

THE NYMPH OF *SIPHLURISCUS CHINENSIS* AND ADDITIONAL IMAGINAL DESCRIPTION: A LIVING MAYFLY WITH JURASSIC ORIGINS
(SIPHLURISCIDAE NEW FAMILY: EPHEMEROPTERA)

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ABSTRACT

The nymph, female imago and egg of *Siphuriscus chinensis* Ulmer are described and figured in detail for the first time based on associated nymphs and imagos from China. Additional characters of the male imago are described. Based upon imaginal and nymphal characters, Siphuriscidae **fam. n.** is established in the Siphonuroidea for *Siphuriscus* and, provisionally, the Jurassic genus *Stackelbergisca* Tshernova. *Siphuriscus ? davidi* Navás, known from one male subimago, is transferred to *Siphonurus davidi* **comb. n.** The family Siphuriscidae is distinguished from all other families of Siphonuroidea by the presence of coxal gills on the fore and middle legs in all stages and in the nymph by the presence of a basal, moveable, dactyl-like appendage on each claw, and labial and maxillary gills. Characters of the nymphal mouthparts, particularly the mandibles and maxillae, suggest that Siphuriscidae is a sister-group of the family Nesameletidae. However, the majority of character states are considered plesiomorphic in the Ephemeroptera, and may contribute valuable information on the origin, phylogeny and biogeography of Ephemeroptera.

Key Words: *Siphuriscus*, *Stackelbergisca*, Siphuriscidae, phylogeny, China, Jurassic

RESUMEN

La ninfa, adulto hembra y huevo de *Siphuriscus chinensis* Ulmer son descritos e ilustrados en detalle por primera vez basados en ninfas y adultos asociados de China. Características adicionales del adulto macho son descritas. Basados en caracteres del adulto y ninfa, Siphuriscidae **fam. n.** esta establecida en la Siphonuroidea para *Siphuriscus* y, provisionalmente, el genero Jurásico *Stackelbergisca* Tshernova. *Siphuriscus ? davidi* Návas, conocido de un subadulto macho, es transferido a *Siphonurus davidi* **comb. n.** La familia Siphuriscidae es distinguida de todas las demas familias de Siphonuroidea por la presencia de branquias coxales en las patas delanteras y medias en todos los estados y en la ninfa por la presencia de apendices basales, movibles, tipo dactil en cada uña, y branquias labiales y maxilares. Características de las partes bucales de la ninfa, particularmente el de las mandibulas y maxilas, sugieren que Siphuriscidae es un grupo hermana de la familia Nesameletidae. Sin embargo, la mayoría de los caracteres de los estados son considerados plesiomórficos en Ephemeroptera, y pueda contribuir información valuable en el origen, filogenia y biogeografía de Ephemeroptera.

Translation provided by author.

Ephemeroptera (mayflies) are among the oldest orders of insects. The earliest record comes from the Upper Carboniferous (Carpenter 1992; Hubbard 1990; Kukulová-Peck 1983, 1985, 1991; McCafferty 1990; Sinitchenkova 1984), and six extant families have been found from the Jurassic (Hubbard & Savage 1981; Hubbard 1990; McCafferty 1990). Because of fragmentary and incomplete specimens and because usually only one life history stage is known, McCafferty (1990) indicated that among extant families only Siphonuridae *sensu lato* is unquestionably represented from the Jurassic.

In 1967, Tshernova established a new genus and species for the Middle Jurassic species *Stackelbergisca sibirica* based on an imaginal forewing print and relatively well-deposited nymphal parts.

Earlier, Ulmer (1920) had described *Siphuriscus chinensis* from extant male imagos and female subimagos from China. In 1976, Edmunds et al. suggested that *Acanthametropus* might be the immature stage of *Siphuriscus*, but this theory was negated by publication of the imago of *Acanthametropus* by Tshernova et al. (1986). Although Ulmer's specimens were redescribed by Demoulin (1955) and McCafferty & Wang (1994), the nymph remained unknown until the present. Demoulin (1974) grouped *Stackelbergisca* and *Siphuriscus* together based on similarities in the wing and proposed a new unnamed subfamily of Siphonuridae.

A second species, *Siphuriscus ? davidi*, was described by Navás (1932), but only a wing fragment was illustrated and the description was inadequate

for generic placement. From the distribution (Sichuan province, "Se-Tchouen"), body length, and wing venation, this appears to be a species of *Siphonurus*, a genus which the senior author has frequently collected from Sichuan province in western China. Pending its redescription, we treat this species as *Siphonurus davidi* (Navás) **comb. n.**

In 1994, nymphs of an unknown genus of mayflies were collected by the senior author from Zhejiang province, southeastern China, and a male and a female imago of *Siphuriscus chinensis* were collected from nearby localities in 1993 and 1999. Brief notes on these specimens were published by Gui (1994). Upon further study, we were able to associate the nymphs with imagos based on characters not previously discussed in the literature, particularly the existence of coxal gills on the forelegs and middle legs. In addition, the wing venation and abdominal color pattern were the same as that described by Ulmer (1920). In this paper, we provide additional description of the male imago, describe the female imago, nymph and egg for the first time, establish the new family Siphuriscidae, and discuss its relationship with *Stachelbergisca*.

Genus *Siphuriscus* Ulmer, 1920

Siphuriscus Ulmer, 1920:61; Demoulin, 1955: 1; Demoulin, 1974: 4; McCafferty & Wang, 1994: 211.

Nymph [(in alcohol) (Figs. 1-20, 28)]

Head hypognathous, upper portion global (Figs. 1-2). Antennae short, 6-segmented, scape thicker than other segments, apical segment of flagellum hair-like (Figs. 2-3). Clypeus large, lateral margins with indentation (Fig. 2). Mouthparts (Figs. 2-11): labrum with Y-shaped suture on dorsal surface and short setae on margins (Figs. 2, 4). Hypopharynx as in Fig. 5, lingua narrow basally and broadened apically, apical margins of lingua and superlinguae with fine hair. Mandible with large blade-like outer incisor and small spine-like inner incisor; a row of hair between incisor and molar area, and a small tuft of hairs present at apex of mola (Figs. 6-7). Maxillae with distinct galea-lacinia fusion suture; distal portion of galea-lacinia with a row of spines and setae (Figs. 8-9); maxillary palps 3-segmented, basal segment a little longer than 2nd, apical segment small, very short; two tufts of gills on inner and outer basal surface of maxillae (Fig. 8). Labium with long, narrow, unfused glossae and paraglossae, aboral surface with long hair; labial palp 3-segmented, 3rd segment shorter than basal two with small rounded constriction apically (Figs. 10-11); postmentum well-developed, with one pair of gill tufts laterally (Fig. 10). Forelegs and middle legs with coxal gill tufts (Fig. 15); tibia and tarsus of all legs subequal in length, to-

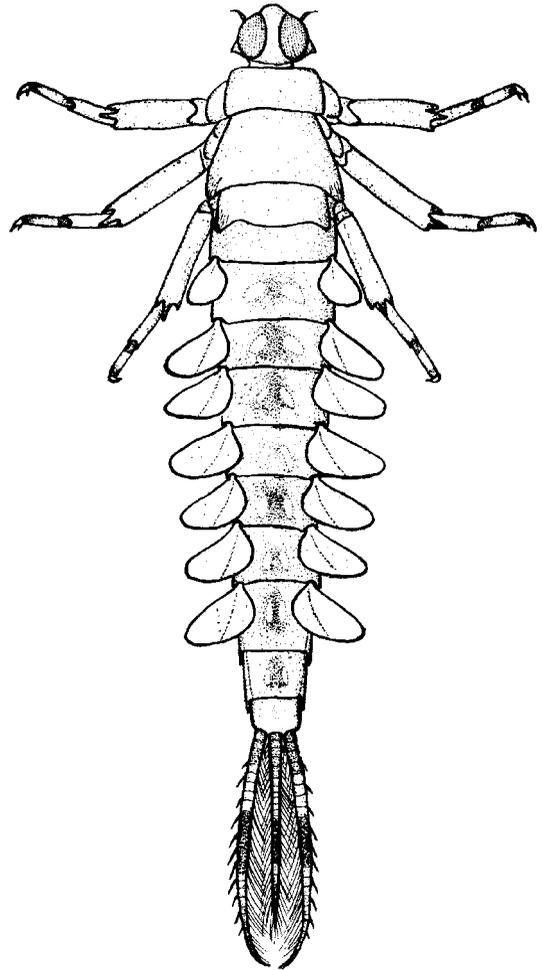
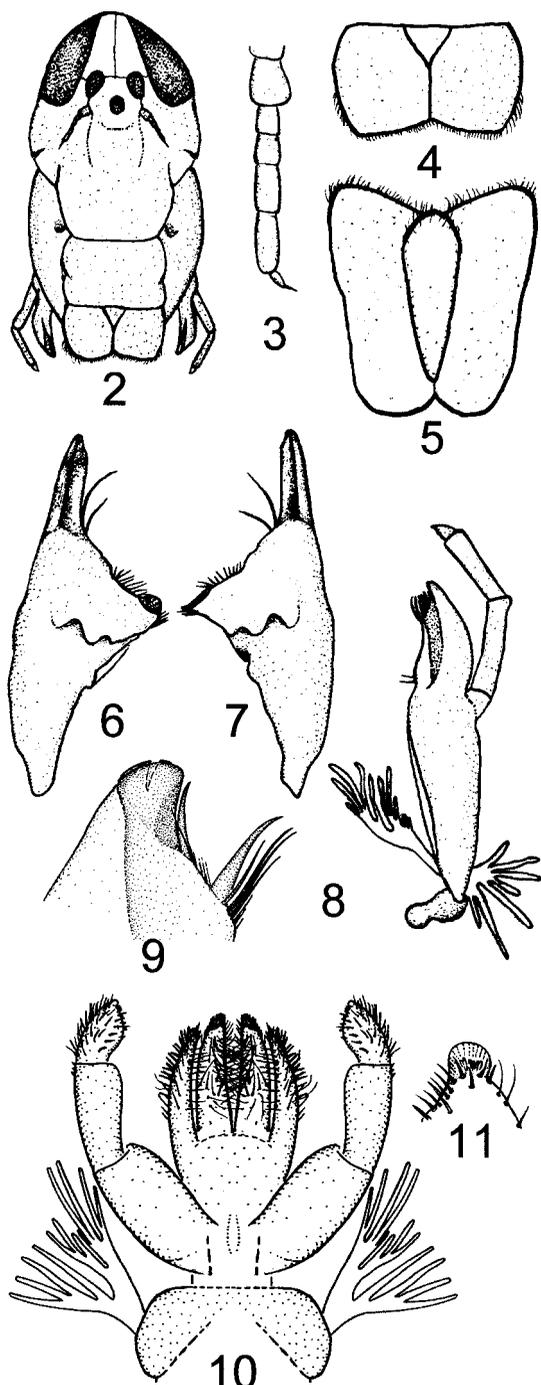


Fig. 1. *Siphuriscus chinensis*, female nymph (habitus).

gether shorter than femur, apex of femur divided into 3 lobes (Figs. 15-17), each with small, stout spines at apex; tibiae of middle and hind legs with patellar-tibial fusion suture; outer margins of all legs with a row of fine hairs (Figs. 15-17). All claws with a broad-based, movable dactyl-like appendage arising from claw base (Figs. 18-19, 28), its inner margin with a row of shallow depressions and its apex long, slender and spine-shaped; inner surface of claw with a shallow groove (Fig. 18). Gills present on abdominal segments 1-7, all gills single, oval, with sclerotized fore costae and submesal sclerotized hind costae (Figs. 1, 12) except costae on first pair of gills small and indistinct (Fig. 14), costae with small blunt setae on surface (Fig. 13); gills 2-7 with small spines apically on anterior margin (Fig. 13); tracheae pigmented. Terga and sterna with very tiny spines on surface, posterior margins of terga with a row of similar spines. Posterolateral projections on ab-



Figs. 2-11. Nymph of *Siphleuriscus chinensis*: 2, head (frontal view); 3, antenna; 4, labrum; 5, hypopharynx; 6, left mandible; 7, right mandible; 8, maxilla; 9, distal detail of maxilla; 10, labium (with apex of postmentum); 11, dorsal detail of apex of labial palp segment 3.

dominal segments 1-9 moderately developed into sharp spines, largest on terga 7-9, tergum 10 with concave posterior margin (Fig. 1). Paraproct with

a stout spine on mesal-posterior angle (Fig. 20). Terminal filament shorter than cerci; lateral margins of terminal filament and inner margins of cerci with dense long hairs, each cercus with spines laterally (Fig. 1).

Imago [(in alcohol) (Figs. 21-27)]

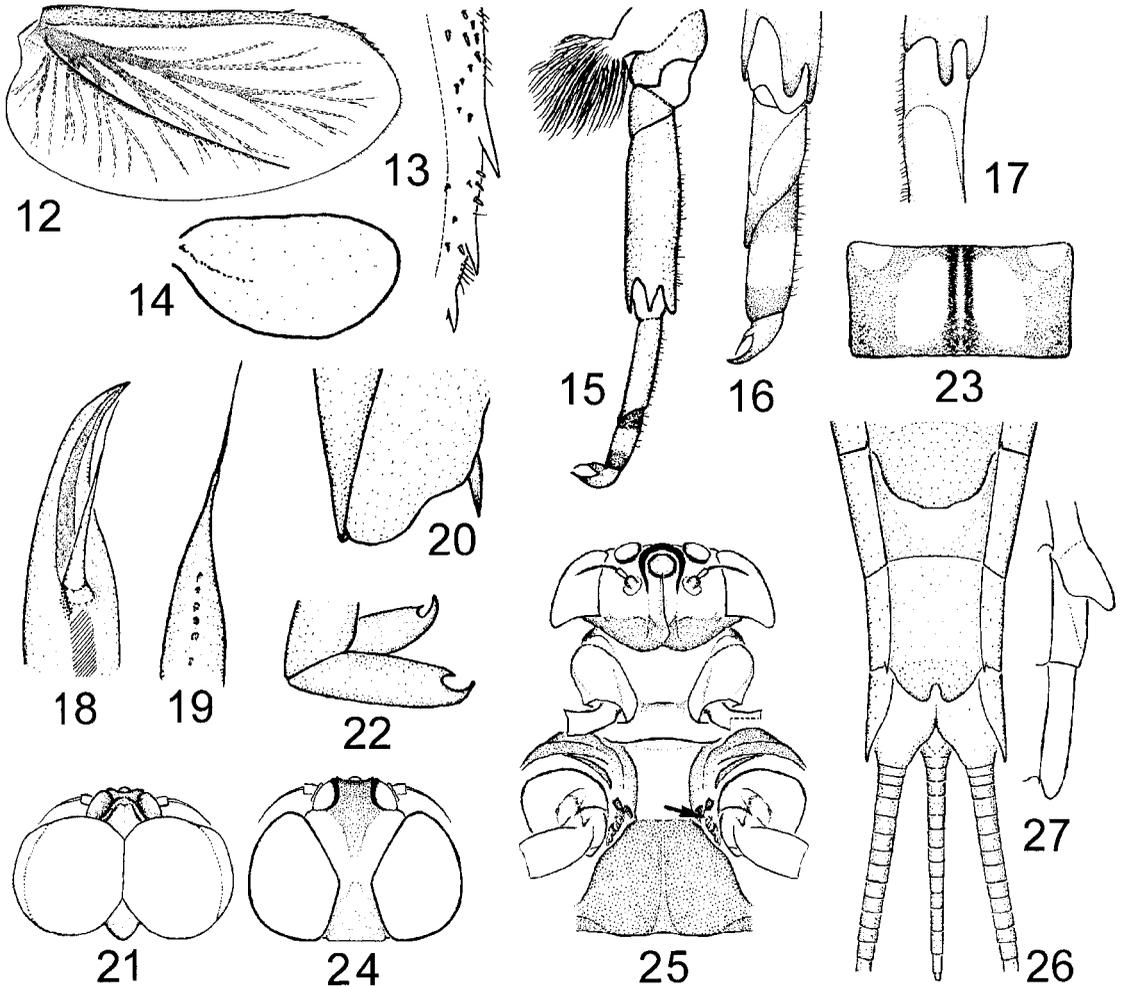
As previously described by Demoulin (1955) and McCafferty & Wang (1994) with following additional characters: compound eyes of ♂ contiguous dorsally, divided into dorsal and ventral portions (Fig. 21); eyes of ♀ separated by width of lateral ocellus (Fig. 24). Head with a horseshoe-shaped carina surrounding median ocellus posteriorly and laterally, a median longitudinal carina running from median ocellus to anterior margin of head (Fig. 25), occiput with posterior projection in ♂ (Fig. 21), broad in ♀ (Fig. 24). Furcasternal protuberances of mesothorax separated posteriorly (Fig. 25). Coxae of fore and middle legs with gill remnants at base (Fig. 25); middle and hind legs with distinct patellar-tibial fusion line; apex of femora of all legs subdivided into 3 lobes. Claws of all legs similar, paired; each hooked, acute with opposing hook (Fig. 22). Ninth sternum of ♀ with concave posterior margin (Fig. 26); sternum 7 of ♀ well developed and extended about half length of sternum 8, median portion of sternum 8 pale, more membranous than surrounding exoskeleton (Figs. 26-27). Terminal filament very short, about 1/10 length of cerci (Fig. 26).

Egg [(description from T. Soldán) (Figs. 29-31)]

Oval, about 1.3 times longer than wide, measurements: 243 μm (238-252 μm) \times 188 μm (185-200 μm), 16 eggs measured. Approximately 15-24 loose attachment structures irregularly scattered around poles, but absent at the poles (Figs. 29-31). Attachment structures measuring 10-35 μm and consisting of two subunits: proximal part elongated, funnel-like, about 3-5 times wider apically than at base; distal part regularly oval or globular, measuring about 7-12 μm in diameter (Fig. 30). Attachment structures similar in length and shape at both poles, but globular distal subunits about twice as wide in diameter on one of the poles. A single micropyle submedial to attachment structures in all eggs examined (Fig. 30). Micropyle roughly oval, bluntly pointed at one side, measuring 10-12 μm \times 15-16 μm ; micropylar rim not developed; sperm guide inconspicuous, connected to bluntly pointed portion of micropyle, measuring about 7.5 μm . Exochorionic surface uniform, consisting of irregular rounded or oval granulation 2.5-4.5 μm in diameter.

Species Included

Siphleuriscus chinensis Ulmer.



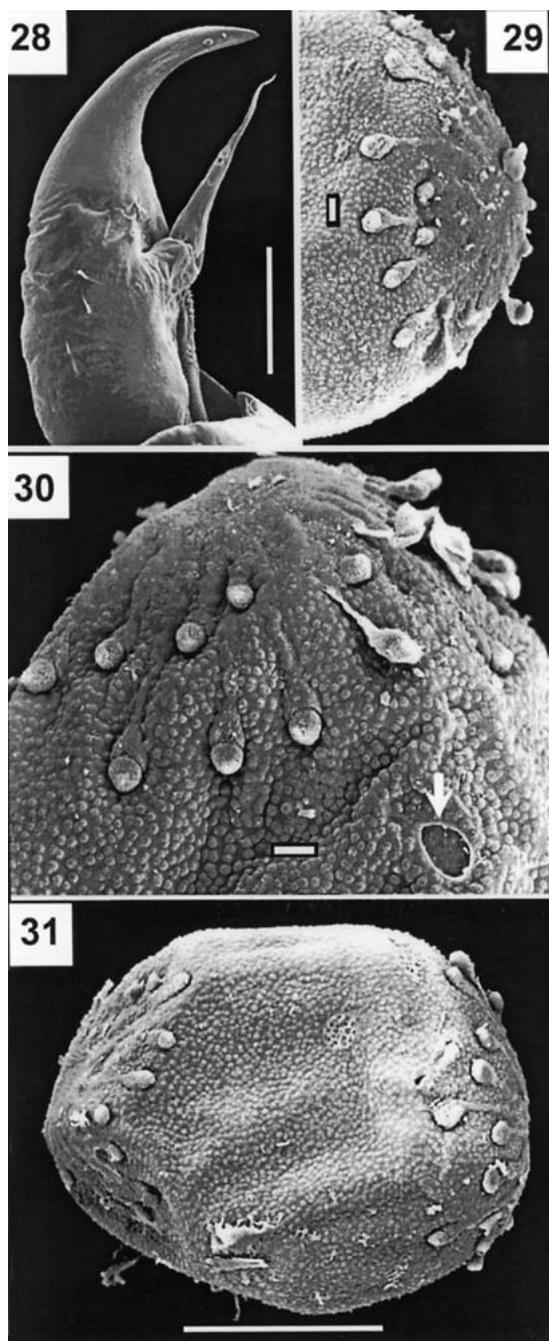
Figs. 12-27. *Siphuriscus chinensis*. Figs. 12-20, nymph: 12-13, gill 4 with apical detail of gill costa (13); 14, gill 1 (tracheation not drawn); 15, foreleg; 16, distal segments of middle leg (ventral); 17, connection between tibia and tarsus of middle leg (dorsal view); 18, apical portion of foreclaw (schematic showing position of groove); 19, detail of dactyl-like appendage of claw; 20, apex of paraproct and margin of tergum 10. Figs. 21-23, male imago: 21, head; 22, foreclaw; 23, tergum 2. Figs. 24-27, female imago: 24, head; 25, pro- and mesosternum (arrow points to gill remnant); 26, sterna 7-9 and caudal filaments; 27, lateral view of sterna 7-9.

DISCUSSION

Siphuriscus is distinguished from all extant genera of Ephemeroptera in the imagos by the combination of straight penes without accessory structures, the deeply divided styliiger plate, the 'siphonuroid' forewing with an exceptionally long and narrow cubital field (as in the Middle Jurassic *Stackelbergisca*), long hind wings (more than half length of forewings), gill remnants on fore and middle coxae, and similar claws. In the nymph, the labial gills, the constricted 3rd segment of the labial palp, and the claws are unique among Ephemeroptera. We believe these characters are sufficiently distinct to follow the recommendation of Demoulin (1974) and establish Siphuriscidae

fam. n. [type genus *Siphuriscus* Ulmer, 1920] for *Siphuriscus* and, provisionally, the Jurassic *Stackelbergisca*, although details of *Stackelbergisca* are not well known (discussed below).

McCafferty & Wang (1994) analyzed relationships between imagos of *Siphuriscus*, *Acanthametropus*, *Analetris*, and Siphonuridae (in the broad sense), showing that *Siphuriscus* was not closely related to the specialized genera included in the psammophilous Acanthametropodidae; they considered the deeply forked MA in the hind wing to be an apomorphy of *Siphuriscus*. Kluge et al. (1995) then summarized relationships of all the family groups where both adults and nymphs were known. Although lacking details of the sub-imago cuticle, we refer to Kluge et al. (1995) for



Figs. 28-31, *Siphuriscus chinensis*. Fig. 28, nymphal claw. Figs. 29-31, egg: 29-30, polar regions of egg with detail of attachment structures and micropyle (Fig. 30, arrow); 31, whole egg. (SEM scale bar = 100 μm in Figs. 28, 31; 10 μm in Figs. 29, 30).

most comparative data. Siphuriscidae share a few common characters with genera of the Northern Hemisphere Siphonuridae and Ameletidae. However, the closest relationship would appear to

be with the Southern Hemisphere Nesameletidae where at least seven of the character states discussed by Kluge et al. (1995) are of similar structure (elongated mandibles with long incisor, modified setae on apex of maxilla, short third segment of maxillary palp, long and narrow unfused glossae and paraglossae, unpaired projection on occiput of male imago, well developed subgenital plate on female sternum 7, and similar adult claws). *Siphuriscus* is easily distinguished from all genera of Nesameletidae in imagos by the greater length of the hind wing ($>1/2$ length of forewing), the deeply divided male styliger plate, penes joined only at base, and the basally forked MA vein in the hind wing; and in the nymph by the presence of well-developed maxillary and labial gills, gills on the pro- and mesothoracic coxae and the unique claw.

Any attempt at cladistic analysis of families within Siphonuroidea is complicated by the fact that the group as presently defined is distinguished by a complex of plesiomorphies (Kluge et al. 1995). In *Siphuriscus*, imaginal structures are considered either plesiomorphic, subject to frequent reversal, or derived by reduction or fusion. Based on the work of paleontologists and morphologists (Smith 1969; Kukulová-Peck 1991, 1992; Gaino & Rebora 1995), we know that the penes of insects have evolved through the loss or fusion of what were ancestrally complex structures and the simpler structure of the penes of *Siphuriscus* would be considered derived, but such reductions are found throughout the order. Similarly, the blade-like outer incisor of the mandible represents a highly specialized algal scraping device found in mayfly nymphs of other families and immature stages of other insect orders; it is considered the most common type of feeding specialization found in immature aquatic insects (Arens 1990). The inner incisor (termed "kinetodontium" by Kukulová-Peck 1991 and Kluge 2000) appears as a spine inserted at the base of the outer incisor ("canine") and its evolutionary status is unclear. Gills at the base of mouthparts and coxae, sometimes called accessory gills to distinguish them from the plate-like abdominal gills (tergaliae of Kluge et al. 1995), are broadly distributed in Ephemeroptera nymphs and persist into the adult stage of several genera of Ephemeroptera, Plecoptera, Odonata, and Trichoptera (Štys & Soldán 1980). The historical evolution of the paraproct has never been studied in Ephemeroptera, but the paraproct of *Siphuriscus* is presumably plesiomorphic based on available outgroups because an acute submedial spine or projection is also found in Siphonuridae, Metretopodidae, Oniscisgastridae and Rallidentidae.

Of the characters discussed in Kluge et al. (1995) and McCafferty & Wang (1994), none will clearly align *Siphuriscus* with other extant families, although initial analysis (Table 1) shows a

TABLE 1. CHARACTER STATES OF SIPHLURISCIDAE, SIPHLONURIDAE, AND NESAMELETIDAE.

Character ¹	Ancestral	Derived	Derived in ²	Source ³
Claw (N)	double (apparently)	single	Siphlo; Nes	A1, A2
Hind: forewing length ratio (A)	>1/2	<1/2	Siphlo; Nes	A1, A2, A3
Hind wing MA fork located (A)	medially or distally	basally	Siphur	B
Prosthecae of mandible (N)	present (w/ brush)	reduced or absent	Siphur; Nes	C, F
Setae on apex of maxilla (N)	free	some fusions	Siphur; Nes	C, D
Penes of male (A)	w/ auxiliary structures	simplified	Siphur; Nes	A1, E
Styliger plate of male (A)	divided	fused	Siphlo; Nes	A1, G
7th sternum of female (A)	simple or extended	with pouch	Siphlo	C
Gill costae (N)	with 2 costae	hind costa weak	Siphlo	C

¹Stage indicated as N (nymph) or A (adult).

²Families abbreviated as Siphlo (Siphonuridae), Nes (Nesameletidae), Siphur (Siphuriscidae).

³Sources: A1, Kukulová-Peck 1991, 1992; A2, Tshernova 1967; A3, Demoulin 1974; B, McCafferty & Wang 1994; C, Kluge et al. 1995; D, Kluge 1998 (see paper for explanation of character); E, Gaino & Rebera 1995; F, numerous authors; general consensus; G, this paper.

potential relationship with Nesameletidae. Table 1 gives a brief summary of characters for which there is general agreement in the literature, and ignores for now the many characters (such as accessory gills) open to more than one interpretation. More detailed analysis is needed to determine if characters such as the structure of apical maxillary setae (Kluge 1998) and the structure of the incisor are synapomorphic. Of all nymphal characters of Siphuriscidae, the most interesting and least understood is the claw. It does not resemble the apically bifurcate foreclaw of Metretopodidae, and only one similar claw is known in Ephemeroptera—that of certain Jurassic nymphs found in association with the imago of *Stackelbergisca sibirica*.

Stackelbergisca includes the type species *S. sibirica* described from the holotype wing (indistinguishable from *Siphuriscus*) and *S. shaburensis* Sinitshenkova. At least two different nymphal types have been associated with the *S. sibirica* imago and *S. shaburensis* is described from nymphs only (Sinitshenkova 1991). Some nymphs (*S. sibirica* in part) have a dactyl-like appendage basally, and others do not (*S. sibirica* in part and *S. shaburensis*), and some have small paired projections on posterior abdominal terga and others do not. The presumed mandibles of *Stackelbergisca* are also not clearly associated with a specimen (Tshernova 1967). From this, we can only conclude that some nymphs with a second basal dactyl-like appendage are present in the same formation as *Stackelbergisca* imagos. Although full double claws are clearly the ancestral state in Ephemeroptera (Kukulová-Peck 1968), the illustrated fossil claw of *Stackelbergisca* does not display enough detail to make any definitive determination of its relationships. Thus, the placement of *Stackelbergisca* in Siphuriscidae is provisional, a placement first suggested by Demoulin (1974) based only on the imaginal wing.

The discovery of the similar nymphal claw which has possibly been retained for more than 100 million years reinforces this placement.

If the relationship between *Siphuriscus* and *Stackelbergisca* is correct, we can say that the *Siphuriscus* lineage arose in the Jurassic, and is a representative of the oldest known extant family with regard to the fossil record. *Stackelbergisca* is among the oldest fossils of Siphonuridae *sensu lato* (Carpenter 1992; Hubbard 1990; McCafferty 1990). However, there are many plesiomorphies in Siphonuridae *sensu stricto* (Table 1) and one other genus from the Jurassic (*Oligisca* Demoulin, 1970, known only from a forewing) is assigned to Siphonuridae *sensu stricto*. The Chinese Siphonuridae have yet to be studied, and discovery of the nymph of species such as *Siphonurus davidi* may require a reevaluation of this hypothesis.

Nelson & Platnick (1984) used some mayfly distribution information provided by Edmunds (1981) as evidence to support the geographic congruence between South America, Australia and New Zealand. Kluge et al. (1995) suggested a Northern Hemisphere (Laurasian) origin for the Southern Hemisphere (Gondwanian) Siphonuroidea. Based upon present findings, their arguments should be qualified because the ancestor of extant Nesameletidae may have had a much broader distribution than previously known. The present distribution [Nesameletidae: *Nesameletus* (New Zealand), *Ameletoides* (Australia), *Metamonius* (Chile, Argentina); Siphuriscidae: *Siphuriscus* (Southeastern China), *Stackelbergisca* (Eastern Siberia)] implies that the ancestor of Nesameletidae and Siphuriscidae may have originated in an ancient, continental mass in the paleo-Pacific region and gives support to the hypothesized Pacifica continent proposed by Nur & Ben-Avraham (1977).

The claw could also represent a more recent, independently evolved structure. The limited series of specimens available to us are sufficient for de-

scription and diagnosis, but many questions remain. The functional morphology of the claw cannot be studied without fresh or living material, and almost nothing is known of the biology of the species. Further study of *Siphuriscus* is essential to understand its biology and evolutionary history.

Siphuriscus chinensis Ulmer, 1920

Siphuriscus chinensis Ulmer, 1920: 62 (male imago, subimago); Demoulin, 1955:1 (subimago); McCafferty & Wang, 1994: 211 (male imago and subimago).

Male imago [(in alcohol) (Figs. 21-23)]

Body length 23 mm; forewing 23 mm; hind wing 13 mm; foreleg 17 mm; middle leg 10 mm; cerci 40 mm; terminal filament 3.5 mm. Compound eyes with gray to dark gray dorsal portion and brown ventral portions. Head and thorax dark brown. Body dark brown with yellowish marks; abdominal terga 1-8 as in Fig. 23, each tergum with pair of yellowish marks and median dark brown stripes. Wings transparent, veins dark brown; Sc and Rs of forewing with distinct vein bullae. Forelegs light brown to brown, femora paler than tibiae and tarsi; middle and hind legs slightly paler than forelegs, femora almost similar to tibiae and tarsi in color. Tergum 10 with slight concave posterior margin. Terminal filament paler than cerci, all filaments with tiny brown setae on surface.

Female imago [(in alcohol) (Figs. 24-27)]

Body length 24-25 mm; forewing 24-25 mm; hind wing 13.5 mm; foreleg 11.5 mm, middle leg 10.7 mm, hind leg 9.5 mm; cerci 38 mm, terminal filament 3 mm. Similar to male, but body paler, venter and thorax yellowish brown. Terga with similar color pattern as male, but paler. Sterna yellowish, each sternum with a pair of indistinct gray marks on median portion, each mark with pale dots. Last ventral abdominal segments shown in Fig. 26.

Nymph [(in alcohol) (Figs. 1-20, 28)]

Body length 22-24 mm, cerci 7.5 mm, terminal filament 6 mm. General color pale yellowish with indistinct brown marks (in life, yellowish green with reddish stripes). Ocelli gray (Fig. 2). Incisors of mandibles strong, reddish. Apex of tibiae yellowish brown; tarsi with 2 brown bands on basal and distal portions (Figs. 15-16). Each tergum with a pair of pale submedian marks, median area dark, especially on terga 2-3, 6 and 8-9 (Fig. 1). Basal and middle portions of caudal filaments with yellowish brown bands (Fig. 1); apically from basal band, every 4th annulation of cerci with spines on outer lateral margin, 10 of them distinct.

Material

P.R. CHINA: 15 nymphs, Zhejiang Province, Guan-Pu-Yang, Nang-Ju, Long-Quan county (28.04°N, 119.08°E), 600 m, 15-VIII-1994, leg. ZHOU Chang-fa & ZHU Chao-Dong; 1♀, Zhejiang Province, Bai-Shan-Zhu, Qingyuan county (27.37°N, 119.04°E), 20-IX-1993, leg. WU Hong; 1♂, Zhejiang Province, Tian-Mu-Shan mountain (30.26°N, 119.34°E), 2-VI-1999, leg. ZHAO Ming-Shui (13 nymphs, 1♂, 1♀ deposited in Department of Biology, Nanjing Normal University, P.R. China; 2 nymphs in Florida A&M University, USA). Egg from 1♀ collected at light trap, Zhejiang Province, Long-Wan-Shan mountains (30.28°N, 119.22°E), 3-VI-1999, leg. Ignac SIVEC, deposited in the Institute of Entomology, Academy of Sciences of the Czech Republic, České Budějovice.

Biology

The nymphs were collected in quiet water of a small mountain stream with a sand and stone substrate. Width of the streambed was between 2 m and 4 m, but at the time of collection the stream was only about 1 m wide and less than 40 mm deep. The stream is in an undisturbed mountainous area with large trees on the bank, and sunlight reaches the water surface only at noon and early afternoon. Living nymphs can jump quickly like small fish when removed from water. They are strong swimmers and can hold tightly to branches or stones with their legs and claws. Gills of observed nymphs did not move. Mayflies collected from the same stream included *Vietnamella*, *Serratella*, *Isonychia*, and some baetid and heptageniid species.

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