size and generally brown to dark brown. Wings suffused brown with dark brown veins. Females and males macropterous. Mesal occipital knob present.

Male genitalia. – T5–8 unmodified; T7–8 typically with patches of sensilla basiconica. T9 anterior sclerite produced mesally, partially dividing membranous field; usually a few sensilla basiconica scattered in membrane. Hemitergites simple, finger-like, extending to posterior margin of T9; apex with dense patch of sensilla basiconica. S6 and metasternum with hair brushes. Penis envelope membranous; tube weakly sclerotized and transversely annulate mesally; sac shorter than tube, apex expanded, multilobed and armed with thick spines; largest spines anteapical; fine long seta-like spines in lateral patches near base of sac; broad basal sclerite present.

Female genitalia. – Subgenital plate massive, completely covering S9 and usually extending beyond lateral margins of abdomen. Apex of plate with shallow, narrow notch. Vagina membranous with accessory glands; spermathecal stalk short; spermatheca small, bulbous.

Egg. – Elongate oval, with wide short collar. Rim of collar smooth with irregular incisions; flange absent; sides with numerous ribs. Chorionic surface smooth except for posterior pole which has shallow FCIs surrounding clusters of pits. Micropyles subequatorial; orifices sessile; canals straight. Anchor pedicel short, cap complexly and finely divided, appearing to consist of numerous fine strands; margins of cap with long finger-like projections.

Larva. – Almost uniformly brown with subtle pattern on dorsal surface. Occipital ridge devoid of setae except near postocular fringe. Pronotal fringe complete, consisting of uniformly long, thick setae. Abdominal tergal fringes of mixed long and short thick setae. S7 posterior fringe incomplete. Clothing hairs red-brown. Anal gills absent. Cercal swimming hairs sparse.

Distribution. – Southeast Asian mainland, Sumatra, Borneo.

Valid species.–
hochii (WU)
* *nigrogeniculatum* (ENDERLEIN)

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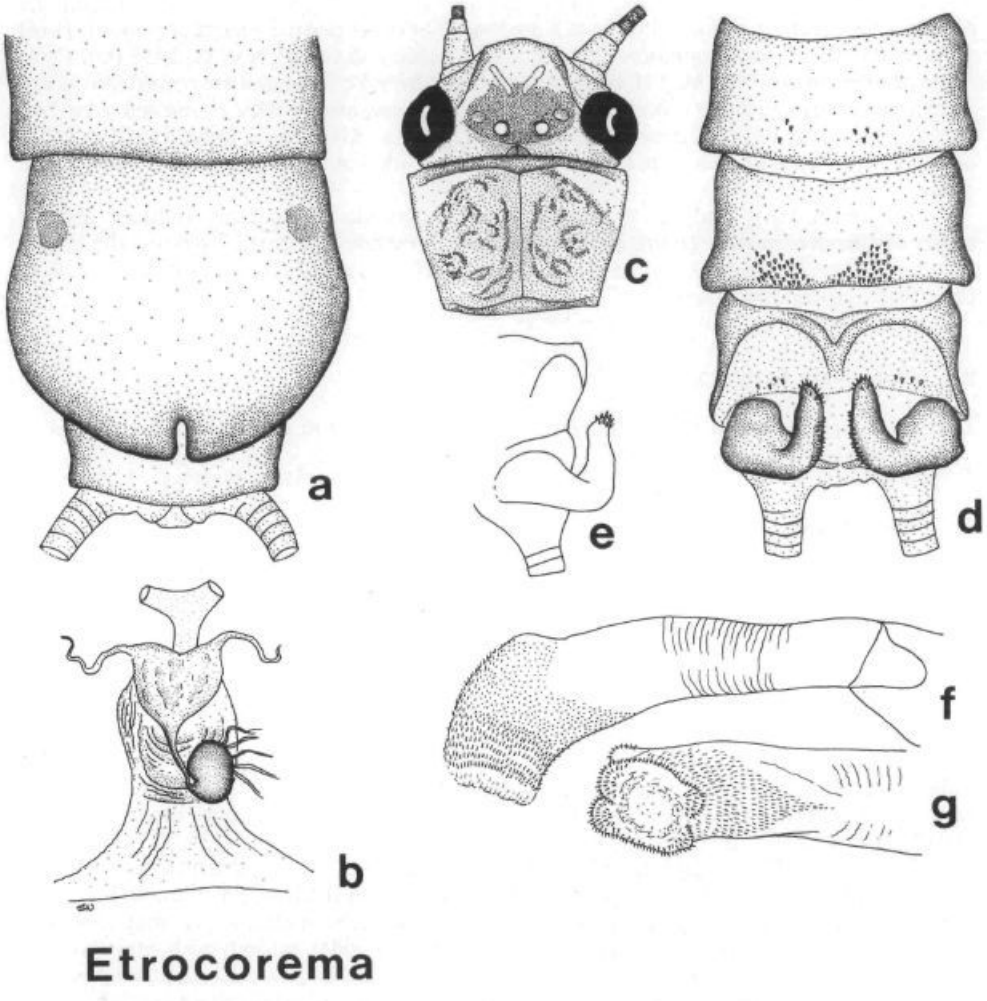

Fig. 18. *Etrocorema nigrogeniculatum* (ENDERLEIN) [India]: Abdominal tip of female (a), vagina (b), head and prothorax (c), abdominal tip of male (d), hemitergite (e), everted penis (f), and ventral view of everted sac (g).

Discussion. – ZWICK (1973) described the lectotype male of *E. nigrogeniculatum* and in other papers (1982b, d, 1984) he clarified the systematics of the genus placing several species and generic names in synonymy. The present concept of a single variable *Etrocorema* species throughout Southeast Asia should be tested by SEM examination of eggs from several populations when additional specimens are available. We observe rather conspicuous differences in head and leg colouration, and a few subtle differences in egg chorion detail and penis setation among the specimens available to us.

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Etrocorema

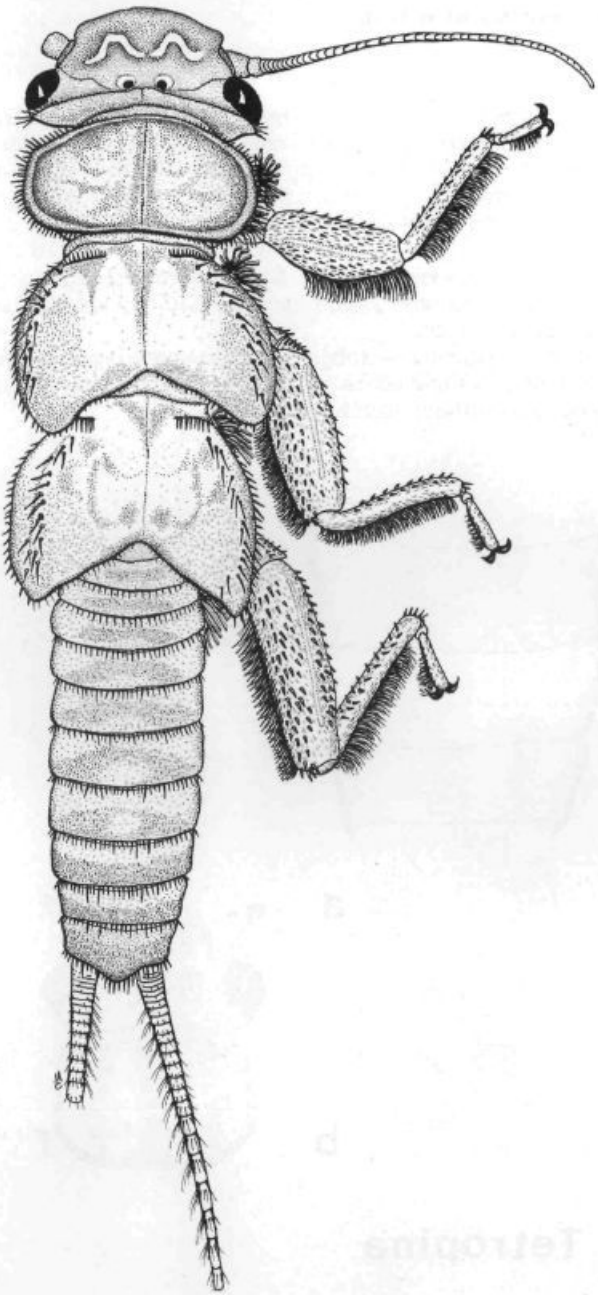

Fig. 19. *Etrocorema nigrogeniculatum* (ENDERLEIN) [Thailand]: Nymph habitus.

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9.9. *Tetropina* KLAPÁLEK

Tetropina KLAPÁLEK (1909). Type species *Ochthopetina fulgescens* ENDERLEIN, orig. desig.

Adult habitus. – Biocellate, medium to large, and generally pale brown; head and pronotum usually with conspicuous pattern of dark on light background. Mesal occipital knob present. Tentorial callosities adjacent to ocelli, directed posteriorly and longer than wide.

Male genitalia. – T5–9 unmodified. T9 with sparse posteromesal patch of sensilla basiconica. Hemitergites simple, short, rounded apically and densely covered with sensilla basiconica on apex. S6–8 and metasternum with hair brushes. Penis envelope membranous; tube armed with wide, rounded scale-like spines; sac shorter than tube, with large basal lobe; sac armed with variably sized spines in a continuous apical band; smaller spines nearer apex; basal sclerite present.

Female genitalia. – Subgenital plate unproduced, or slightly produced. Vagina small, membranous without accessory glands. Spermathecal stalk longer than vagina; spermatheca bulbous and without accessory glands.

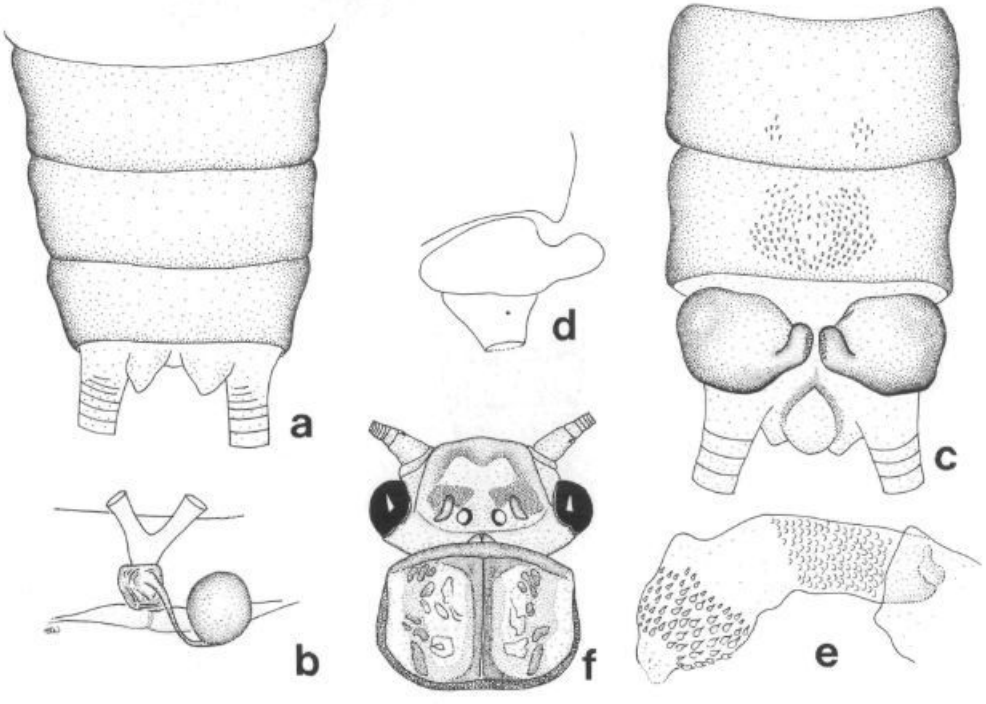

Fig. 20. *Tetropina larvata* KLAPÁLEK [Malaysia]: Abdominal tip of female (a), vagina (b), head and prothorax (f), abdominal tip of male (c), hemitergite (d), and everted penis (e).

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Tetropina

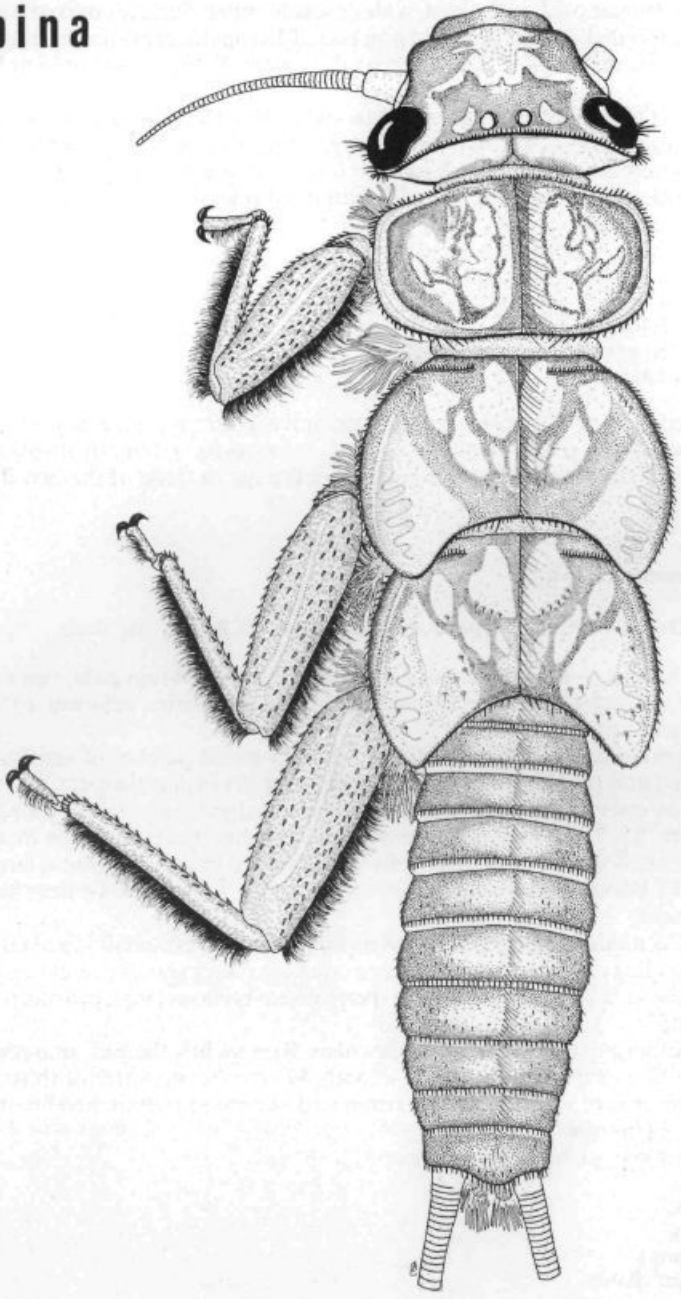

Fig. 21. *Tetropina larvata* KLAPÁLEK [Malaysia]: Nymph habitus.

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Egg. – Elongate oval, with short, wide or sessile collar. Surface covered with shallow FCIs which surround shallow pits or raised processes. Micropyles in posterior third; orifices sessile, sometimes surrounded by FCI rosette; canals straight. Eclosion line present below micropylar row. Anchor cap complexly lobed; pedicel short.

Larva. – Distinctly patterned in yellow and brown. Occipital setal row complete. Lateral pronotal fringe incomplete. Abdominal tergal fringes of stout setae; stout intercalary setae mainly in anterolateral patches. Black clothing hairs present. S7 posterior fringe complete. Cerci without swimming hairs. Mesal longitudinal row of long silky setae on body dorsum. Anal gills present.

Distribution. – Borneo, Malaysia.

Valid species.–
* *fulgescens* (ENDERLEIN)
* *kraepelini* (KLAPÁLEK), n. comb.
* *larvata* KLAPÁLEK

Discussion. – ZWICK (1984) gave comparative figures for male genitalia and eggs of the Bornean species, *T. larvata* and *T. fulgescens*. *T. kraepelini* is tentatively placed in this genus on the basis of the overwhelming similarity of the egg to those of the two Bornean species.

9.10. *Neoperlops* BANKS

Neoperlops BANKS (1939). Type species *Neoperlops gressitti* BANKS, orig. desig.

Adult habitus. – Biocellate, large and generally pale. Wings pale, veins brown. Macropterous. Mesal occipital knob present. Tentorial callosities adjacent to ocelli, directed anteriorly, and longer than wide.

Male genitalia. – T5–9 unmodified. T9 with mesal patches of sensilla basiconica on slightly raised humps. Hemitergites short, acute apically in dorsal aspect, and without sensilla basiconica on apex; inner basal side of hemitergites slightly swollen, forming a basal callus-like structure. S5–7 and metasternum with hair brushes. Penis envelope membranous; tube armed with small spines; sac armed with variably sized triangular spines; largest spines form median and 2 lateral patches near apex; membranous, unarmed lobe near base of sac. Basal sclerite present.

Female genitalia. – Subgenital plate slightly produced as a small mesal tab, often recessed and not extending over S9. Vagina membranous, accessory glands present on anterior angles. Spermathecal stalk longer than vagina; spermatheca bulbous large, bearing a single small accessory gland.

Egg. – Elongate oval with short wide collar. Rim slightly flanged, smooth and irregularly incised. Chorion coarsely punctate or smooth. Micropyles in posterior third; orifices sessile. Eclosion line absent. Anchor pedicel composed of numerous bunched fibers; usually short.

Larva. – Unknown.

Distribution. – China, Viet Nam.

Valid species.–
cheni (WU)
* *gressitti* BANKS
* *obscuripennis* BANKS

Discussion. – ZWICK's (1984) treatment provides the systematic basis for this group. Only scattered, fragmentary material has been available for our study.

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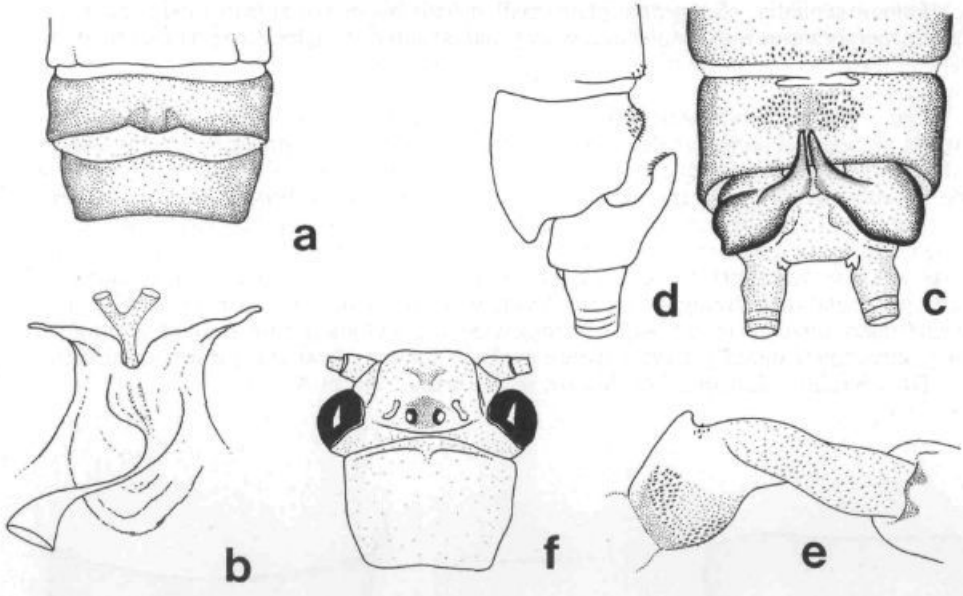

Neoperlops

Fig. 22. *Neoperlops gressitti* BANKS [China]: Abdominal tip of female (a), vagina (b), head and prothorax (f), abdominal tip of male (c, in lateral view d), and everted penis (e).

9.11. *Perla* GEOFFROY

Perla GEOFFROY (1762). Type species *Perla bipunctata* PICTET, desig. ICZN Opinion 6451 (1963).
Esera NAVÁS (1909). Type species *Esera fraterna* NAVÁS = *Perla grandis* (RAMBUR).

Adult habitus. – Triocellate, medium to large, and generally brown to dark brown. Wings suffused, veins dark brown. Females macropterous, males macropterous or brachypterous. Mesal occipital knob weak or absent.

Male genitalia. – T5–7 unmodified, T8 sometimes membranous mesally. Sclerotized anterior margin T9 projecting into mesal field, partially dividing tergum; mesal field with a group of spiny projections, sometimes grouped in longitudinal rows. Hemitergites short, rounded apically and covered apically with sensilla basiconica; projecting portion of hemitergite longer than wide; basal callus absent. Sterna usually without noticeable hair brushes, but sometimes weakly manifested. Penis envelope membranous; tube short, weakly sclerotized with sclerites produced into small, spine-like projections; sac shorter than tube, bulbous, and variously armed with slender spines, sometimes organized into an apical brush. Basal sclerite absent.

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Female genitalia. – Subgenital plate small, usually bilobed or at least weakly excavated. Vagina membranous with slender accessory glands at anterior angles. Length of spermathecal stalk subequal to vagina; stalk slender, spermatheca usually inflated with at least one accessory gland.

Egg. – Elongate oval with short, wide, slightly stalked collar. Rim usually smooth or slightly incised, not flanged; sides weakly to strongly ribbed. Chorion variable, granular, pitted, or with complexly produced projections of FCIs. Micropyles subequatorial; orifices sessile, or with slightly raised, thin lips; canals straight. Anchor mushroom-like; pedicel short.

Larva. – Typically patterned with brown and yellow. Abdominal terga with at least paired light spots, sometimes with complete pale bands. Pronotal disk with large, simple pale areas. Area between posterior ocelli typically with at least a small pale spot. Occiput with a complete setal row. Pronotal fringe complete with mixed long and short setae. Abdominal tergal fringes usually with at least 1 or 2 long setae. Black clothing hairs present. S7 posterior fringe incomplete mesally. Cercal swimming hairs present. Anal gills present or absent.

Distribution. – Europe, Asia Minor, the Caucasus, North Africa.

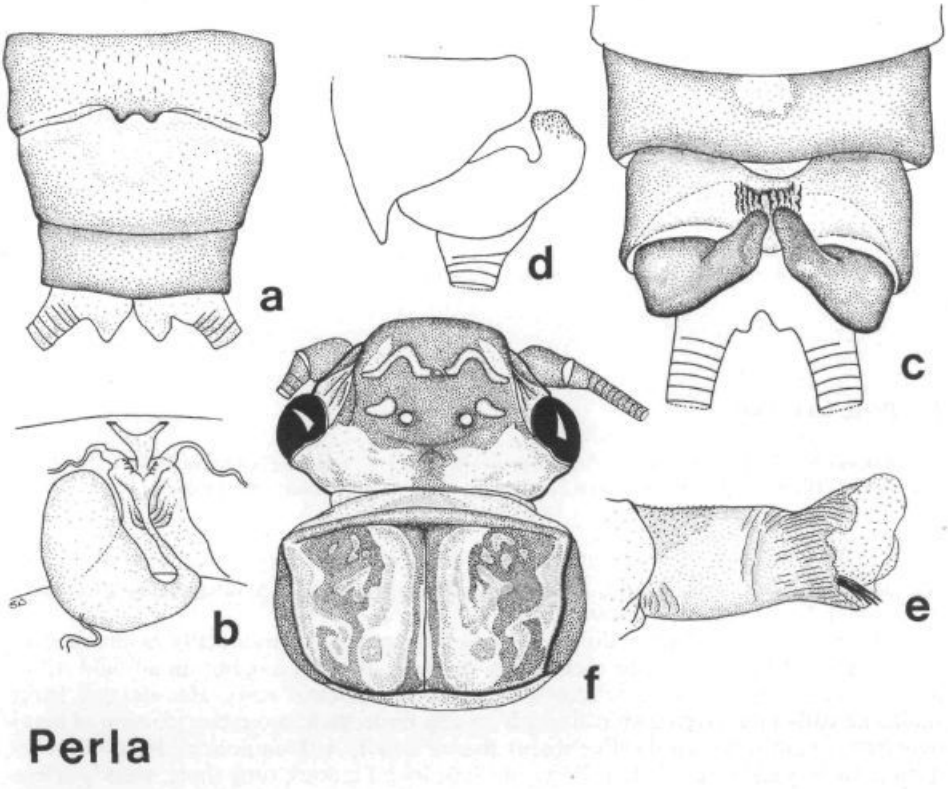

Fig. 23. *Perla burmeisteriana* CLAASSEN [Yugoslavia]: Abdominal tip of female (a), vagina (b), head and prothorax (f), abdominal tip of male (c, in lateral view d), and everted penis (e).

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Perla

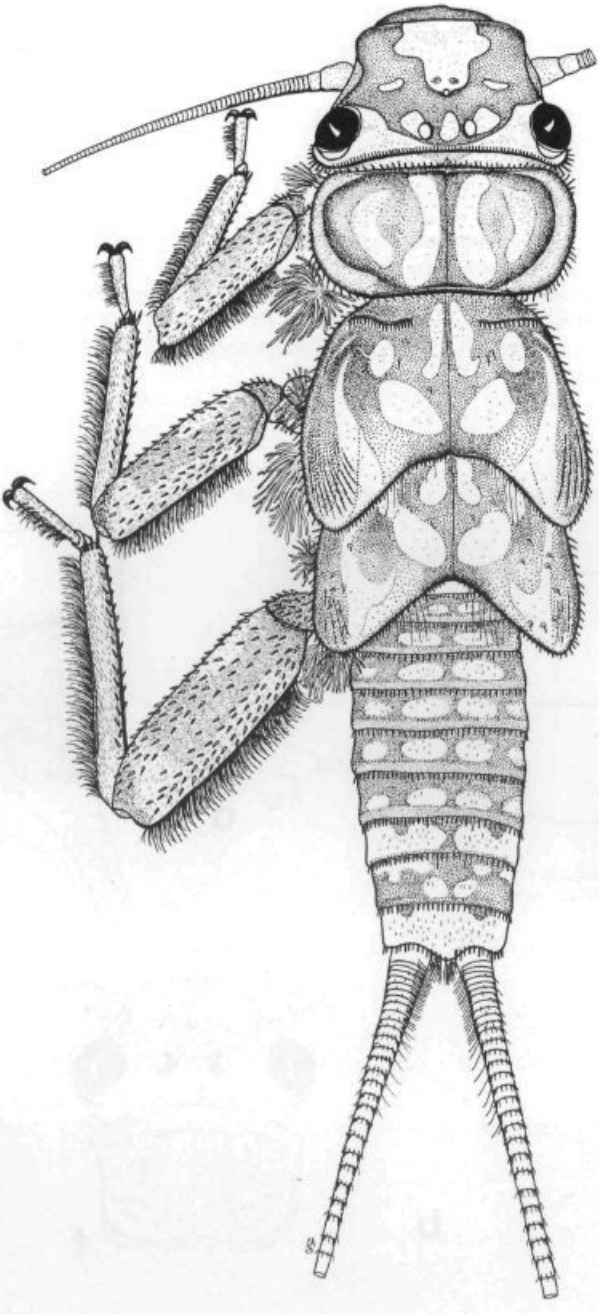

Fig. 24. *Perla burmeisteriana* CLAASSEN [Germany]: Nymph habitus.

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Valid species.–
* *bipunctata* PICTET
* *burmeisteriana* CLAASSEN
* *grandis* RAMBUR
* *illiesi* BRAASCH & JOOST
* *kiritschenkoi* ZHILTZOVA
* *marginata* (PANZER)
* *pallida* GUÉRIN
* *persica* ZWICK

Discussion. – *Perla* is presently considered to be a circum-Mediterranean genus with populations extending eastward to the Caucasus and Iran. Populations also occur in the British Islands, but none are known from Scandinavia. The numerous Asian species formerly described or placed in *Perla* by various authors (ILLIES, 1966; ZWICK, 1973) belong to *Kamimuria, Paragnetina* and other genera. Potamon species such as *P. burmeisteriana* are endangered or extinct in many localities.

9.12. *Eoperla* ILLIES

Eoperla ILLIES (1956). Type species *Perla ochracea* KOLBE, monotypy.

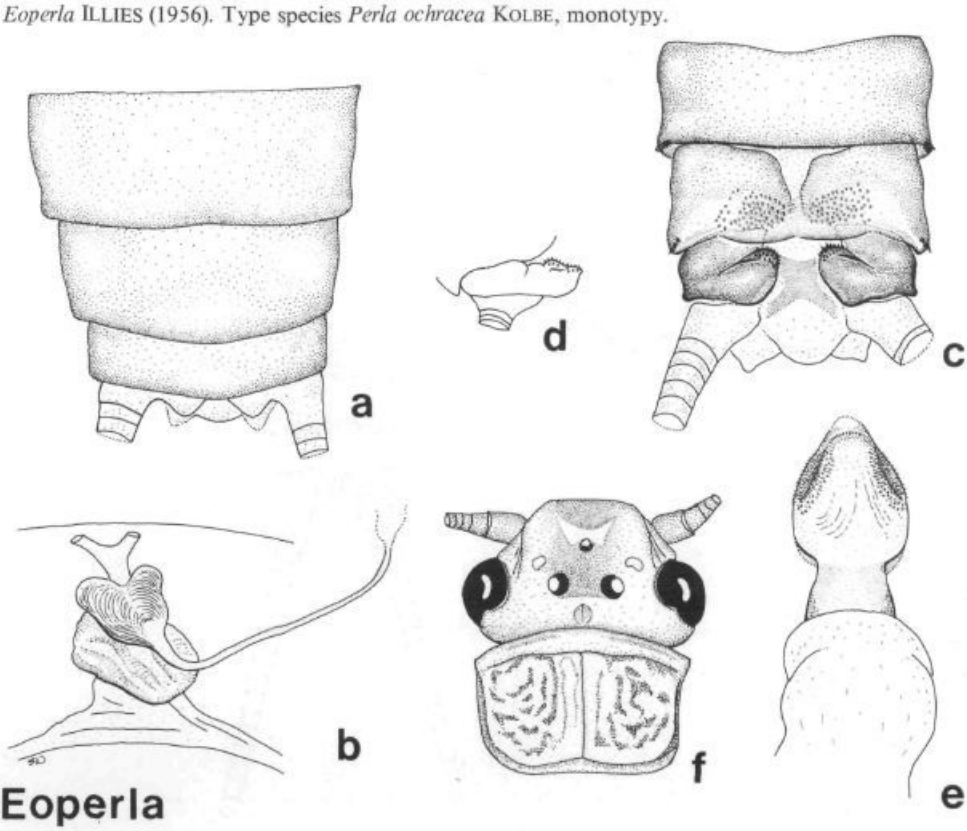

Fig. 25. *Eoperla ochracea* (KOLBE) [Greece]: Abdominal tip of female (a), vagina (b), abdominal tip of male (c), hemitergite (d), everted penis (e), and had and prothorax (f).

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Eoperla

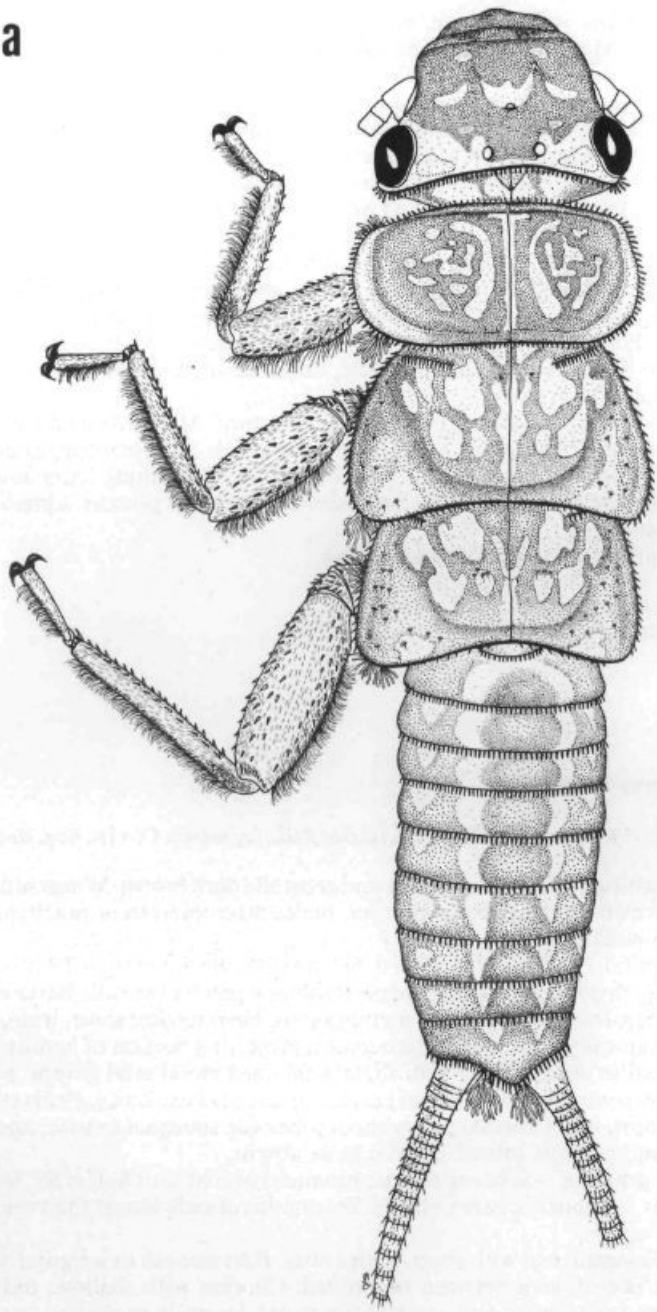

Fig. 26. *Eoperla ochracea* (KOLBE) [Greece]: Nymph habitus.

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Adult habitus. – Triocellate, medium size and pale brown or yellowish. Wings pale. Macropterous. Mesal occipital knob present.

Male genitalia. – T5–8 unmodified. Sclerotized anterior margin T9 projecting into mesal field, partially dividing tergum; dense posteromesal patch of sensilla basiconica almost separated on midline. Hemitergites short, wide, truncate apically and apex covered with sensilla basiconica; projecting portion of hemitergite wider than long; basal callus absent. S2–8 with only slightly enlarged mesal setal groups, not usually organized into definite brushes. Penis envelope membranous; tube short and weakly sclerotized apically; sac subequal to tube, apex armed with a pair of lateral patches of slender spines. Basal sclerite absent.

Female genitalia. – Subgenital plate unproduced. Vagina membranous, accessory glands absent. Spermathecal stalk longer than vagina and slender; spermatheca small.

Egg. – Elongate oval with short, wide collar. Collar rim flanged and shallowly incised, sides ribbed. Posterior pole deeply pitted; shallow indistinct FCIs cover most of surface. Micropyles in posterior third; orifices sessile, canals straight. Anchor mushroom-like; pedicel short, cap flat.

Larva. – Distinctly patterned in yellow and brown. Abdomen with pale lateral bands extending to at least T8. Occiput with complete setal row. Pronotal fringe complete. Abdominal tergal fringes of uniformly short, thick setae. Black clothing hairs absent. S7 posterior fringe complete. Cercal swimming hairs absent. Anal gills present. Lateral submental lobe with basal suture.

Distribution. – Circum-Mediterranean.

Valid species.–
* *ochracea* (KOLBE)

9.13. *Dinocras* KLAPÁLEK

Perla (Dinocras) KLAPÁLEK (1907). Type species *Perla cephalotes* CURTIS, orig. desig.

Adult habitus. – Triocellate, large and generally dark brown. Wings suffused with brown, veins dark brown. Females macropterous, males macropterous or brachypterous. Mesal occipital knob weak.

Male genitalia. – T5–8 unmodified. Sclerotized anterior margin T9 projecting into mesal field, partially dividing tergum; dense posteromesal patch of sensilla basiconica broadly continuous; posterolateral angles of T9 membranous. Hemitergites short, wide, rounded apically and covered apically with sensilla basiconica; projecting portion of hemitergites longer than wide; basal callus absent. S6–7 with slightly enlarged mesal setal groups, not organized into brushes; S7–9 sometimes with mesal patches of sensilla basiconica. Penis envelope membranous; tube short, unsclerotized and without lobes; sac subequal to tube, apex armed with incomplete band of short spines. Basal sclerite absent.

Female genitalia. – Subgenital plate produced over at least half of S9, unnotched. Vagina membranous, without accessory glands. Spermathecal stalk longer than vagina; spermatheca an enlarged sac.

Egg. – Elongate oval with short, wide collar. Rim smooth to irregularly incised, without flange; sides ribbed, area between ribs pitted. Chorion with shallow, indistinct FCIs. Micropyles in posterior third; orifices semi-triangular, lower lip projecting above chorionic surface; canals straight. Anchor mushroom-like; pedicel slender, length about equal to cap diameter; cap consisting of numerous fine strands.

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Larva. – Typically dark brown with paired pale spots on abdominal terga. Pale areas on pronotal disc form a complex pattern; preoccipital area with large oval pale spots adjacent to eyes, but most of area posterior to ecdysial suture brown. Occiput with complete setal row. Pronotal fringe complete. Abdominal tergal fringes of uniformly short, thick setae. Black clothing hairs absent. S7 posterior fringe complete. Cercal swimming hairs absent. Anal gills present. Lateral submental lobes with basal suture.

Distribution. – Europe.

Valid species.–
* *cephalotes* (CURTIS)
* *ferreri* (PICTET)
* *megacephala* (KLAPÁLEK)

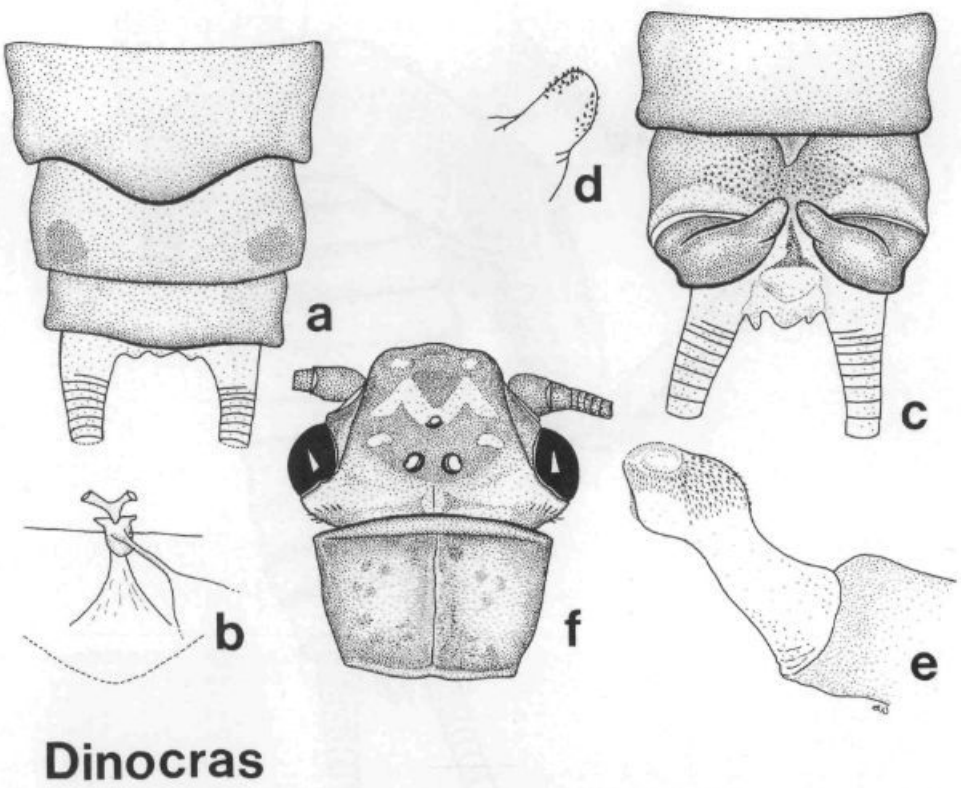

Fig. 27. *Dinocras megacephala* (KLAPÁLEK) [Yugoslavia]: Abdominal tip of female (a), vagina (b), abdominal tip of male (c), hemitergite (d), everted penis (e), and head and prothorax (f).

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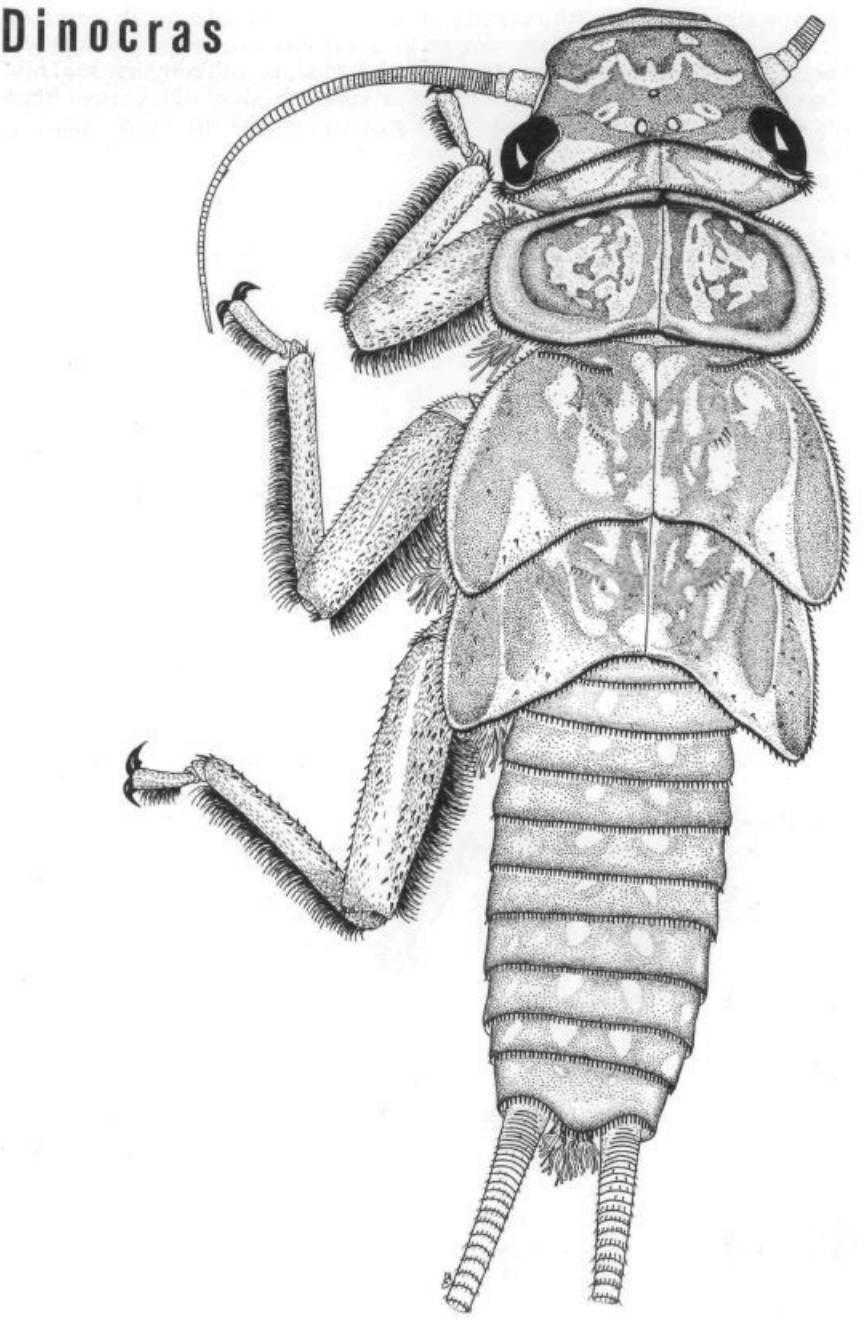

Fig. 28. *Dinocras megacephala* (KLAPÁLEK) [Yugoslavia]: Nymph habitus.

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10. Tribus NEOPERLINI

10.1. *Furcaperla* SIVEC, n. gen.

Type species. – *Tylopyge bifurcata* WU= *Furcaperla bifurcata* here designated.

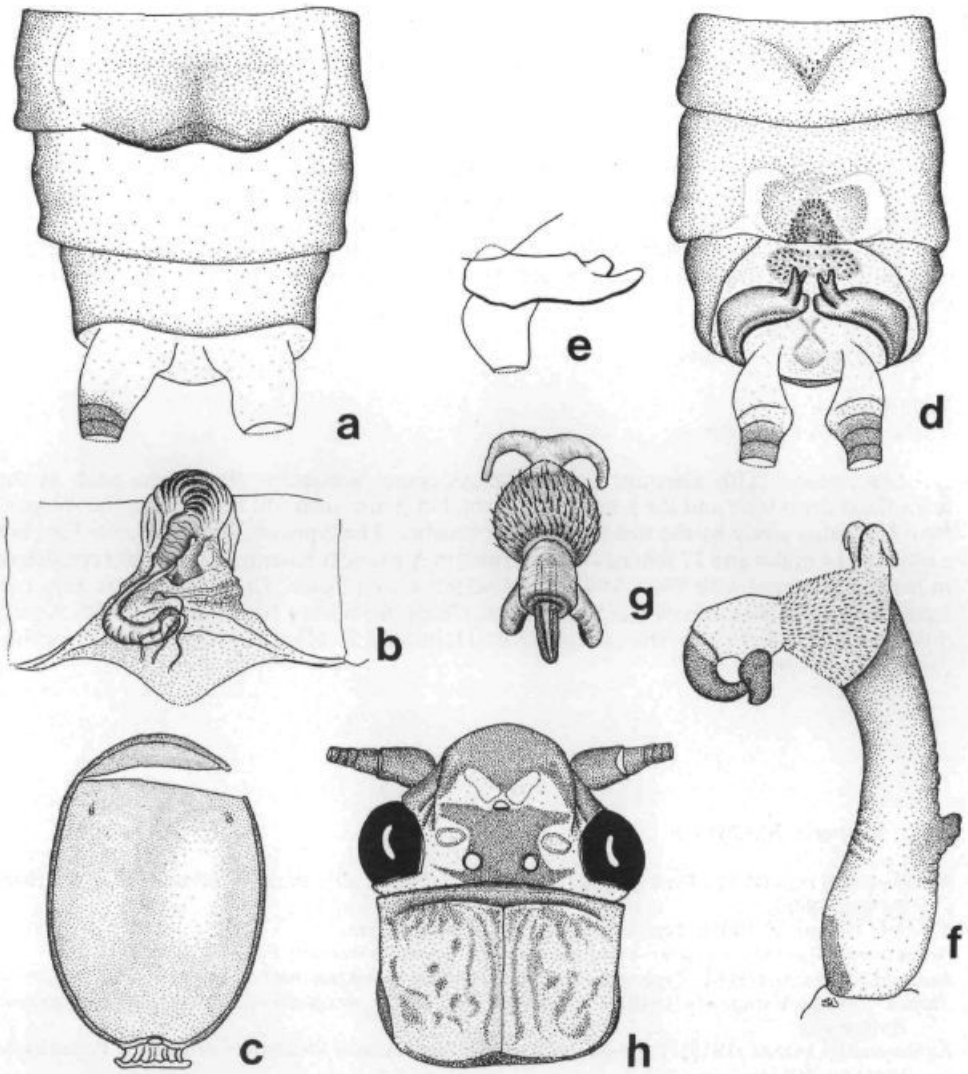

Fig. 29. *Furcaperla bifurcata* (WU) [China]: Abdominal tip of female (a), vagina (b), egg (c), abdominal tip of male (d), hemitergite (e), everted penis (f), dorsal view of everted sac (g), and head and prothorax (h).

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Adult habitus. – Triocellate, medium to large brown species. Wings suffused with brown, veins dark brown. Macropterous. Male basal cercal segment slightly enlarged. Mesal occipital knob absent.

Male genitalia. – T5, 6 unmodified. T7 with a sparse mesal patch of sensilla basiconica. T8 with a sclerotized mesal knob covered with sensilla basiconica. T9 with a wide mesal sclerite, covered with sensilla basiconica, and produced into low lateral knobs. Hemitergites with a pair of small finger-like projections. S4–7 and metasternum with hair brushes. Penis envelope membranous; tube weakly sclerotized, weakly annulate and with a small mesal lobe; sac shorter than tube, and bearing a pair of basal membranous lobes and 3 large claw-like sclerotized, apical hooks; sac armed in basal half with triangular spines; basal sclerite present.

Female genitalia. – Subgenital plate slightly produced into a short, arcuate, apically notched structure. Vagina membranous with numerous anterior folds; accessory glands absent. Spermathecal stalk short; spermatheca slender with a few long accessory glands.

Egg. – Elongate oval with slightly stalked, wide collar. Rim flanged, margin scalloped. Chorionic surface finely punctate throughout. Micropyles in posterior third; orifices sessile; canals straight.

Larva. – Unknown.

Distribution. – China.

Valid species.–
* *bifurcata* (WU), n. comb.

Discussion.– This aberrant genus displays some Neoperlini characters, such as the sclerotized penis tube and the hemitergite form, but it also seems to be allied to the *Neoperlops-Tetropina* group by the metasternal hair brushes. The types of *T. bifurcata* are lost, but a series of 14 males and 12 females in the Museum Alexander Koenig in Bonn, are consistent in hemitergal detail with WU's (1947–48) description and figure. These specimens were collected by J. Klapperich from Kuatun, Fukien, China, from May 10, to June 5, 1937. An additional male in the British Museum of Natural History was collected by M. S. Young in Foochow, China, 1935–36.

10.2. *Neoperla* NEEDHAM

Pseudoperla BANKS (1892). Type species *Perla occipitalis* PICTET, orig. desig. Preoccupied (BRONN, 1848; PICTET, 1845).
Neoperla NEEDHAM (1905). Replacement for *Pseudoperla* BANKS.
Ochthopetina ENDERLEIN (1909). Type species *Ochthopetina aeripennis* ENDERLEIN, orig. desig.
Javanita KLAPÁLEK (1909). Type species *Perla caligata* BURMEISTER, monotypy.
Tropidogynoplax ENDERLEIN (1910). Type species *Tropidogynoplax fuscipes* ENDERLEIN= *O. aeripennis* ENDERLEIN.
Formosina KLAPÁLEK (1913). Type species *Neoperla hatakeyamae* OKAMOTO, orig. desig. Preoccupied (BECKER, 1911).
Formosita KLAPÁLEK (1914). Replacement for *Formosina* KLAPÁLEK.
Oodeia KLAPÁLEK (1921). Type species *Neoperla dolichocephala* KLAPÁLEK, orig. desig.
Simpliperla WU (1962). Type species *Simpliperla obscurofulva* WU, monotypy. n. syn.

Adult habitus. – Biocellate, small to medium, usually pale brown, exceptionally black. Wings suffused, veins brown. Macropterous. Mesal occipital knob absent.

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Male genitalia. – T5–6 unmodified. T7 typically with projecting lobe or raised process. T8 usually with mesal raised process, varying from simple, slightly raised hump to elaborate, sclerotized, tongue-like and sometimes bifurcate process. T9 typically with slightly raised humps. T7–9 processes, or membrane, with patches of sensilla basiconica. Hemitergites with anterior process simple, finger-like; apical margins of basal piece covered with sensilla basiconica. Sterna without hair brushes. Penis envelope membranous; tube typically sclerotized, at least basally, sometimes armed with lateral patches of spines or spiny lobes; lobes sometimes unarmed or sclerotized. Sac usually longer than tube, variably lobed and armed.

Female genitalia. – Subgenital plate unproduced or weakly produced. Vagina with or without sclerites, sometimes lined with fine spines; accessory glands absent. Spermathecal stalk lined with fine, golden brown spines, or unlined; frequently long and coiled, sometimes short and uncoiled. Spermatheca reduced to small membranous bag for species with complex stalk, and somewhat enlarged for other species into a slender, long, membranous bag.

Egg. – Shape, collar form and chorionic surface detail variable. Frequently striate or with ornate FCIs and punctations, occasionally smooth. Collar present or absent, stalked or sessile. Micropyles in posterior third; orifices sessile or with raised lip. Eclosion line present or absent. Anchor variable.

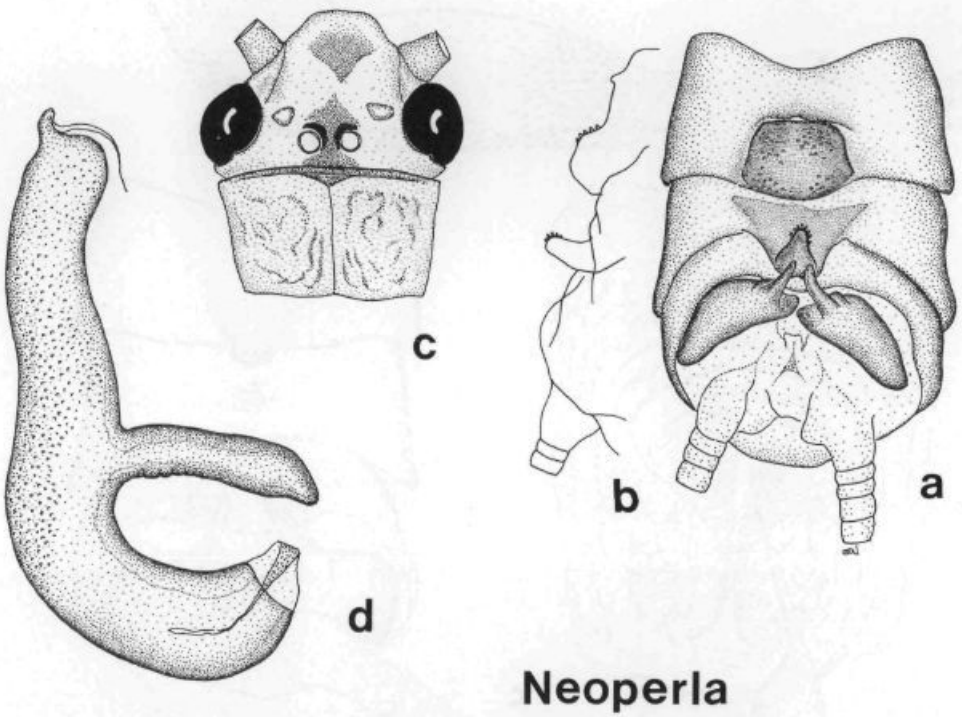

Fig. 30. *Neoperla flavescens* CHU [China]: Abdominal tip of male (a, in lateral view b), head and prothorax (c), and penis (d).

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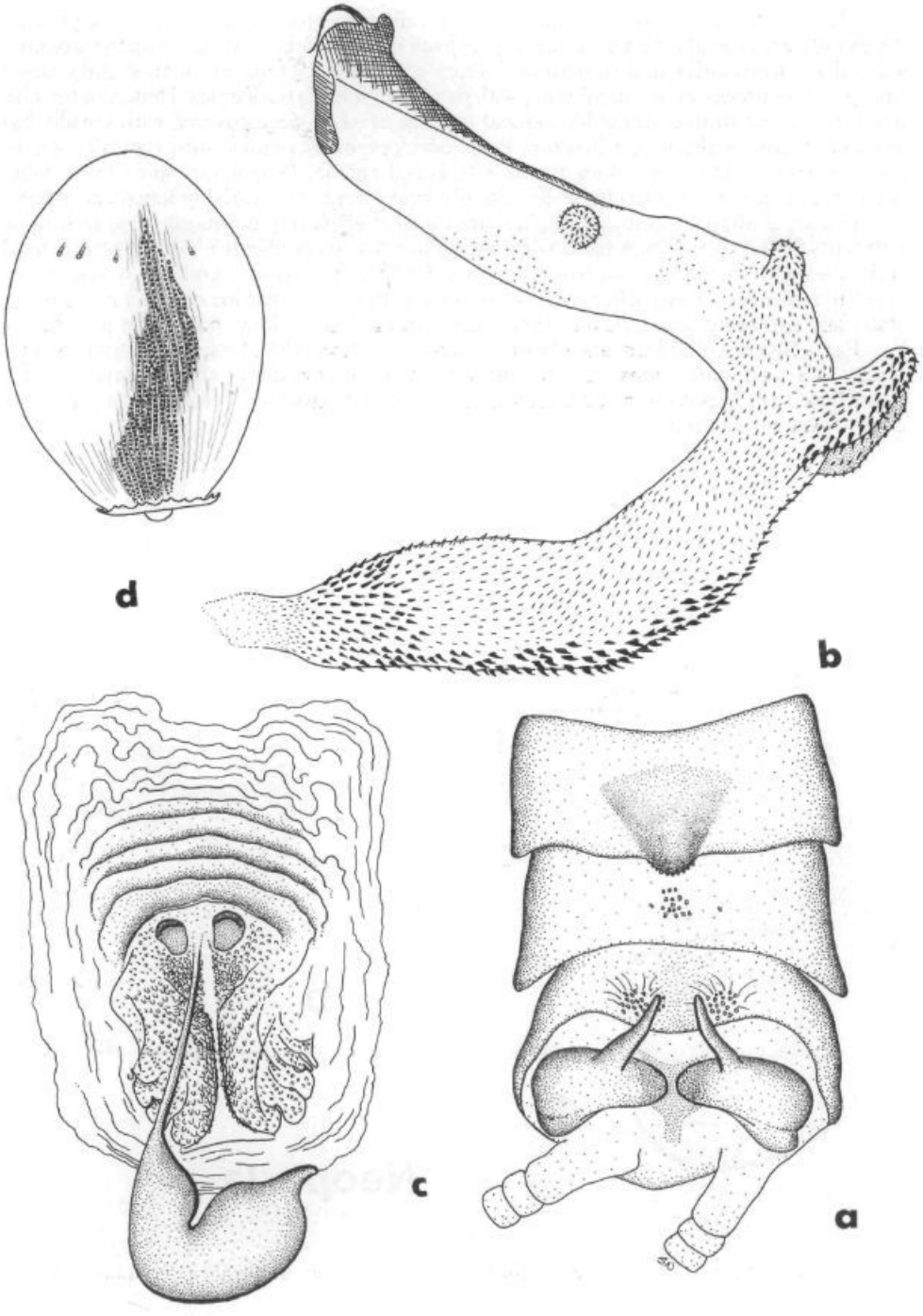

Fig. 31. *Neoperla obliqua* BANKS [Philippines]: Abdominal tip of male (a), everted penis (b), vagina (c), egg (d).

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Neoperla

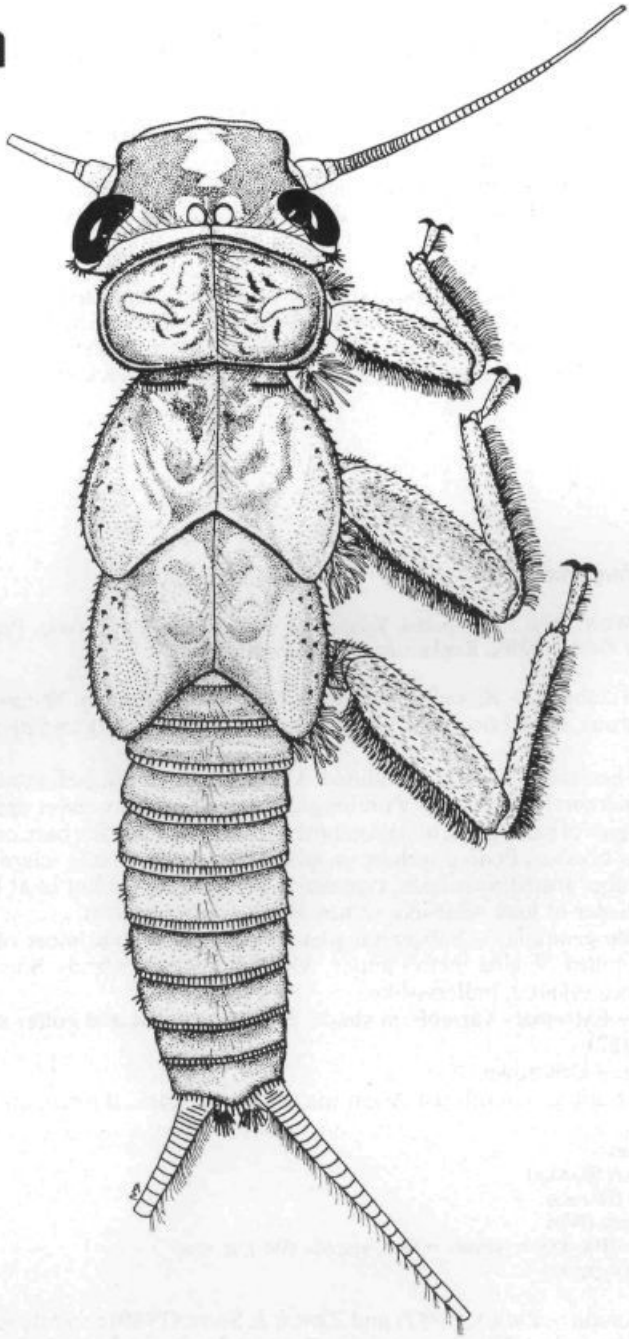

Fig. 32. *Neoperla angulata* (WALKER) [Sri Lanka]: Nymph habitus.

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Larva. – Generally brown with subtle pattern. Occipital ridge bare. Pronotum usually without complete lateral fringe. Abdominal tergal fringes typically of short, thick setae. S7 posterior fringe complete or incomplete. Cerci usually without swimming hairs, but present in at least one species. Anal gills present. Black clothing hairs typically present.

Distribution. – Nearctic, Ethiopian, and widely distributed over Asian mainland and southeast to New Guinea.

Valid species. – One hundred eighty two *Neoperla* species are currently recognized following work over the past decade by ZWICK, SIVEC, STARK, and others. Included in this number are 19 species described by WU, CHU, or WU & CLAASSEN for which type material is lacking, and 29 African species names. ZWICK is currently revising the African species and UCHIDA is revising the Japanese species. Much additional material from mainland Asia, particularly China, will be needed to clarify the situation in this region. *Simpliperla* is placed as a provisional synonym since the only known distinguishing character, absence of modified T7, is now known to occur in *Neoperla illiesi* ZWICK and *N. tenuispina* KLAPÁLEK (ZWICK, 1983).

10.3. *Chinoperla* ZWICK

Sinoperla WU (1948). Type species *Sinoperla nigroflavata* WU, orig. desig. Preoccupied (PING, 1928). *Chinoperla* ZWICK (1980). Replacement for *Sinoperla* WU.

Adult habitus. – Biocellate, small, brown to dark brown. Wings suffused, veins dark. Macropterous. Mesal occipital knob present. Sc vein usually ending in basal third of forewing.

Male genitalia. – T5–8 unmodified. T9 with slender, bilobed, mesal sclerite arising from anterior margin. Hemitergites with long slender anterior processes approaching T9 sclerite; inner margins of basal piece of hemitergite with patch of sensilla basiconica. S3–4, sometimes 5 with hair brushes. Penis envelope membranous; tube partially sclerotized basally; sac subequal to tube; armed near apex, typically with short spines but in at least one species with a dense cluster of long setal-like spines. Basal sclerite present.

Female genitalia. – Subgenital plate variable, covering most of S9, or unproduced, usually notched. Vagina membranous, without accessory glands. Spermathecal stalk short; spermatheca inflated, balloon-like.

Egg. – Extremely variable in shape, chorionic detail and collar structure according to ZWICK (1982).

Larva. – Unknown.

Distribution. – Southeast Asian mainland, Sumatra, Borneo, and India.

Valid species.–
* *fascipennis* (BANKS)
* *nigriceps* (BANKS)
nigroflavata (WU)
* *nigrifrons* (BANKS), n. comb. = *furcomacula* (WU), n. syn.
* *reducta* (GEIJSKES)

Discussion. – ZWICK (1982) and ZWICK & SIVEC (1980) recently gave details for several *Chinoperla* species. The type species, *C. nigroflavata,* unfortunately, is known only from WU's (1948) figures, and is the only described *Chinoperla* which apparently lacks the

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shortened Sc vein (ZWICK, 1982). We are provisionally placing *S. furcomacula* (WU, 1973) as a synonym of *C. nigrifrons* (BANKS, 1939). Both species are from Hainan, and there is little to distinguish WU's figure of external male genitalia from the type of *C. nigrifrons*.

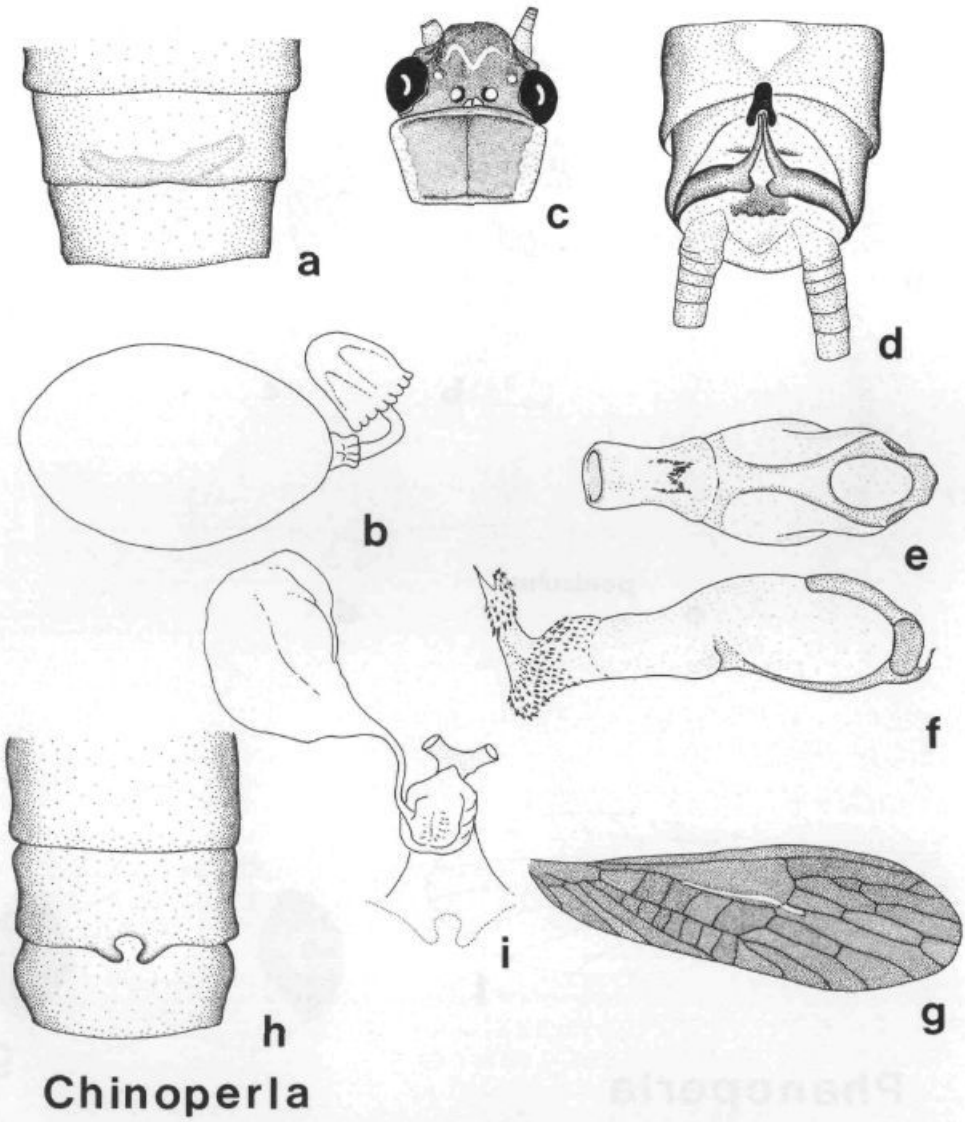

Fig. 33. *Chinoperla nigriceps* (BANKS) [India]: Abdominal tip of female (a), egg (b), abdominal tip of male (d), head and prothorax (c), ventral view of penis (e), everted penis (f), fore wing (g); *C. nigrifrons* (BANKS) [Taiwan]: Abdominal tip of female (h), vagina (i).

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10.4. *Phanoperla* BANKS

Phanoperla BANKS (1938). Type species *Perla limosa* HAGEN, orig. desig.
Dyaperla BANKS (1939). Type species *Dyaperla anomala* BANKS, orig. desig.

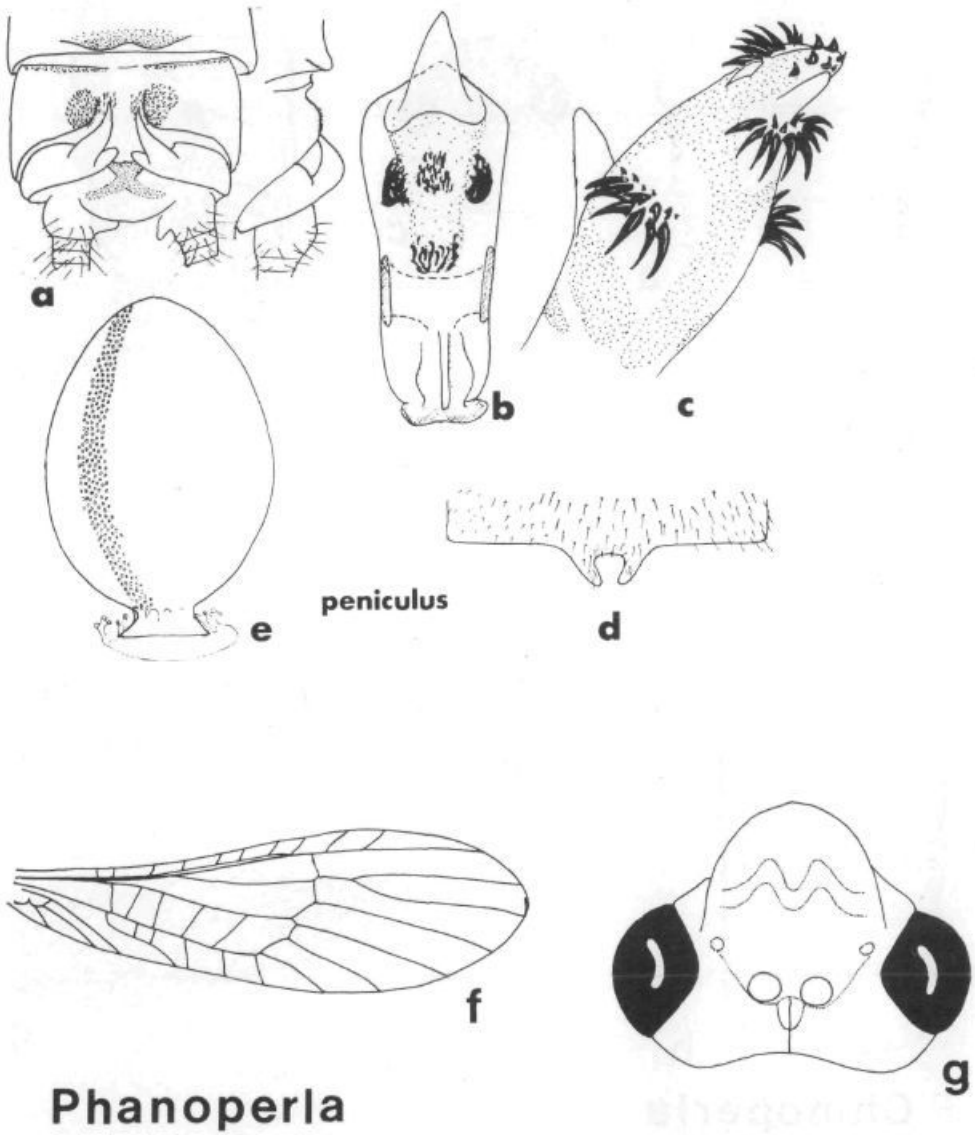

Fig. 34. *Phanoperla peniculus* KAWAI [India]: Abdominal tip of male (a), ventral view of penis (b), everted sac of penis (c), female subgenital plate (d), egg (e); *Phanoperla* sp.: fore wing (f), head (g).

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Adult habitus. – Biocellate or triocellate, small to medium size, pale to dark brown species. Cu2 of forewing curved basally, and joining Cul at an almost right angle. Mesal occipital knob present.

Male genitalia. – T5–7 unmodified. T8 sometimes with mesal lobe, usually unmodified. T9 typically unsclerotized mesally, and bearing a pair of mesal humps covered with sensilla basiconica; membrane usually with a small patch of sensilla basiconica. Hemitergites with a simple, usually acute anterior process. Penis envelope membranous; tube weakly sclerotized, usually with several small sclerites; sac short and usually heavily armed with large, black spines and scattered smaller spines; basal sclerite present.

Female genitalia. – Subgenital plate slightly produced and typically bilobed. Vagina membranous or with small sclerites; accessory glands absent. Spermathecal stalk usually slender with a small, elongate, sausage-like spermatheca; at least one species with stalk enlarged and densely setose internally.

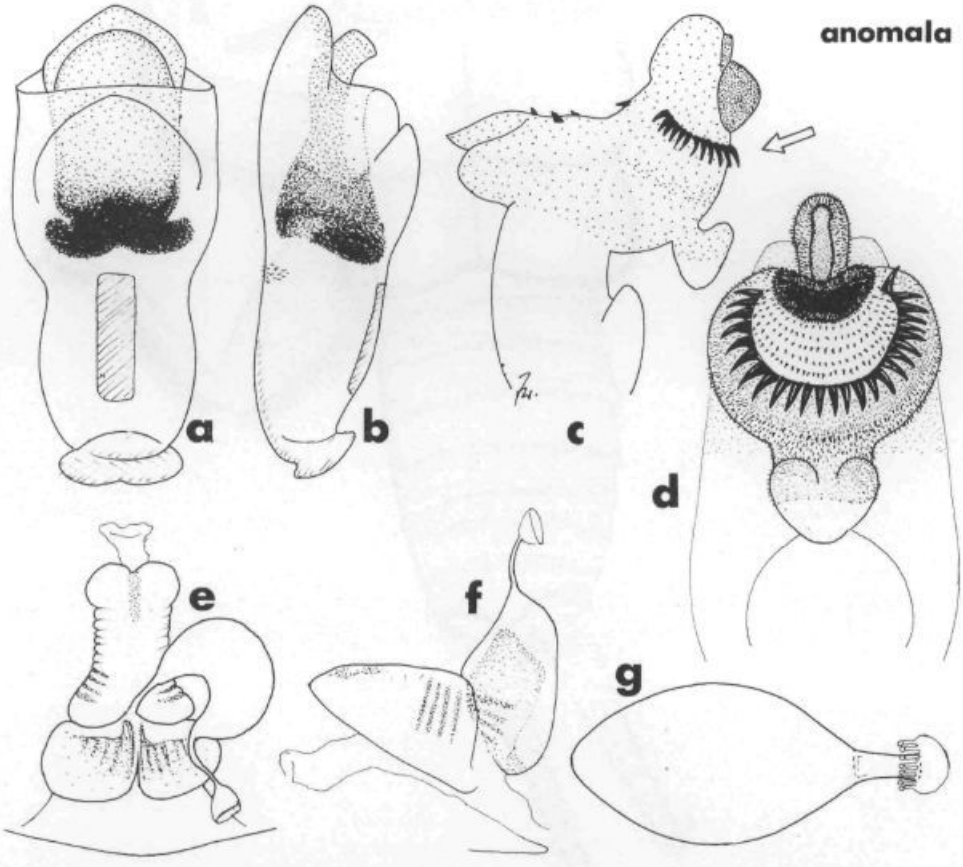

Fig. 35. *Phanoperla anomala* (BANKS) [Borneo]: Dorsal (a), and lateral view of penis, everted sac of penis (c,d), vagina (dorsal e, lateral f), egg (g).

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Phanoperla

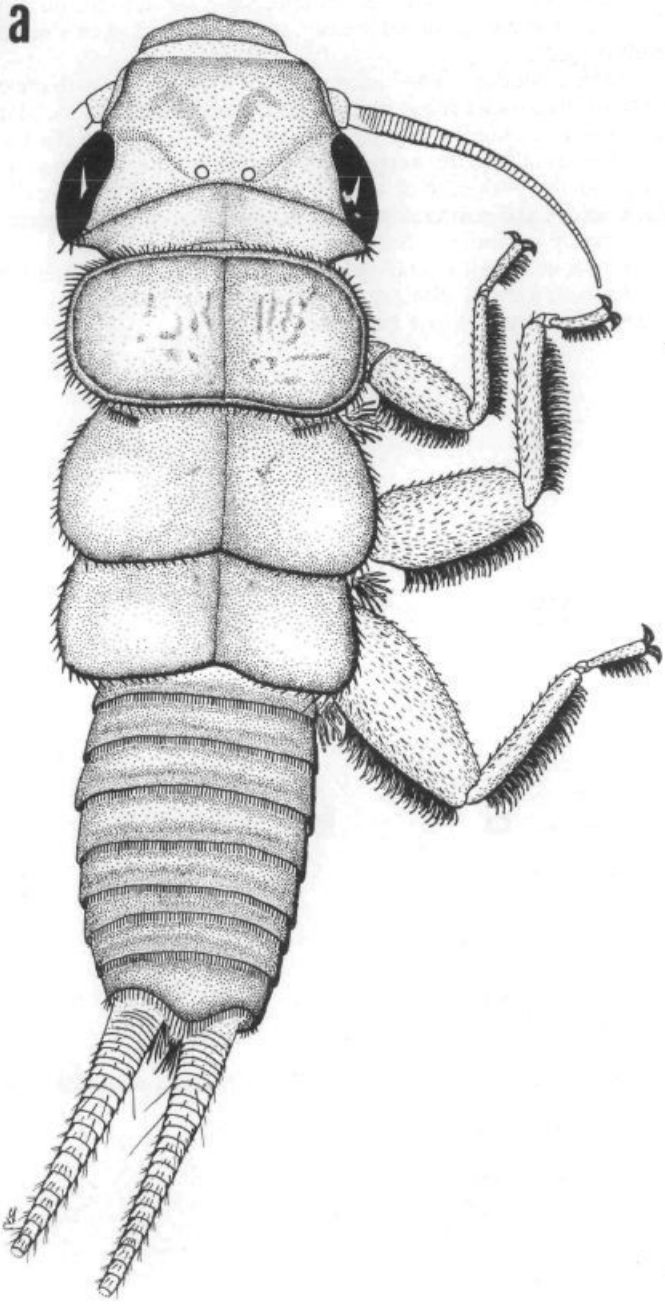

Fig. 36. *Phanoperla* sp. [Thailand]: Nymph habitus.

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Egg. – Elongate oval with variable collar. Chorion smooth to ornate. Micropyles in posterior third; orifices sessile. Anchor cap typically with finger-like projections; pedicel of variable length.

Larva. – Usually pale brown without distinctive pattern. Occipital ridge with or without setae. Pronotum fringed primarily with long slender setae. Abdominal tergal fringes uniform; terga with dense red-brown clothing hairs. S7 posterior fringe complete. Cerci typically short, stout and without swimming hairs. Anal gills present; gills PSC 2, 3 reduced; one pair PSC3 gills. Thoracic sternal plates with posterior fringes of setae. Lateral lobes of submentum with basal suture.

Distribution. – Southern Oriental Islands and mainland Southeast Asia, Indian subcontinent, Sri Lanka and the Himalayas.

Valid species. – Thirty four species have recently been described by ZWICK (1982, 1983, 1986), ZWICK & SIVEC (1985) and STARK (1983). ZWICK (1982) recognized 7 species groups based on egg and penis characters.

11. *Miniperla* KAWAI

Miniperla KAWAI (1967). Type species *Miniperla japonica* KAWAI, orig. desig.

Adult habitus.–Triocellate, small and generally pale with dark markings. Wings transparent, veins except costal area brown; C and Sc yellow. Macropterous.

Male genitalia.–T3 with a slightly sclerotized, weakly produced mesal lobe. T4–8 with sclerotized anterior margin usually broadly bilobed; mesal field of T4–8 membranous. T9 with mesal membranous area bounded by raised sclerotized bars. Hemitergites slender, finger-like, extending forward over posterior margin T9. S3–4 with mesal hair brushes. Penis characters unknown.

Female genitalia.–Subgenital plate truncate, short, and barely projecting over anterior margin of S9. Vaginal characters unknown.

Egg.–Unknown.

Larva.–Unknown.

Distribution.–Japan.

Valid species.–
japonica KAWAI

Discussion.– This small, distinctive species is known only from KAWAI's (1967) description of a series from the now polluted Lake Biwa outflow. Speciemens have not been available for our study.

12. Species not included in the lists of valid species

The following list includes species unrecognizable from the original descriptions for which the typic material is lost:

Agnetina chrysodes NAVÁS, 1919; *Paragnetina lutescens* NAVÁS, 1911; *P. schenklingi* KLAPÁLEK,1921; *P. tonkinensis* NAVÁS, 1919;*Perla aegyptiaca* PICTET, 1841; *P. apicata* NAVÁS, 1918; *P. cadaverosa* MCLACHLAN, 1875; *P. carletoni* BANKS, 1920; *P. caucasica* GUÉRIN, 1838; *P. caudata* KLAPÁLEK, 1921; *P. cellulata* NAVÁS, 1919; *P. cocandica* MCLACHLAN, 1875; *P. comstocki* WU, 1937; *P. costata* NAVÁS, 1918; *P. cymbele* NEEDHAM, 1909; *P. flavata* NAVÁS, 1923 (not *Kamimuria flavata* NAVÁS, 1933); *P. immersa* MCLACHLAN, 1875; *P. impunctata* PICTET, 1841: *P. infumata* NAVÁS, 1923; *P. ione* NEEDHAM, 1909; *P. navasa* CLAASSEN, 1923; *P. picteti* LUCAS, 1849; *P. servillei* PICTET, 1841; *P. stankovici* ŠAMAL,1935; *P. simplex* CHU, 1929: *P. xenocia* BANKS, 1914; *Phasganophora media* WU, 1935; *Kamimuria atricornis*

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KLAPÁLEK, 1912; *K. cheni* WU, 1947; *K. chingtechenensis* WU, 1935; *K. chungnanshana* WU, 1938; *K. crassispina* WU, 1947; *K. jeanneli* WU, 1935; *K. kirinensis* WU, 1938; *K. longispina* WU, 1947; *K. magna* WU 1938; *K. manchuriana* WU, 1938; *K. melli* WU, 1935; *K. nigriceps* NAVÁS, 1919; *K. notalis* NAVÁS, 1927; *K. robusta* WU, 1947; *K. sibirica* KLAPÁLEK, 1916; *K. taoi* WU, 1936; *K. tenuispina* WU, 1947; *K. tienmushanensis* WU, 1938; *Neoperla brachyura* NAVÁS, 1918; *N. chui* WU & CLAASSEN, 1934; *N. curvispina* WU, 1948; *N. infuscata* WU, 1935; *N. longispina* WU, 1937; *N. lushana* WU, 1935; *N. minor* CHU, 1929; *N. rotunda* WU, 1948; *N. sinensis* CHU, 1928; *N. tingwushanensis* WU, 1935; *N. trilobata* WU, 1935; *N. truncata* WU, 1948; *N. tuberculata* WU, 1937; *Ochthopetina ramosa* NAVÁS, 1919; *O. vitalis* NAVÁS, 1923; *Togoperla bifoveolata* KLAPÁLEK, 1921.

POVZETEK

Perline predstavljajo številčno najbogatejšo poddružino v okviru plekopterske družine Perlidae (vrbnice). V Evropi so zastopane le z majhnim številom vrst (15), svoj pravi razcvet pa so doživele v toplih predelih sveta, predvsem v tropski Aziji, kjer se njihovo število povzpne v več sto različnih vrst. Mnoge med njimi predstavljajo prave orjake te skupine žuželk, na žalost pa tudi ene najbolj ogroženih predstavnikov tekočih voda. Vse intenzivnejše poseganje v naravno okolje je bilo tudi v tem delu sveta usodno za marsikatero od teh zanimivih in tudi gospodarsko pomembnih živalskih vrst, tako da jih danes poznamo le kot ohranjene muzejske primerke, medtem ko so v naravi po vsej verjetnosti že izumrle. Kolikšno pa je število tistih, ki bodo izginile prej, preden jih bomo uspeli opisati, najbrž ne bomo izvedeli nikoli.

Pričujoča študija je rezultat desetletnega intenzivnega dela. Pregledali smo skoraj ves material, ki je na voljo v muzejih po svetu in preučili vse dostopne in obstoječe tipe posameznih, že opisanih vrst. Ugotovili smo, da je precejšnje število tipov izgubljenih ali uničenih, v sistematiki te skupine pa je bila nepopisna zmešnjava. Mogoče je tudi to eden od razlogov, da se z obdelavo te skupine žuželk vse od preloma stoletja pa do danes ni ukvarjal tako rekoč nihče. Ves starejši muzejski material je le slučajno oziroma vzporedno nabran pri lovu nočnih metuljev na svetlobne pasti. Azijski predstavniki družine Perlidae imajo v nasprotju z evropskimi vrstami lastnost, da jih privlači svetloba. Nekoliko številnejši material, ki smo ga sami nabrali na ekspedicijah v Azijo, ter dokaj obsežen material z Japonske in iz Severne Amerike predstavlja, žal, le obrobje razširjenosti te skupine žuželk, medtem ko je bil razpoložljivi material z najbolj zanimivih območij, to je osrednje Azije, lahko bi rekli, zgolj simboličen. Tako je ta študija daleč od popolnosti dejanskega stanja, a največ, kar lahko trenutno ugotovimo. Posebno skrbno smo se posvetili izdelavi ključev za določanje rodov, ki so za obravnavano skupino vrbnic narejeni prvič v takem obsegu.

S tem prikazom želimo vzpodbuditi limnologe in entomologe na obravnavanih območjih k intenzivnejšemu terenskemu delu. Le terensko delo s čim večjim številom zbranih osebkov različnih vrst ter ekološkimi opazovanji je pogoj za podrobnejšo in temeljitejšo obdelavo znotraj posameznih rodov. Tako bodo potrjeni ali pa izpopolnjeni sorodstveni odnosi med posameznimi rodovi, ni pa izključena možnost, da bi odkrili nove, do sedaj še nepoznane rodove. Brez dvoma pa se bo z intenzivnejšim raziskovanjem v prihodnje še precej povečalo število novoodkritih vrst.

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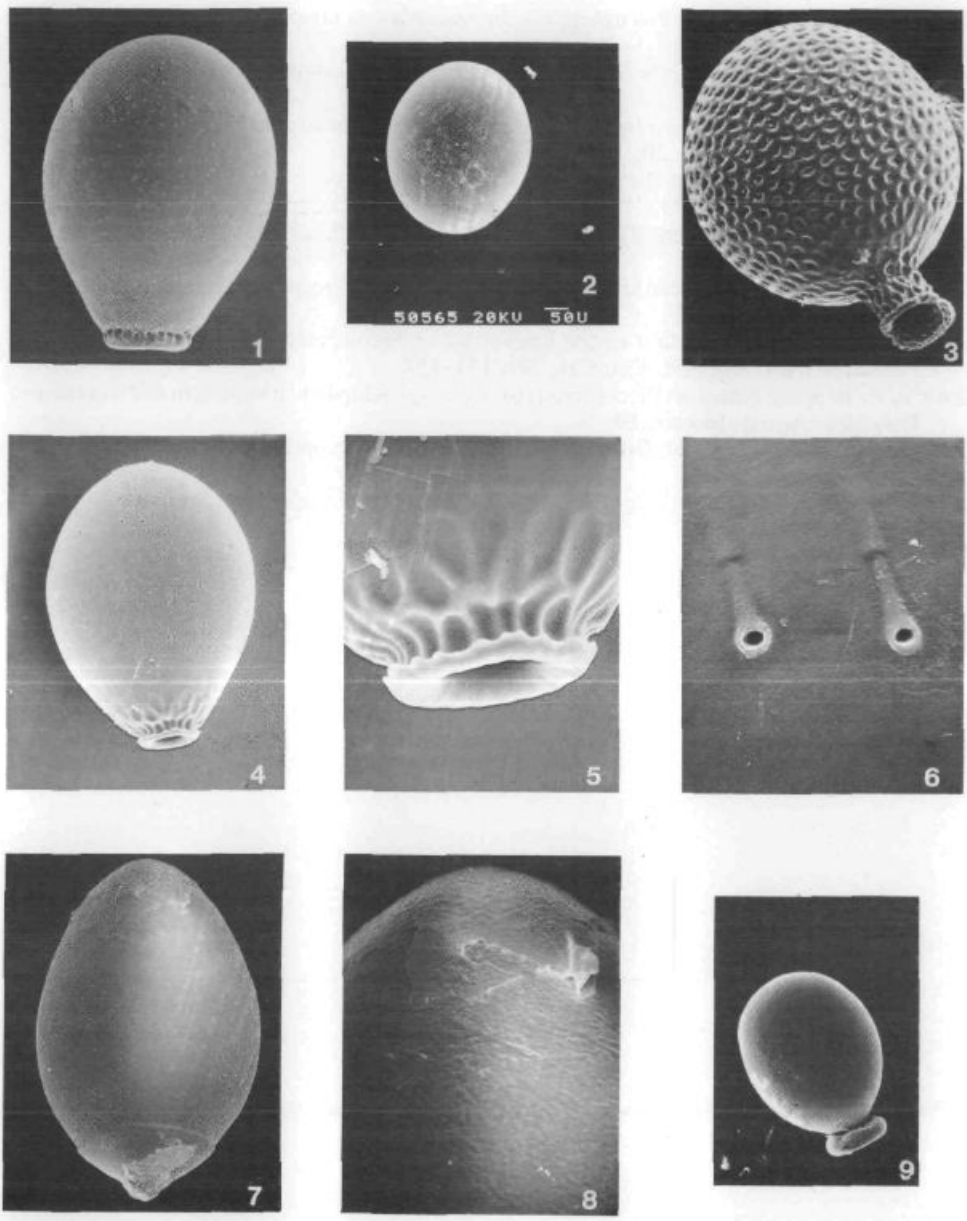

Fig. 37. SEM photomicrographs of eggs: *Togoperla* sp. [Thailand]: Egg lateral, 200× (1); *Togoperla limbata* (PICTET) [Japan]: Egg lateral, 150× (2); *Paragnetina media* WALKER [USA]: Egg lateral, 250× (3); *Oyamia* sp.: Egg lateral, 280× (4), collar, 1000× (5), detail of chorion and micropyles, 2000× (6); *Marthamea beraudi* (NAVÁS) [Lebanon]: Egg lateral, 306× (7), polar end, with micropyles, 850× (8): *Kamimuria* sp. [Japan]: Egg lateral, 150× (9).

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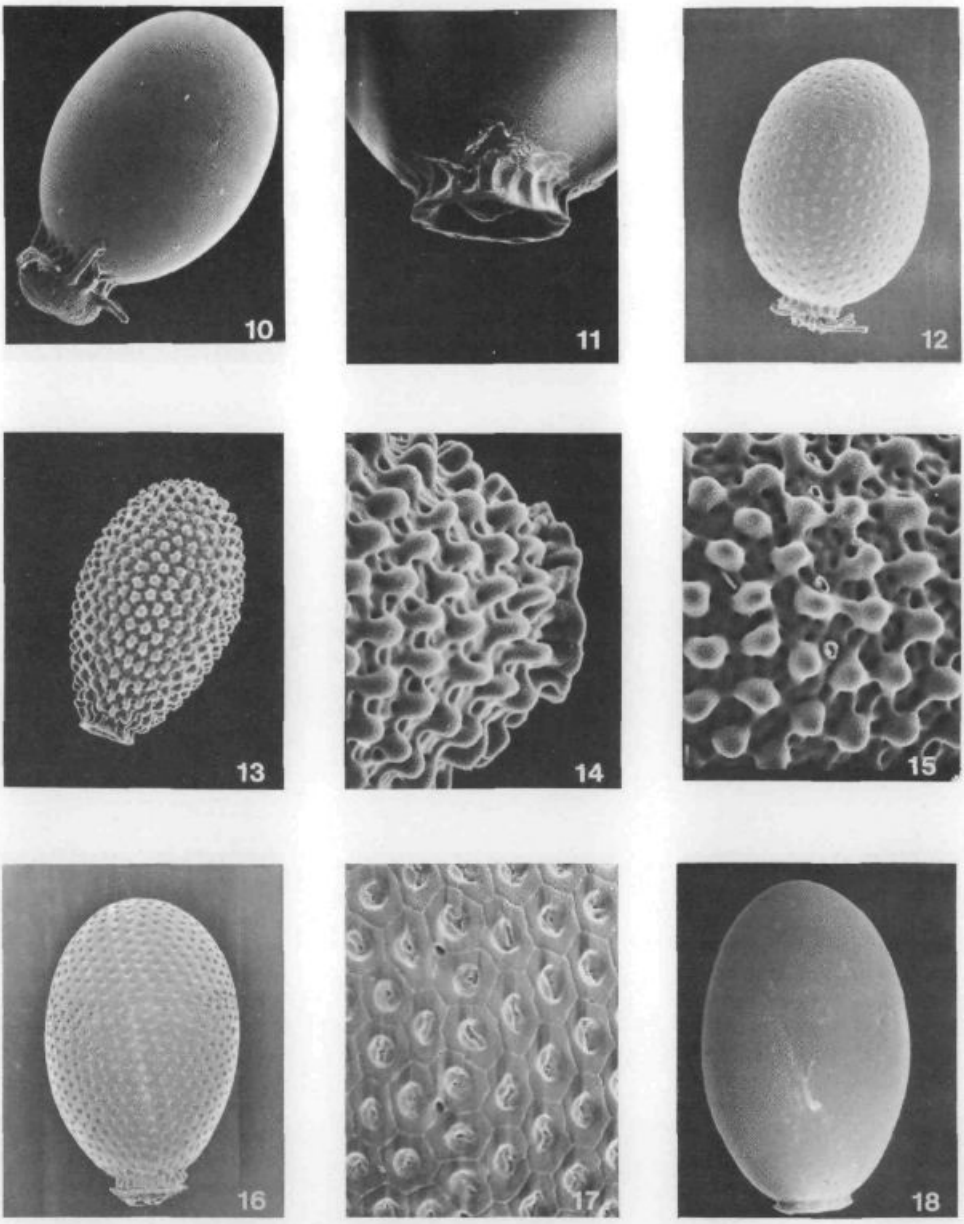

Fig. 38. SEM photomicrographs of eggs: *Etrocorema nigrogeniculatum* (ENDERLEIN) [Malaysia]: Egg lateral, 200× (10), collar, 400× (11); *Tetropina* sp. [Malaysia]: Egg lateral, 200× (12); *Perla burmeisteriana* CLAASSEN [Switzerland]: Egg lateral, 200× (13), collar end 700× (14), detail of chorion and micropyles, 700× (15); *Perla pallida* GUERIN [Yugoslavia]: Egg lateral, 230× (16), detail of chorion and micropyles, 950× (17); *Perla grandis* RAMBUR [Switzerland]: Egg lateral 270× (18).

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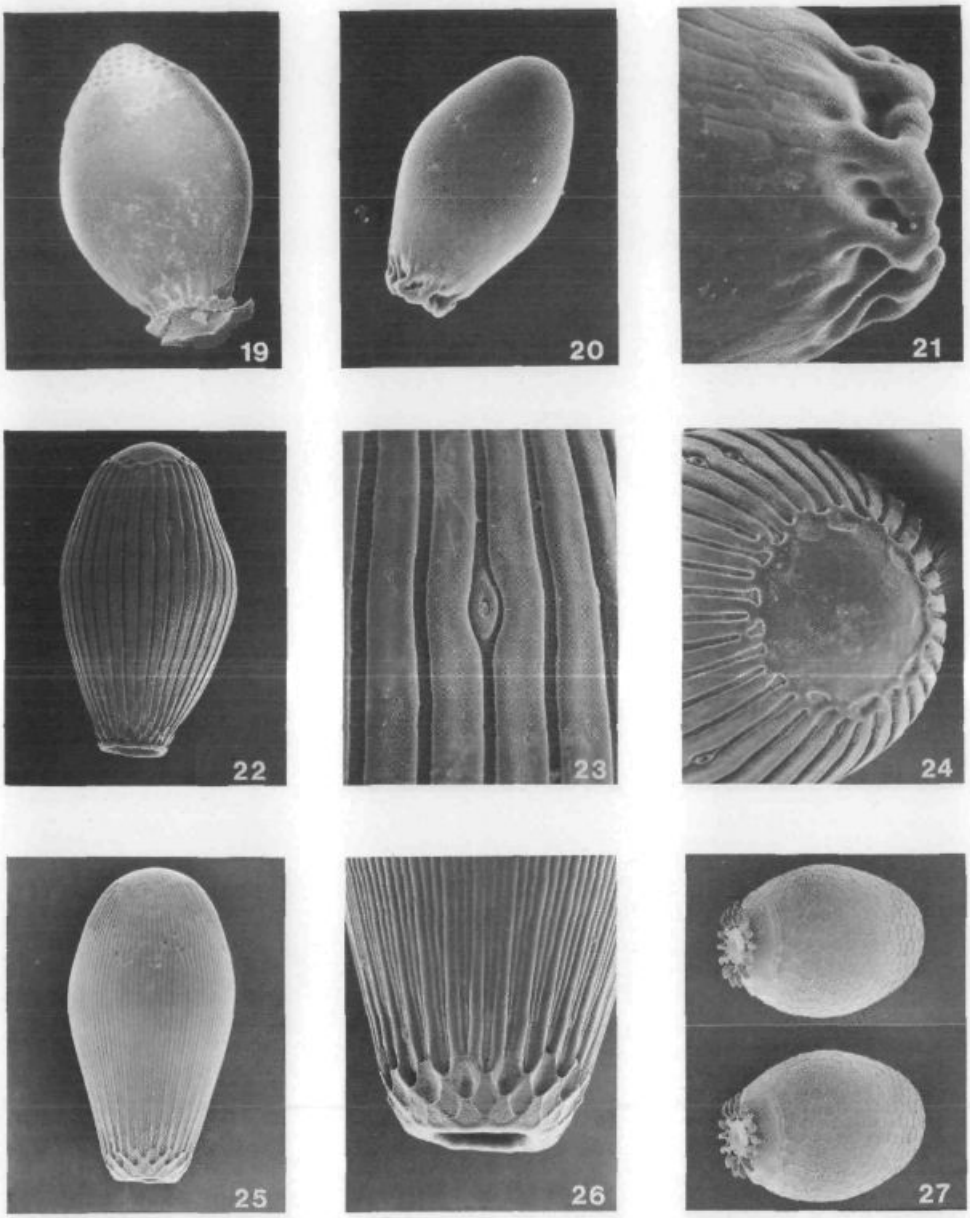

Fig. 39. SEM photomicrographs of eggs: *Eoperla ochracea* (KOLBE) [Algeria]: Egg lateral, 220× (19); *Dinocras megacephala* (KLAPÁLEK) [Switzerland]: Egg lateral, 200× (20), collar end, 700× (21); *Neoperla* sp. [China]: Egg lateral, 270× (22), detail of chorion and micropyle, 1200× (23), polar end, 550× (24); *Neoperla lahu* STARK [Thailand]: Egg lateral, 300× (25), collar end, 750× (26); *Neoperla* sp. [Sumatra]: Eggs lateral, 230× (27).

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