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A revision of *Epeorus* (*Proepeorus*) in China, with descriptions of two new species (Ephemeroptera, Heptageniidae)

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ABSTRACT

The genus *Epeorus* Eaton, 1881 is diverse in China but has never been specifically studied before. In this revision, eight species in *Epeorus* (*Proepeorus*) from China are recognised, including two new species, *Epeorus* (*Proepeorus*) *gibbus* **sp. nov.**, *Epeorus* (*Proepeorus*) *falcatus* **sp. nov.** and additional five new records for this country. Both new species have unique shape of imaginal penis and tubercles on nymphal terga. The variation of *Epeorus* (*Proepeorus*) in China shows this subgenus may not be a monophyletic taxon.

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morphology

Introduction

The genus *Epeorus* Eaton, 1881 is known as one of the most species-rich genus of family Heptageniidae. Up to now, 100 species have been reported around the world (Sivaruban et al. 2013; Boonsoong and Braasch 2013; Sartori and Brittain 2015; Hrivniak et al. 2017, 2019, 2020a) and most species of this genus distribute in Holarctic and Oriental regions. As a vast territory and possessing both parts of Holarctic and Oriental regions, China hosts a high number of *Epeorus* species. However, only very limited species of them have been reported scatteredly before.

Historically, several subgenera of *Epeorus* have been proposed (Burks 1953; Edmunds and Traver 1954; Tshernova 1981; Kluge 1997, 2004; Braasch 2006). As a summary, Kluge (2004) divided genus *Epeorus* (= *Epeorus* s.l. or *Epeorus*/fg3) into seven subgenera: *Proepeorus*, *Epeorus* (= *Epeorus*/fg4), *Belovius* (= *Belovius*/g2), *Albertiron*, *Iron* (= *Iron*/g2), *Ironopsis* (= *Ironopsis*/g2) and *Caucasiron*. Meanwhile, some competitive opinions were also proposed. Braasch (2006) and Braasch and Boonsoong (2010) disagreed to the combination of genus *Iron* (= *Iron*/g1) and *Epeorus* (including other *Epeorus*/fg3 species except *Iron*/g1). Webb and McCafferty (2008a) did not recognise any subgenera of genus *Epeorus* (including *Iron*), seeing them as paraphyletic groups. In a word, the classification of genus *Epeorus* is controversial.

For convenience sake and to be consistent with several recent related works (Boonsoong and Braasch 2013; Hrivniak et al. 2017, 2019), here we follow the theory of Kluge (2004).

Kluge (2004) established subgenus *Epeorus* (*Proepeorus*) (hereafter *Proepeorus*) as a 'plesiomorphon' (a taxon characterised by plesiomorphies only, see Kluge 2004, p. 16), which possesses similar diagnostic characters as *Epeorus* (*Epeorus*) (=Epeorus/fg4 *sensu* Kluge 2004, hereafter *Epeorus* s.str.) in nymph: 1) slightly elongated gill lamellae I and unfolded gill lamellae VII (contrary to subgenus *Iron*, *Ironopsis* and *Caucasiron*, they have well-elongated gill lamellae I and distinct folded gill lamellae VII); 2) gill lamellae II–VII with anal rib on anal margin (in contrast to subgenus *Belovius* and *Albertiron*, they have anal rib situated at a distance from anal margin). We can only distinguish *Proepeorus* from *Epeorus* s.str. by the presence of median titillators on imaginal penis lobes. Therefore, many Asian species belonging to *Proepeorus* or *Epeorus* s.str. without descriptions of adult stages were unable to be classified into any subgenus. Under this circumstance, up to now, only seven *Proepeorus* species have been described, including five Nearctic species and two Asian species (*E. (P.) anatolii* Sinitshenkova, 1981 and *E. (P.) nipponicus* (Uéno, 1931)).

In China, species of genus *Epeorus* have been reported frequently since the 1920s (Table 1), but most of them, especially some endemic species, were described from either adult or nymphal stage only. This condition makes them difficult to be classified in any subgenus in most cases. Meanwhile, many undescribed and newly recorded *Epeorus* species were found in our recent samplings. In order to deepen understanding about this genus in China, we checked all related materials in our collection, and as a first step, eight species belonging to subgenus *Proepeorus* are recognised and compared in this report.

Table 1. List of species of *Epeorus* recorded in China (according to Zhou et al. 2015 etc.), classification of subgenera is according to Kluge (2004).

	Species	Subgenus (Kluge 2004)	Reference
1	<i>Epeorus assimilis</i> Eaton, 1885	<i>Epeorus</i> (<i>Epeorus</i>)	Su et al. (1995)
2	<i>Epeorus melli</i> (Ulmer, 1925)	<i>Epeorus</i> (<i>Epeorus</i>)	Ulmer (1925) and Zhou et al. (2007)
3	<i>Epeorus latifolium</i> Uéno, 1928	<i>Epeorus</i> (<i>Belovius</i>)	Imanishi (1940)
4	<i>Epeorus pellucidus</i> (Brodsky, 1930a)	<i>Epeorus</i> (<i>Belovius</i>)	Zhou et al. (1998), Bae and Liu (1999) and Quan et al. (2002)
5	<i>Epeorus aesculus</i> (Imanishi, 1934)	<i>Epeorus</i> (<i>Iron</i>)	Tshernova et al. (1986), Bae and Liu (1999) and Quan et al. (2002)
6	<i>Epeorus montanus</i> (Brodsky, 1930b)	<i>Epeorus</i> (<i>Iron</i>)	Braasch 1999
7	<i>Epeorus curvatulus</i> Matsumura, 1931	<i>Epeorus</i> (<i>Iron</i>)	Imanishi (1940), Bae and Liu (1999) and Quan et al. (2002)
8	<i>Epeorus dayongensis</i> Gui & Zhang, 1992	Incertae sedis	Gui and Zhang (1992)
9	<i>Epeorus herklotsi</i> (Hsu, 1936a)	Incertae sedis	Hsu (1936a)
10	<i>Epeorus ngi</i> Gui, Zhou & Su, 1999	Incertae sedis	Gui et al. (1999)
11	<i>Epeorus extraordinarius</i> Chen, Wang & Zhou, 2010	<i>Epeorus</i> (<i>Caucasiron</i>)	Chen et al. (2010)
12	<i>Epeorus erratus</i> Braasch, 1981	Incertae sedis	Braasch (1981) and Kang and Yang (1994)
13	<i>Epeorus pinguoyuanensis</i> You, 1987	Incertae sedis	You (1987)
14	<i>Epeorus sagittatus</i> Tong & Dudgeon, 2003	Incertae sedis	Tong and Dudgeon (2003)
15	<i>Epeorus dominans</i> (Navás, 1936)	Incertae sedis	Navás (1936)
16	<i>Epeorus famulans</i> (Navás, 1936)	Incertae sedis	Navás (1936)
17	<i>Epeorus minor</i> (Hsu, 1936b)	Incertae sedis	Hsu (1936b)
18	<i>Epeorus sinensis</i> (Ulmer, 1925)	Incertae sedis	Ulmer (1925)
19	<i>Epeorus jacobii</i> (Braasch, 1978)	Incertae sedis	Braasch (1999)
20	<i>Epeorus rheophilus</i> (Brodsky, 1930b)	<i>Epeorus</i> (<i>Ironopsis</i>)	Braasch (1999)

Material and methods

The nymphs were collected by hand net and the adults were collected by light trap (using led and mercury lamp). Some adults were reared from nymphs in the field. The materials were stored into ethanol (more than 75%).

In addition to *Propeorus* species, some other *Epeorus* species for morphologic comparisons were also examined in this study, contain some Chinese species belong to subgenus *Iron*, *Belovius* and *Epeorus* s.str. or incertae sedis. Sample sites of these materials are as follows:

Epeorus (Epeorus) melli (Ulmer, 1925): 55 nymphs Lianhua Village (108°11'869"E, 26°22'377"N, 1546 m a.s.l.), Lei-gong-shan Reserve, Guizhou Province, collected by Peng LI, Zhi-Jie WANG, 17-18-IX-2005

Epeorus nguyeni (Webb & McCafferty, 2008b) (first record for China): 4 nymphs, Punwen Town (1032 m a.s.l.), Xishuangbanna, Yunnan Province, collected by Ning DING, 1-IV-2013

Epeorus (Belovius) pellucidus (Brodsky, 1930a): 80 nymphs, Dadingshan Forest Park, Raohe County, Heilongjiang Province, collected by Juan-Yan LUO, Wei ZHANG, Ze HU, 20-VII-2016

Epeorus (Iron) alexantri Kluge & Tiunova, 1989 (first record for China): 20 nymphs, Halaha River (1050 m a.s.l.), Aer mountain, Inner Mongolia, collected by Li SHI, Ming-Run TIAN, Yu-Xuan ZHU, Xue-Feng GAO, 25-VII-2014

All specimens were examined under a stereomicroscope and photographed with a digital camera fitted with a micro-lens. Some small structures, such as gills and mouthparts, were observed and photographed with a microscope camera. Gills, mouthparts and microstructure of terga and legs were drawn from slides.

Diagnostic characters and terminology were used according to Kluge (2004, 2015), Zhou et al. (2007), Braasch and Boonsoong (2010) and Hrivniak et al. (2017). The terms 'arrow-like setae' (see Tong and Dudgeon 2003: fig. 26) and 'setose pads' (see Ditsche-Kuru and Koop 2009: Figures 2 and 3) were used for the nymphal characters. The term 'myo-sigillum' refers to the marking on abdominal sterna (see Kluge 2015). Abbreviation: 'a.s.l.': above sea level; 'C': Costa; 'Sc': Subcosta; 'MA': Medius anterior; 'MP': Medius posterior.

Results

Epeorus (Propeorus) nipponicus (Uéno, 1931)

Figs 1A–C, 6B, 12C, 13C, 14E–F, 15A, I, 16C

Epeorus nipponicus Uéno, 1931, p. 97, Figure 4 (male imago). Types: male imago, from Japan.

Epeorus curvatulus (nec Matsumura, 1931): Imanishi 1934, p. 392, Figure 3 (male, female, nymph); Imanishi 1940, p. 250, Figure 38 (nymph, first record from China); Bae 1997, p. 410; Bae and Liu 1999, p. 5; Quan et al. 2002, p. 253. Synonymised by Ishiwata 2001, p. 74.

Materials examined

Six male imagoes, Yalu River (668 m a.s.l.), Boketu Town, Yakeshishan City, Inner Mongolia, collected by Chang-Fa ZHOU, Hui XIE, 2-VIII-2007; 1 female imago, Zhuoer River (755 m a.s.

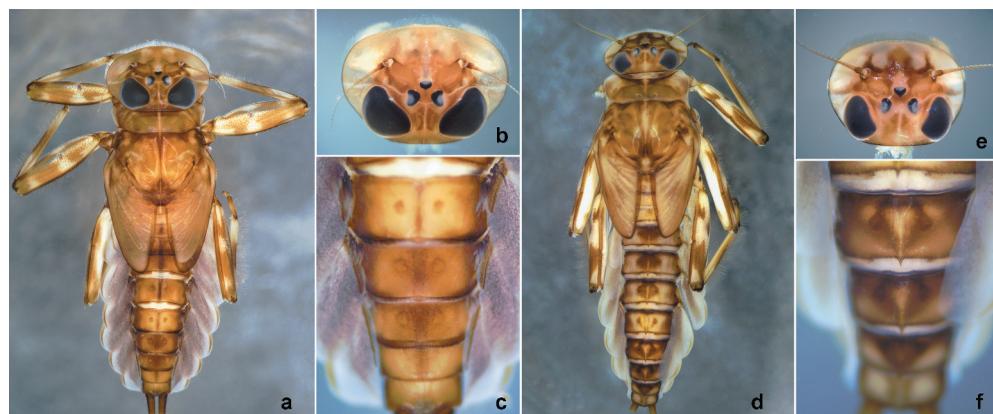


Figure 1. Nymph of *Epeorus* spp.: (a–c) *Epeorus (Proepeorus) nipponicus*: (a) Nymphal habitus, (b) Head capsule, (c) Abdominal terga VII–X; D–F: *Epeorus (Proepeorus) unispinosus*: (d) Nymphal habitus, (e) Head capsule, (f) Abdominal terga VII–X.

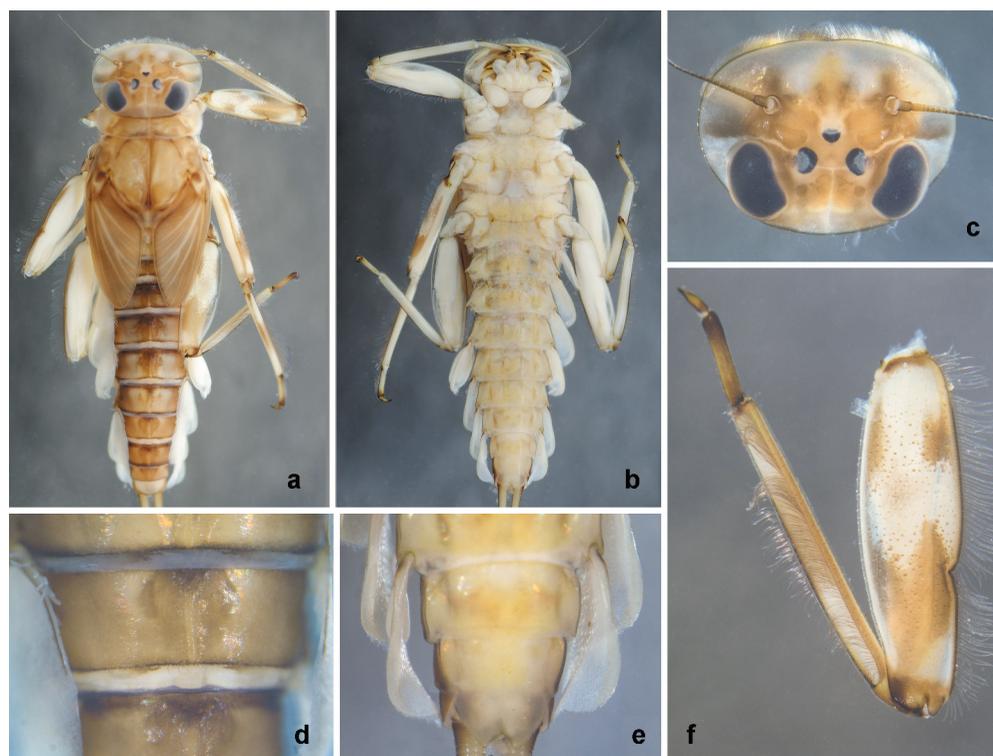


Figure 2. Nymphal habitus and structures of *Epeorus (Proepeorus) gibbus* sp. nov.: (a) Nymphal habitus (dorsal view); (b) Nymphal habitus (ventral view); (c) Head capsule; (d) Abdominal tergum (segment VII); (e) Gill VII (ventral view); (f) Middle leg.

I.), Taerqi Town, Yakeshishan City, Inner Mongolia, collected by Chang-Fa ZHOU, Hui XIE, Shi-Lei WANG, 4-VIII-2007; 30 nymphs, Wangyedian (1288 m a.s.l.), Kelaqi, Chifeng City, Inner Mongolia, collected by Yu-Xuan ZHU, Xue-Fen GAO, Wei-Jie SUN, 25-VII-2014; 4

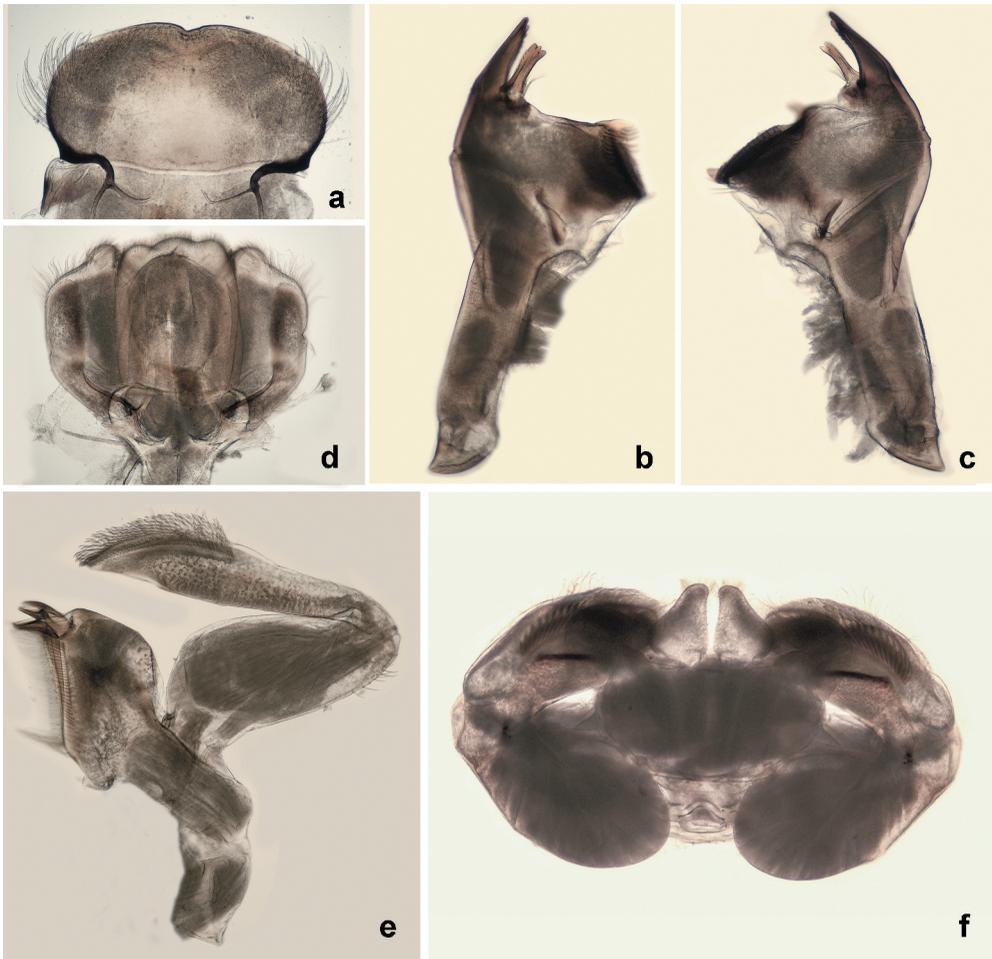


Figure 3. Mouthparts of *Epeorus (Proepeorus) gibbus* sp. nov. (digital photos): (a) Labrum; (b) Left mandible; (c) Right mandible; (d) Hypopharynx; (e) Maxillae; (f) Labium.

female imagoes, Songjianghe Town, Fusong County, Jilin Province, collected by Shi-Lei WANG, Gui ZHAO, 28-VII-2008; 30 nymphs, Dadingshan Forest Park, Raohe County, Heilongjiang Province, collected by Juan-Yan LUO, Wei ZHANG, Ze HU, 20-VII-2016.

Diagnosis and remarks

Nymph of this species can be characterised by conspicuous paired C-shaped markings near frontal margin of head (Figure 1(b)) and brownish median line with a pair of submedian brownish spots on each abdominal tergum from segments III–VIII (Figure 1A, C). In adults, it can be distinguished from other congeners by the rounded and laterally expanded penis lobes of male imago (Figures 12(c) and 13(c)) and trapezoidal subgenital plate of female imago (Figure 14(e,f)). *Epeorus (Proepeorus) anatolii* Sinitschenkova, 1981 have the similar characters in nymphal (e.g. the colouration pattern of abdominal terga) and imaginal stages (e.g. shape of penes, see Sinitschenkova 1982: Figure 1). Although we can distinguish *E. (P.) anatolii* from *E. (P.) nipponicus* by the absence

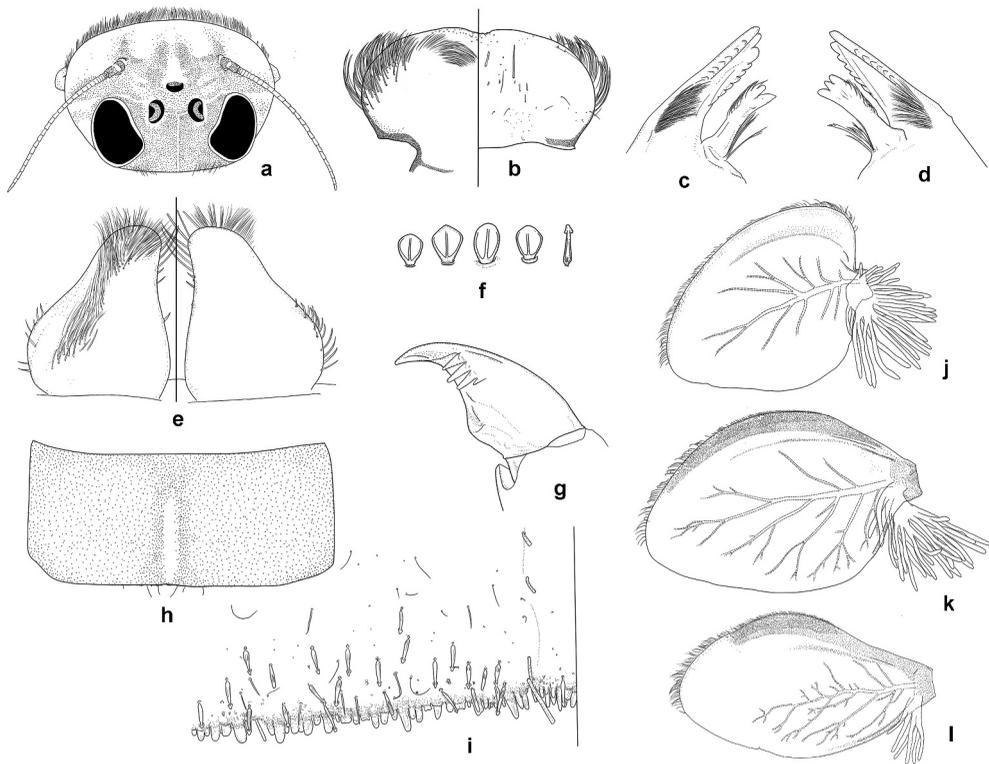


Figure 4. Nymph of *Epeorus (Proepeorus) gibbus* **sp. nov.**: (a) Head capsule; (b) Labrum (ventral view on left, dorsal view on right); (c) Right mandible; (d) Left mandible; (e) Glossae of labium (dorsal view on left, ventral view on right); (f) Femoral setae; (g) Claw; (h) Abdominal tergum VII (dorsum); (i) Posterior margin of tergum VII (vertical line is midline of tergum); (j) Gill I; (k) Gill II; (l) Gill VII.

of C-shaped markings on head capsule, assuming the variability of colouration in nymphs, the relationship of these two species should be confirmed upon further more detailed morphological comparison and molecular evidence.

Distribution

China (Inner Mongolia, Jilin, Heilongjiang and Liaoning), Japan.

***Epeorus (Proepeorus) unispinosus* Braasch, 1980**

Figs 1D–F, 6C–D, 15B, 16E

Epeorus sp. Uéno, 1955, p. 313, Figures 100–110 (nymph).

Epeorus unispinosus Braasch, 1980, p. 62, Figure 5. Types: nymph, from Nepal.

Materials examined

14 nymphs, Shaolu Village, Tianmu Mountain, Zhejiang Province, collected by Juan-Yan LUO, Wei ZHANG, Zhen-Xing MA, Ming ZHANG, 14-IV-2017; 70 nymphs, unnamed creek in front of Tian-Mu Hotel, West Tianmu Mountain, Zhejiang Province, collected by Juan-Yan LUO, Wei ZHANG, Zhen-Xing MA, Ming ZHANG, 16-IV-2017; 3 nymphs, Zhoujiatan, West

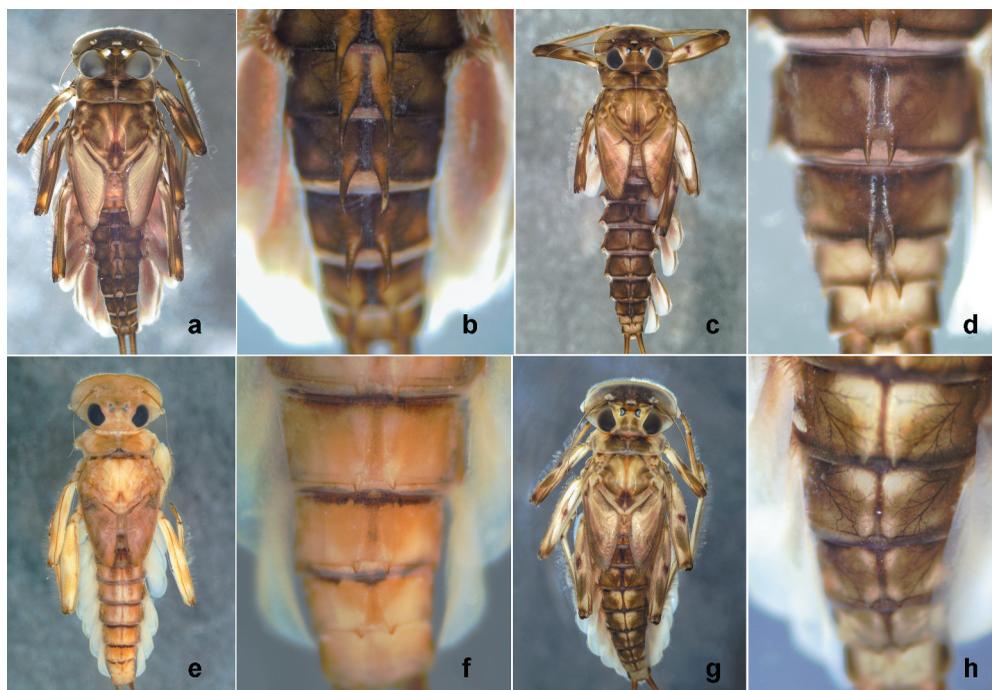


Figure 5. Nymphal habitus and abdominal terga of *Epeorus (Proepeorus)* spp.: A–B: *E. (P.) aculeatus*, (a) Nymphal habitus, (b) Abdominal terga VII–X; C–D: *E. (P.) bispinosus*, (c) Nymphal habitus, (d) Abdominal terga VII–X; (e, f): *E. (P.) bifurcatus*, (e) Nymphal habitus, (f) Abdominal terga VII–X; (g, h) *E. (P.) rhithralis*, (g) Nymphal habitus, (h) Abdominal terga VII–X.

Tianmu Mountain, Zhejiang Province, collected by Juan-Yan LUO, Wei ZHANG, Zhen-Xing MA, Ming ZHANG, 18-IV-2017; 30 nymphs, Huangtukeng Village, Anhui Province, collected by Chang-Fa ZHOU, 1-V-1996; 12 nymphs, Zhongmiao (783m a.s.l.), Chang'an District, Xi'an City, Shaanxi Province, collected by Sheng XU, Zhao XIE, V-2012.

Diagnosis and remarks

This species can be recognised by the presence of an unpaired median spine on each abdominal tergum from segments II–IX (Figure 1(d,f)) and paired distinct pale round maculae on head (Figure 1(e)). Adults are unknown.

E. (P.) unispinosus was originally described by Uéno (1955) based on an incomplete nymphal specimen (without gill I) collected in Nepal as *Epeorus* sp. Braasch (1980) proposed the name *Epeorus unispinosus* to this species but provide no new information about it. Our materials are complete, the structures of gill lamellae (slightly expanded gill I and unfolded gill VII, Figure 6(d)) show that it is a member of the subgenus *Proepeorus* or *Epeorus* s.str. Since the nymphal characteristics of *E. (P.) unispinosus* and *Epeorus (Proepeorus) gibbus* **sp. nov.** are very similar (see remarks of *E. (P.) gibbus* **sp. nov.** below), we temporarily regard *E. (P.) unispinosus* as a *Proepeorus* species.

Distribution

China (Zhejiang, Anhui, Shaanxi), Nepal.

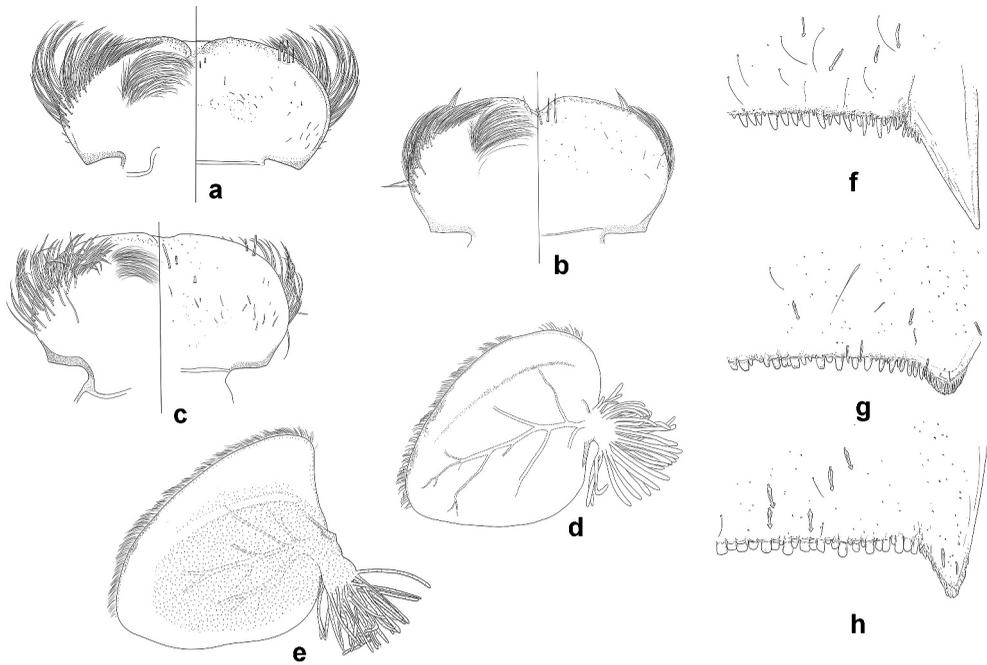


Figure 6. Nymphal structures of *Epeorus* spp.: (a–c) Labrum, (a) *Epeorus (Epeorus) melli*, (b) *Epeorus (Proepeorus) nipponicus*, (c) *E. (P.) unispinosus*; (d, e) Gill I, (d) *E. (P.) unispinosus*, (e) *E. (P.) bifurcatus*; (f–h) Posterior margin of tergum VII, (f) *E. (P.) bispinosus*, (g) *E. (P.) rhithralis*; (h) *E. (P.) bifurcatus*.

***Epeorus (Proepeorus) gibbus* sp. nov. Zhou**

Figs 2–4, 10A–B, E–F, 11A–D, 12A, 13A–B, 14A–B, 15G, 16F

Materials examined

Holotype. male imago, Chanyuan Temple (30°19'16.7"N, 119°26'55.7"E), west Tianmu Mountain, Zhejiang Province, collected by He-Ying WANG, Xiao-Li YING, 5-IV-2019. Paratypes: 2 female imagoes, 10 nymphs, same as the holotype; 2 male imago, unnamed creek in front of Tian-Mu Hotel, West Tianmu Mountain, Zhejiang Province, collected by Juan-Yan LUO, Wei ZHANG, Zhen-Xing MA, Ming ZHANG, 15-IV-2017; 1 male, 10 nymphs, Three Mile Pavilion, West Tianmu Mountain, Zhejiang Province, collected by He-Ying WANG, Xiao-Li YING, 8-IV-2019; 20 nymphs, One Mile Pavilion, West Tianmu Mountain, Zhejiang Province, collected by Yin-Fang WANG, Zhen-Xing MA, 6-IV-2019.

Nymph (in ethanol). Body length 10.5–14.0 mm (female), 9.5–10.0 mm (male), caudal filaments 11.5 mm. The body is generally yellowish brown (Figure 2(a)).

Head. ellipsoid, head width/length ratio 1.32–1.35, anterior margin evenly convex with a row of dense setae directed anteriorly, posterolateral margin slightly narrowed (indistinct in male), posterior margin slightly convex to nearly straight. Colouration of head yellowish brown, with a pair of indistinct pale spots near anterior margin, area near anterolateral margin obviously paler (Figures 2(c) and 4(a)); posterior margin with two tufts of setae. **Labrum:** anterior and lateral margins evenly convex and with a median

emargination, ventral surface with long lateral bristles and brush of median fine setae; dorsal surface with four bristles antero-medially; each side with one long bristle medially, two bristles near anterolateral margin and scattered setae in different size (Figures 3(a) and 4(b)). **Mandibles:** outer incisor with 2 (left mandible) or 3 (right mandible) apical teeth and serrated margins, inner incisor of right mandible with 2 apical teeth; left inner incisor slender and nearly straight, with 3 apical rounded teeth; both inner incisors with serrated outer margins. Prosthema represented by a tuft of plumose setae (Figure 3(b,c) and 4(c,d)). **Maxillae:** with 4 fimbriated setae at base of apex (Figure 15(g)); basal segment of maxillary palp with a row of bristles along distal half of outer margin, apical segment 1.3× length of basal segment (Figure 3(e)). **Hypopharynx:** lingua with 2 anterolateral lobes, both lingua and superlinguae with fine dense setae anteriorly (Figure 3(d)). **Labium:** with narrow separation between glossae; dorsum of glossa with a row of longitudinal dense setae, base of outer margin with a tuft of bristles, inner margin with a row of spine-like bristles (Figures 3(f) and 4(e)); apical segment of labial palpi slightly shorter than basal segment, apical/basal segment length ratio 0.80 (Figure 3(f)).

Thorax. Yellowish brown with irregular markings. Femora pale, with a median dark spot and irregular brown markings, outer margin of femora with a row of long setae and sparse short setae (Figure 2(f)), dorsal surface of femora with scattered spatulate and arrow-like setae (Figure 4(f)). Tibiae with an indistinct median brown band, tarsi brown, with darker base and apex, dorsal margins of tibiae and tarsi with a row of dense setae (Figure 2(f)). Forefemora/foretibiae length ratio 1.0, midfemora/midtibiae length ratio 1.1, hind femora/hind tibiae length ratio 1.2. Claw with 4 subapical denticles (Figure 4(g)).

Abdomen. Brown with dark brown markings. Each tergum of segments II–IX with a pair of submedian brown spots (among them, spots on terga V–VI more distinct) and a longitudinal median ridge (look like a median pale stripe) (Figures 2(a,d) and 4(h)). Posterior margins of terga with dense round pointed denticles in different size (Figure 4(i)). Sterna colourless (mature nymph with same colouration as imago). Gill I slightly expanded beneath abdomen, with a row of setae along anterior margin, distal half of anterior margin with ventral setose pads (Figure 4(j)). Gills II–VI similar in shape, with sclerotised costal and anal margin and well developed ventral setose pads (Figure 4(k)). Gill VII narrowed both basally and distally, slightly curved (Figures 2(e) and 4(l)). Cerci yellowish brown, basal segments with row of dorsal setae.

Male imago (in ethanol). Body length 10.0–11.0 mm, forewing 10.0–11.5 mm, hindwing 4.0–4.5 mm, cerci 25.0–31.0 mm. Body pale brown with brownish black markings (Figure 10(a)).

Head. Face fold colourless. Median area light brown, antennae brown. Ocelli basally dark, apically whitish. Compound eyes pale to grey (dark brown when alive), with darker basal half; distance between compound eyes less than width of median ocellus (Figure 10(e)).

Thorax. Dark brown. Prosternum dark brown in anterior half, brown in posterior half (Figure 10(e)). Median depression of mesothoracic furcasternum convergent anteriorly (Figure 10(f)). Wings transparent but with semi-hyaline stigma region. Forewings with brown veins, basally paler, costal brace dark brown; stigma region with 13–14 cross veins between C and Sc; MA forked 2/3 of distance from base to margin, MP forked 1/4 of distance from base to margin; hindwings transparent, MP forked 1/3 of distance from base to margin (Figure 10(b)).

Legs. Forelegs dark brown, basal half of femora paler than other parts, ratios of femora: tibiae: tarsi = 2.8: 3.6: 5.7, order of tarsal segments arranged in descending order: 1, 2, 3, 4, 5. Middle and hind legs pale brown, femora of all legs with a median brown macula. Ratio of femora: tibiae: tarsi in middle legs = 2.5: 2.3: 1.1, order of tarsal segments arranged in descending length 1, 5, 2, 3, 4. Ratio of femora: tibiae: tarsi in hind legs = 2.6: 2.2: 1.0, order of tarsal segments arranged in descending length 5, 1, 2, 3, 4. Claws on each leg dissimilar, one blunt and one hooked.

Abdomen. Pale to light brown. Terga II–IX with similar markings: anterior margin with a brown transverse band; median brown band with a slender longitudinal pale line inside it; posterior margin with a dark brown transverse band (Figure 11(a)). Tergum X with a median brown band bordering posterior margin. Colouration pattern of sterna II–VIII similar (Figure 11(b)): 1) a reddish-brown median broad band; 2) a pair of oblique stripes located by sides of anterior of median band (medio-anterior myo-sigilla, indistinct in some individuals and segments); 3) a pair of round blanks inside the median band (medio-posterior myo-sigilla). Sternum IX with a median brown band; styliger light brown, with straight posterior margin. Forceps segments I–II light brown, segments III–IV pale, combined length of segments III–IV obviously longer than half of segment II. Penis lobes divergent in apical half, expanded laterally forming a lateral hooked apex, each penis lobe with a medio-apical emargination. Median titillators small but distinct (Figures 12(a) and, 13(a,b)). Cerci dark brown basally and paler distally, with dark annulations.

Female imago (in ethanol). Body length 10.0 mm, forewing 10.0 mm, hindwing 4.0 mm, cerci 23.0 mm. Body brownish, colouration pattern similar to male imago but paler (Figure 11(c,d)). Thorax light brown, wings as in male. Legs with similar colouration to male, length ratios of femora: tibiae: tarsi of middle legs = 2.6: 2.4: 1.1; length ratios of femora: tibiae: tarsi of hind legs = 2.6: 2.3: 1.1 (fore legs missing). Colouration pattern of abdomen as in male, median brown band indistinct on abdominal terga VI–IX in some individuals (Figure 11(c)). Posterior margin of subgenital plate rounded, sternum IX deeply emarginated divided into two round pointed apices (Figure 14(a,b)).

Etymology

The epithet *gibbus* is from Latin, means bulging or protuberant, referring to its unique medial ridge on abdominal terga of nymph.

Biology

Nymphs inhabits in the small-sized mountain streams (0.5–5.0 m wide, 0.1–0.5 m deep, recorded from ca. 300–700 m a.s.l.), and they are found underneath stones in moderately to fast flowing sections with rocky and stony substrate. The emergence of subimagos was observed in the morning (9:00 AM–11:00 AM).

Diagnosis and remarks

This species can be recognised among other congeners by the following characters: 1) penis of male imago with laterally expanded pointed apex and small median titillator; 2) distinct abdominal colouration pattern in imago; 3) head capsule of nymph with a pair of indistinct pale spots; 4) abdominal terga of nymphs without any spine but with a longitudinal median ridge, posterior margins of each terga with row of blunt denticles.

E. (P.) gibbus **sp. nov.** most resembles *E. (P.) unispinosus* Braasch, 1980 by having similar structures of mouthparts (e.g. labrum and mandibles, see Figures 4(b), 6(c) and 16(e,f)), gills (Figures 4(j) and 6(d)) and colouration pattern of abdominal (Figures 1(d) and 2(a)). However, *E. (P.) gibbus* **sp. nov.** can be distinguished from the latter by the absence of median unpaired spine on posterior margin of abdominal tergum (Figure 1(e)) and the indistinct paired spots on head capsule (which distinct in *E. (P.) unispinosus*, Figure 1(e)).

We collected these two related species *E. (P.) gibbus* **sp. nov.** and *E. (P.) unispinosus* in the same stream from west Tianmu mountain. The nymphs of *E. (P.) gibbus* **sp. nov.** were found inhabiting upper sites of the stream (altitude above ca. 300 m) while *E. unispinosus* inhabit lower water (ca. 150–300 m).

Distribution

China (Zhejiang).

Epeorus (Proepeorus) aculeatus Braasch, 1990

Figs 5A–B, 12D, 13F, 15D, 16I

Epeorus aculeatus Braasch, 1990, p. 7, Figures 1–8 (nymph). Types: nymph, from Thailand.

Epeorus aculeatus: Nguyen and Bae 2004, p. 19 (nymph); Webb and McCafferty 2006a, p. 65 (male).

Materials examined

One male imago, Futian Village, Eryuan Town, Niujie County, Yunnan Province, collected by Wei ZHNAG, Zhen-Xing MA, 3-11-IV-2018; 1 nymph (1400 m a.s.l.), Jianfeng River, Zhonghe Town, Tengchong City, Yunnan Province, collected by Hui XIE, Yan-Yan JIA, Ping CHEN, 20-VII-2008; 8 nymphs, Laomane (1255 m a.s.l.), Menghai County, Xishuangbanna, Yunnan Province, collected by Ning DING, 21-III-2008; 6 nymphs, Mengyuan Village, Mengla County, Xishuangbanna, Yunnan Province, collected by Yun-Lei ZHOU, 14-III-2013; 2 nymphs, Dutian Village (103°54'47.99"N, 23°11'5.67"E), Wenshan City, Yunnan Province, collected by Zhen-Xing MA, 17-X-2020; 5 nymphs, Xiaoyaodian Village (103°56'6.27"N, 23°17'56.55"E), Wenshan City, Yunnan Province, collected by Zhen-Xing MA, 17-X-2020.

Diagnosis and remarks

E. (P.) aculeatus can be distinguished from other congeners by the following characters. In male imago (Figures 12(d) and 13(f)): 1) penes are fused basally and widely divergent apically, each penis lobe shallowly notched apically; 2) base of penes with small median titillators; 3) unique colouration of abdominal terga and sterna (see Webb and McCafferty 2006a: Figures 1–2). In nymph: posterior margin of abdominal terga II–IX with a pair of long submedian spines (Figure 5(b)).

Kluge (2004) placed *E. (P.) aculeatus* in the subgenus *Epeorus* s.str., but the presence of median titillators on penes of male indicates that *E. (P.) aculeatus* is belonging to subgenus *Proepeorus*. In addition, some new records of Chinese 'paired-spines' species (with submedian paired spines or tubercles on nymphal terga, including *Epeorus rhithralis* Braasch, 1980, *Epeorus bispinosus* Braasch, 1980 and *Epeorus bifurcatus* Braasch & Soldán,

1979), which have a close relation with *E. (P.) aculeatus* but have not been described in adult stages, are also included in this work and regarded as *Proepeorus* species for the time being.

Distribution

China (Yunnan), Thailand, Vietnam.

***Epeorus (Proepeorus) rhithralis* Braasch, 1980**

Figs 5G–H, 6G, 15E, 16L

Epeorus rhithralis Braasch, 1980, p. 60, Figure 4(b–l) (nymph). Types: nymph, from Nepal.

Materials examined

20 nymphs, Daping Village (103°5'44.32"N, 22°55'59.6"E), Jinping County, Yunnan Province, collected by Zhen-Xing MA, 20-X-2020; 8 nymphs, Wola Village (102°51'31.2588"N, 23°3'40.81"E), Jinping County, Yunnan Province, collected by Zhen-Xing MA, 21-X-2020.

Diagnosis and remarks

E. (P.) rhithralis is differentiated from other congeners by the paired tubercles on terga (Figure 5(g,h)), pointed denticles on posterior margin of terga (Figure 6(g)) and colouration pattern of femur (Figure 5(g)). This species most resembles *Epeorus inthanonensis* Braasch & Boonsoong, 2010 by having similar paired tubercles and pointed denticles on posterior margin of abdominal terga. As mentioned in the research of Braasch and Boonsoong (2010), *E. (P.) rhithralis* can be separated from *E. inthanonensis* according to different size of gill I: *E. inthanonensis* has smaller gill I than gill II–VI, while *E. (P.) rhithralis* with gill I larger than all other gills. However, according to figures from original description of *E. (P.) rhithralis* (Braasch, 1980: Figure 4(j–l)), its gill I is slightly expanded anteriorly and obvious smaller than gill III. Considering that the colouration pattern of the femur of specimens in China is same as *E. (P.) rhithralis* (with one median spot surrounded by irregular marking, see Braasch 1980: Figure 4(g)) but significantly different from that of *E. inthanonensis* (only with one median spot, see Braasch and Boonsoong 2010: fig. 75), this species in China is temporarily designated as *E. (P.) rhithralis*. Adults are unknown.

Distribution

China (Yunnan), Nepal.

***Epeorus (Proepeorus) bispinosus* Braasch, 1980**

Figs 5C–D, 6F, 15F, 16K

Epeorus bispinosus Braasch, 1980, p. 60, Figure 3(b–l) (nymph). Types: nymph, from Nepal.

Epeorus (Epeorus) bispinosus: Kluge 1997, p. 205.

Materials examined

3 nymphs, Tengchong County, Baoshan City, Yunnan Province, collected by Ran LI, 22–23-VIII-2020; 4 nymphs, Yaojiaping, Lushui City, Yunnan Province, collected by Ran LI, 20-VIII-2020.

Diagnosis and remarks

The nymph of *E. (P.) bispinosus* can be distinguished from other congeners by the paired sharp and slender spines (Figure 5(c,d)) and the pointed denticles on abdominal terga (Figure 6(f)). This species was described based on nymph by Braasch (1980) and other stages are unknown. Kluge (1997, 2004) regarded this species as a member of *Epeorus* s. str. In this work, this species is temporarily classified into *Proepeorus* because it is closely related to *E. (P.) aculeatus*.

Distribution

China (Yunnan), Nepal, Tajikistan.

***Epeorus (Proepeorus) bifurcatus* Braasch & Soldán, 1979**

Figs 5E–F, 6E, H, 15C, 16J

Epeorus bifurcatus Braasch & Soldán, 1979, p. 270, Figures 15–22 (nymph). Types: nymph, from Vietnam.

Epeorus bifurcatus: Nguyen and Bae 2004, p. 21 (nymph); Braasch and Boonsoong 2010, p. 23.

Materials examined

2 nymphs, Pingshan County, Yibin City, Sichuan Province, collected by Bei-Xin WANG, 19-XI-2019; 20 nymphs, Baijin Town, Huishui County, Guizhou Province, collected by Chang-Fa ZHOU, 11-IX-2000; 30 nymphs, Dali Ancient City, Yunnan Province, collected by Jia-Chang QIN, Peng LI, 25-VII-2009.

Diagnosis and remarks

E. (P.) bifurcatus is recognised among Asian *Epeorus* species by a pair of small submedian spines on terga II–IX (Figure 5(e,f)), a row of blunt denticles along posterior margin of terga and triangular gill I (Figure 6(e,h)). This species most resembles *E. (P.) bispinosus* in the paired submedian spines on terga and triangular gill I, but *E. (P.) bispinosus* can be distinguished from it by the acute denticles along the posterior margins of terga. Shape of submedian spines of *E. (P.) bifurcatus* are variable: more developed and sharper in some individual. Adults are unknown.

Distribution

China (Yunnan, Guizhou, Sichuan), Vietnam, Thailand.

***Epeorus (Proepeorus) falcatus* sp. nov. Zhou**

Figs 7–9, 10C–D, G–H, 11E–H, 12B, 13D–E, 14C–D, 15H, 16H

Materials examined

Holotype: male imago, Wudong Village (26°22'55.4"N, 108°10'01.8"E), Leishan County, Guizhou Province, collected by Zhen-Xing MA, Xu-Hong-Yi ZHEN, 1–5-VIII-2019. Paratypes: 3 male imagoes 2 female imagoes 10 nymphs, same as holotype; 5 nymphs, Huaping Nature Reserve, Guangxi Province, collected by Zhen-Xing MA, 20–21-VIII-2020; 30 nymphs, Jintong Mountain, Shaoyang City, Hunan Province, collected by Zhen-Xing MA, 23-VIII-2020.

Nymph (in ethanol). Body length 10.0–12.0 mm (female), 8.5–9.5 mm (male), caudal filaments 14.0–15.0 mm (female), 11.0 mm (male). Body generally pale to brown (Figure 7(a)).

Head. ellipsoid, head width/length ratio 1.39, anterior and lateral margins evenly convex, posterior margin slightly convex (nearly straight); anterior margin with a row of dense setae directed anteriorly, posterior margin with two tufts of setae. Head

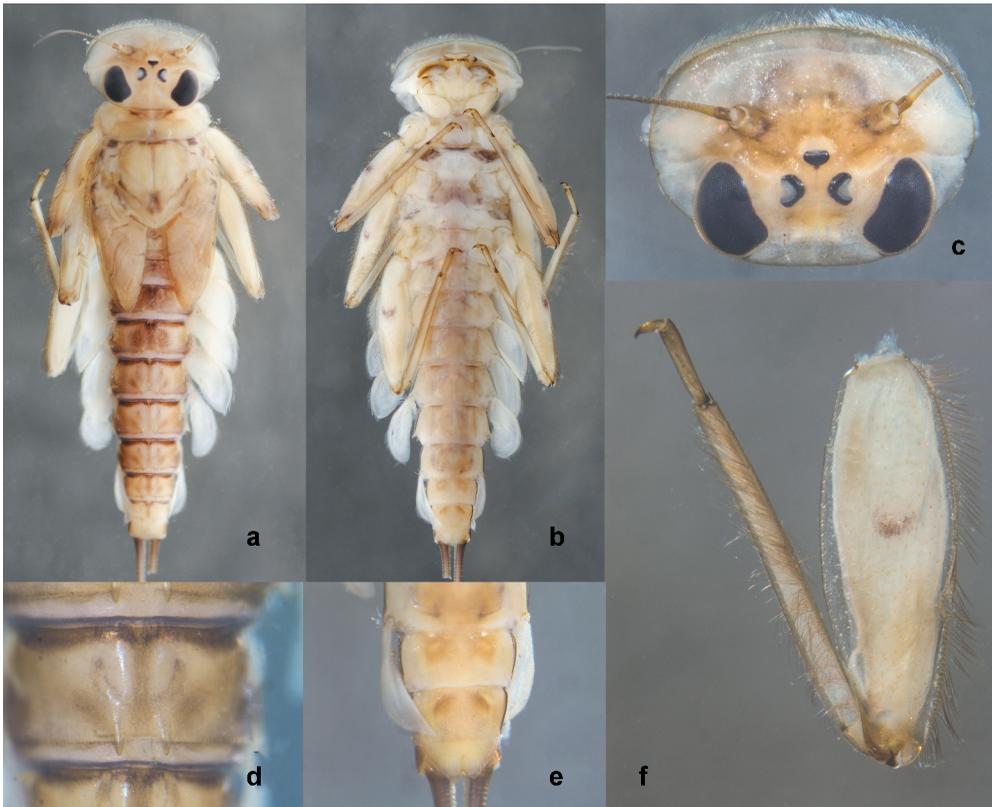


Figure 7. Nymphal habitus and structures of *Epeorus (Proepeorus) falcatus* sp. nov.: (a) Nymphal habitus (dorsal view); (b) Nymphal habitus (ventral view); (c) Head capsule; (d) Abdominal tergum (segment VII); (e) Gill VII (ventral view); (f) Middle leg.

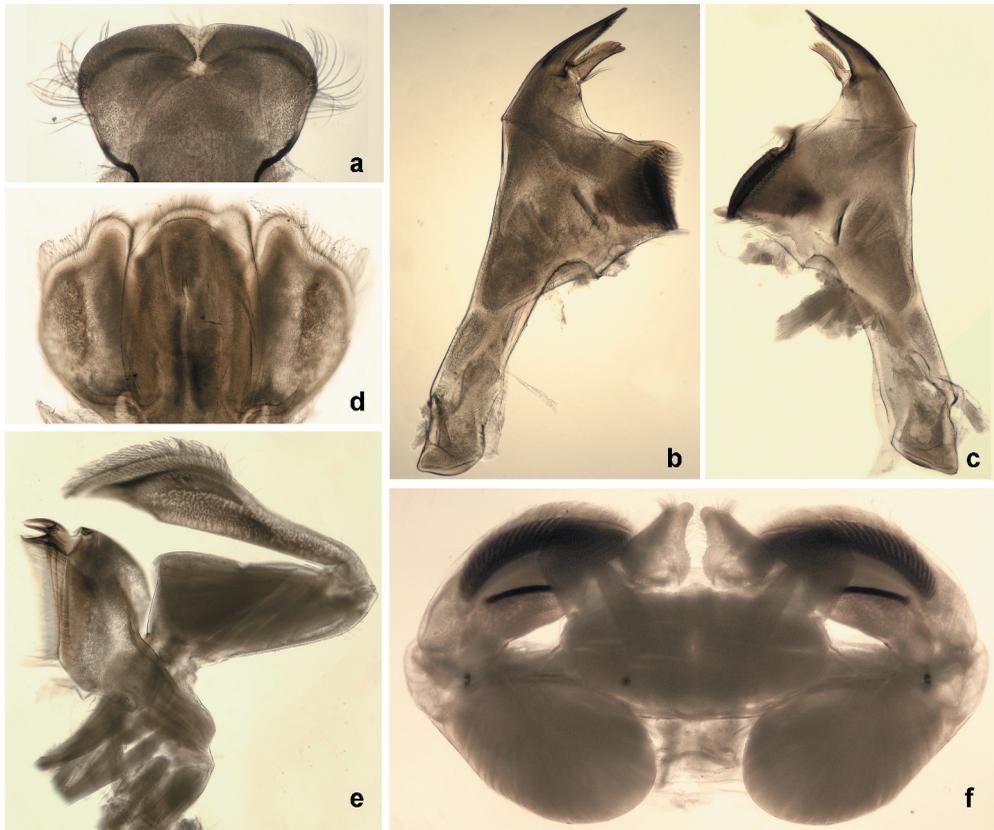


Figure 8. Mouthparts of *Epeorus (Proepeorus) falcatus* sp. nov. (digital photos): (a) Labrum; (b) Left mandible; (c) Right mandible; (d) Hypopharynx; (e) Maxillae; (f) Labium.

generally pale, with median brown or dark grey irregular markings (Figures 7(c) and 9 (a)). **Labrum:** lateral margins straight and widened anteriorly, anterior margin with a distinct median notch, dorsal surface with 6 bristles antero-medially and 2 bristles near each side of anterolateral margin. Ventral surface with a row of bristles along lateral margin extend to anterior margin and brush of fine setae medially (Figures 8 (a) and 9(b)). **Mandibles:** outer incisor with 2 (left mandible) or 3 (right mandible) apical lobes and serrated margins, inner incisor with 2 (right mandible) or 3 (left mandible) apical lobes and serrated outer margins. Prosthema represented by a tuft of plumose setae (Figures 8(b,c) and 9(c,d)). **Maxillae:** with 1 fimbriated setae at base of apex of maxilla (Figure 15(h)); basal segment of maxillary palp slightly expanded proximally and with a tuft of (4–5) distal bristles on outer margin; apical segment 1.35× length of basal segment, with slender basal half and extremely expanded distal half (Figure 8(e)). **Hypopharynx:** lingua with anterolateral lobes (Figure 8(d)). **Labium:** with narrow U-shaped separation between glossae; glossa triangular, with a shallow subapical projection, dorsum with a row of longitudinal dense setae, both

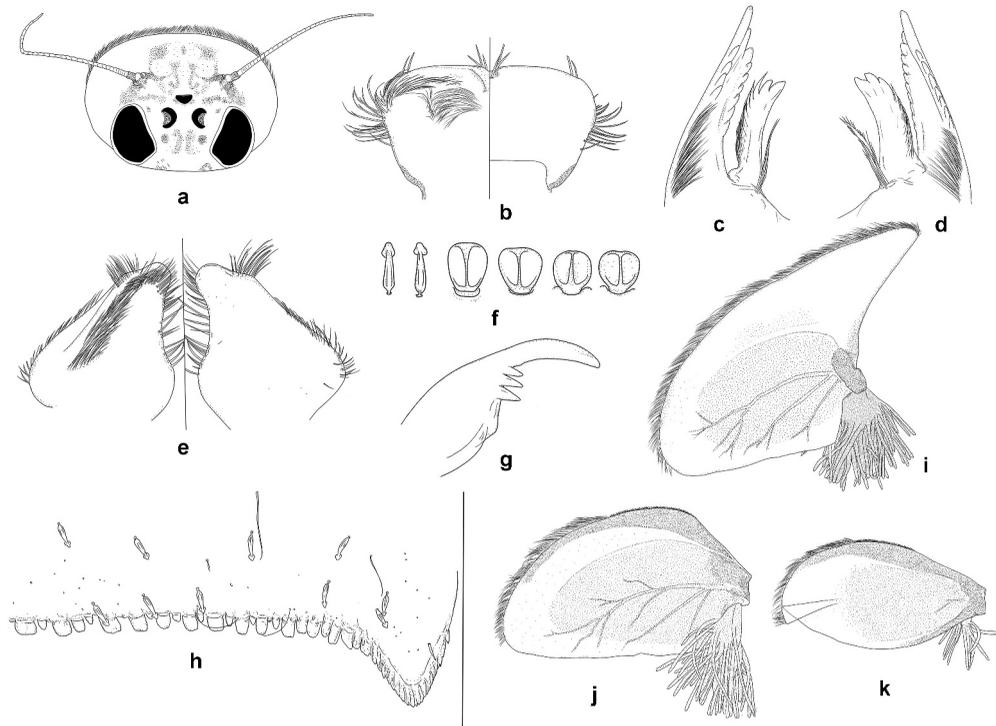


Figure 9. Nymph of *Epeorus* (*Proepeorus*) *falcatus* **sp. nov.**: (a) Head capsule; (b) Labrum (ventral view on left, dorsal view on right); (c) Right mandible; (d) Left mandible; (e) Glossae of labium (dorsal view on left, ventral view on right); (f) Femoral setae; (g) Claw; (h) Posterior margin of tergum VII (vertical line is midline of tergum); (i) Gill I; (j) Gill II; (k) Gill VII.

inner margin and outer margin of glossa with a row of bristles; apical segment of labial palpi slightly shorter than basal segment, apical/basal segment length ratio 0.86 (Figures 8(f) and 9(e)).

Thorax. pale to brown with irregular markings. Femora pale, with a medial dark spot (indistinct in some individuals) and irregular brown markings, outer margin with a row of long setae and sparse short setae (Figure 7(f)), dorsum with scattered blunt spatulate and arrow-like setae (Figure 9(f)). Proximal and medial portion of tibiae slightly darkened, base and apex of tarsi darkened (Figure 7(f)). Forefemora/foretibiae length ratio 0.96, mid femora/mid tibiae length ratio 1.08, hind femora/hind tibiae length ratio 1.22. Claws with 3 subapical denticles (Figure 9(g)).

Abdomen. Pale with brown markings. Terga segments II–IX with paired small submedian spines and a median longitudinal dark stripe. Terga II–IV with paired submedian irregular pale spots. Each tergum with transverse brown band along anterior margin (Figure 7(a,d)). Posterior margins of terga with blunt denticles and mixed with smaller round pointed denticles (Figure 9(h)). Sterna colourless (sterna VII–IX with paired brown stripes in some individuals) (Figure 7(e)). Gills: gill I moderately expanded anteriorly and narrowed apically, outer margin with a row of fine setae (Figure 9(i)); gills II–VI similar, distal half of costal margin with a row of long setae

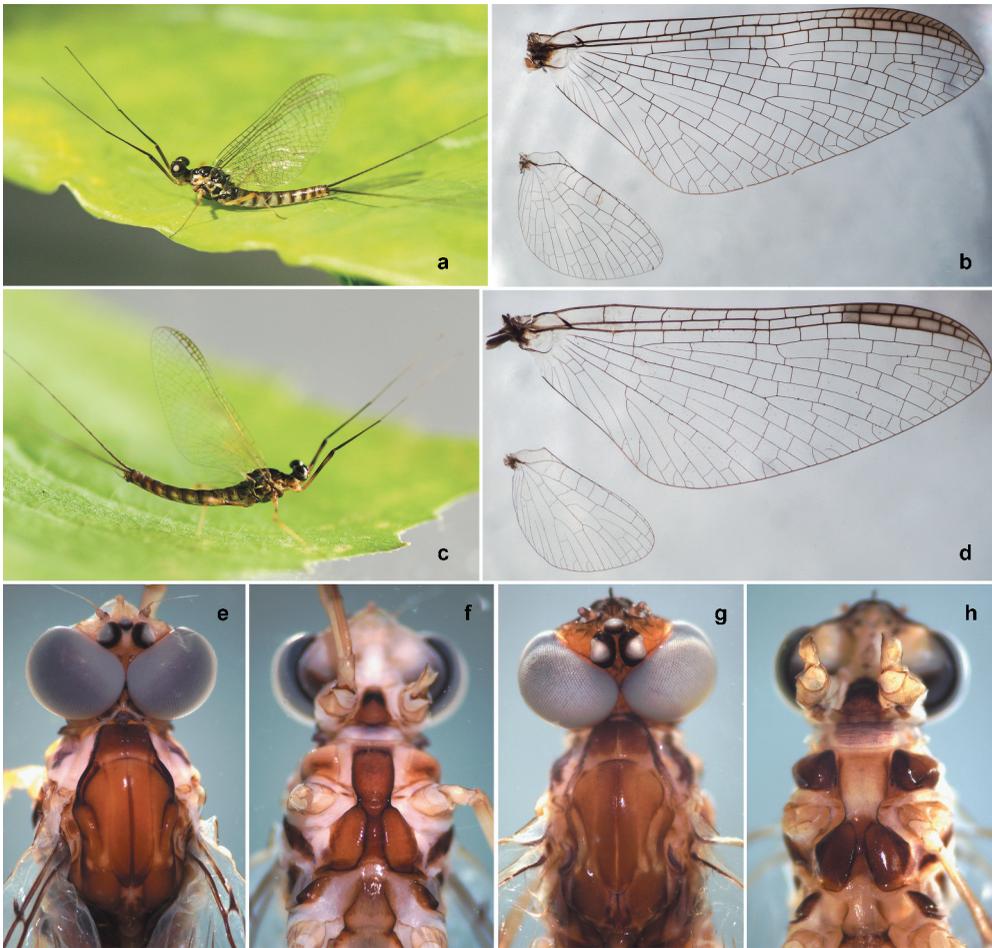


Figure 10. Male adults of two new species: (a, b) *Epeorus (Proepeorus) gibbus* **sp. nov.**, (a) General view, (b) Wings; (c, d) *Epeorus (Proepeorus) falcatus* **sp. nov.**, (c) General view, (d) Wings; (e, f) Thorax of *Epeorus (Proepeorus) gibbus* **sp. nov.**, (e) Dorsal view, (f) Ventral view; (g, h) Thorax of *Epeorus (Proepeorus) falcatus* **sp. nov.**, (g) Dorsal view, (h) Ventral view.

(Figure 9(j)); gill VII oval, with long anal rib, slightly curved and without distinct fold (Figures 7(e) and 9(k)). Cerci pale to brown, with a row of dorsal setae along basal segments.

Male imago (in ethanol). Body length 9.0–10.0 mm, forewing 9.5–10.0 mm, hindwing 3.0–3.5 mm, cerci 28.0–34.0 mm. Body generally brownish (Figure 10(c)).

Head. Face fold dark brown, antennae brown, median area brown. Compound eyes pale (dark brown when alive), contiguous, with darker basal half (Figure 10(g)).

Thorax. Dark brown. Prosternum dark brown, median depression of mesothoracic furcasternum convergent anteriorly (Figure 10(h)). Most area of wings transparent except semi-hyaline stigma area. Forewings with brown veins and dark brown costal brace, stigma region with 9–10 cross veins between Sc and C; MA forked

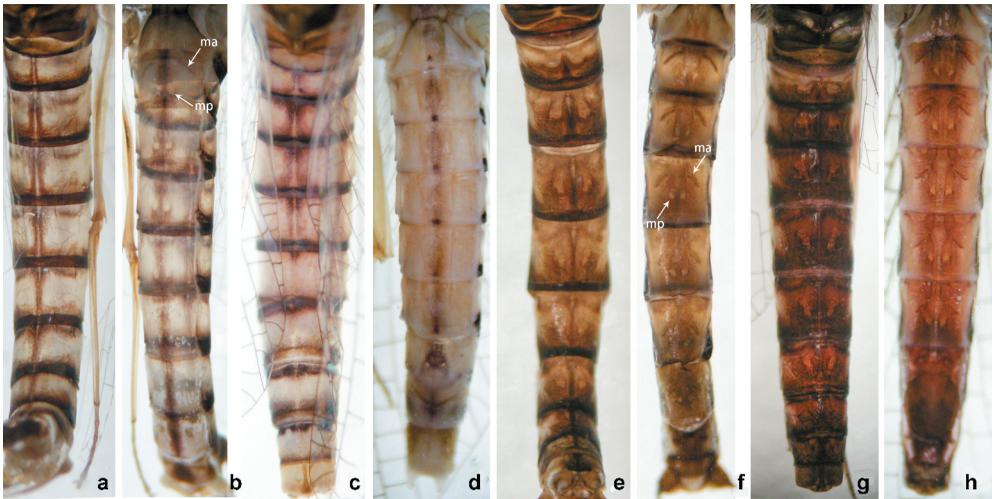


Figure 11. Abdominal terga of imagoes of two new species: (a–d) *Epeorus (Proepeorus) gibbus* **sp. nov.**, (a) Dorsal view of male, (b) Ventral view of male, (c) Dorsal view of female, (d) Ventral view of female; (e–h) *Epeorus (Proepeorus) falcatus* **sp. nov.**, (e) Dorsal view of male, (f) Ventral view of male, (g) Dorsal view of female, (h) Ventral view of female; Abbreviations: ma, medio-anterior myo-sigillum; mp, medio-posterior myo-sigillum.

2/3 of distance from base to margin, MP forked 1/3 of distance from base to margin; hindwings transparent, MP forked 1/2 of distance from base to margin (Figure 10(d)).

Legs. Forelegs brown, with dark brown tibiae and distal half of femora, paler basal half of femora and tarsi, ratios of femora: tibiae: tarsi = 2.5: 3.2: 5.5, order of tarsal segments arranged in descending order: 1, 2, 3, 4, 5. Middle legs light brown, ratios of femora: tibiae: tarsi = 2.2: 2.1: 1.3, order of tarsal segments arranged in descending length 1, 2, 3, 5, 4 (hind legs missing). Femora of all legs with a median dark brown macula. Claws of each leg dissimilar, one blunt, one hooked.

Abdomen. Light brown, with darker maculae. Terga II–IX with similar colour pattern (Figure 11(e)): indistinct brown transverse band along anterior margin; median area brown, with a longitudinal median dark stripe and a pair of paler irregular maculae (like the fusion of two dots); posterior half of each tergum darker and with a dark brown transverse band along posterior margin extended to lateral margin. Tergum X pale, with a median dark stripe. Colouration of sterna II–VIII similar (Figure 11(f)): 1) dark brown median band; 2) a pair of distinct brown oblique stripes near anterior margin (medio-anterior myo-sigilla, progressively fading posteriorly); 3) a pair of small round blanks inside the median band (medio-posterior myo-sigilla). Sternum IX brown, with longitudinal dark band laterally; styliger light brown, posterior margin slightly convex medially. Forceps segments I–II brown, III light brown and IV pale, combined length of segments III–IV subequal to half of segment II; penis lobes widely divergent, with sharp lateral hooked tips directed dorsally and medio-apical emargination. Submedian titillators distinct (Figures 12(b), 13(d,e)). Cerci with dark annulations.



Figure 12. Genitalia of male: (a) *Epeorus (Proepeorus) gibbus* **sp. nov.** (ventral view); (b) *Epeorus (Proepeorus) falcatus* **sp. nov.** (ventral view); (c) *Epeorus (Proepeorus) nipponicus* (ventral view); (d) *Epeorus (Proepeorus) aculeatus* (ventral view).

Female imago. Body length 10.5 mm, forewing 10.5 mm, hindwing 3.5 mm, cerci 20.5 mm. General reddish-brown, colouration of body similar to male imago. Thorax paler than in male, wings same as male. Length ratios of femora: tibiae: tarsi of fore legs = 2.6: 2.6: 2.1; length ratios of femora: tibiae: tarsi of middle legs = 2.7: 2.6: 1.3; length ratios of femora: tibiae: tarsi of hind legs = 3.0: 2.5: 1.1. Colour pattern of abdominal terga same as male imago but darker (Figure 11(g)). Abdominal sterna somewhat different to male imago (Figure 11(h)): sterna VII–IX darker than other segments. Subgenital plate extended to posterior margin of sternum VIII and with rounded posterior margin, sternum IX with shallow median emargination (Figure 14(c,d)).

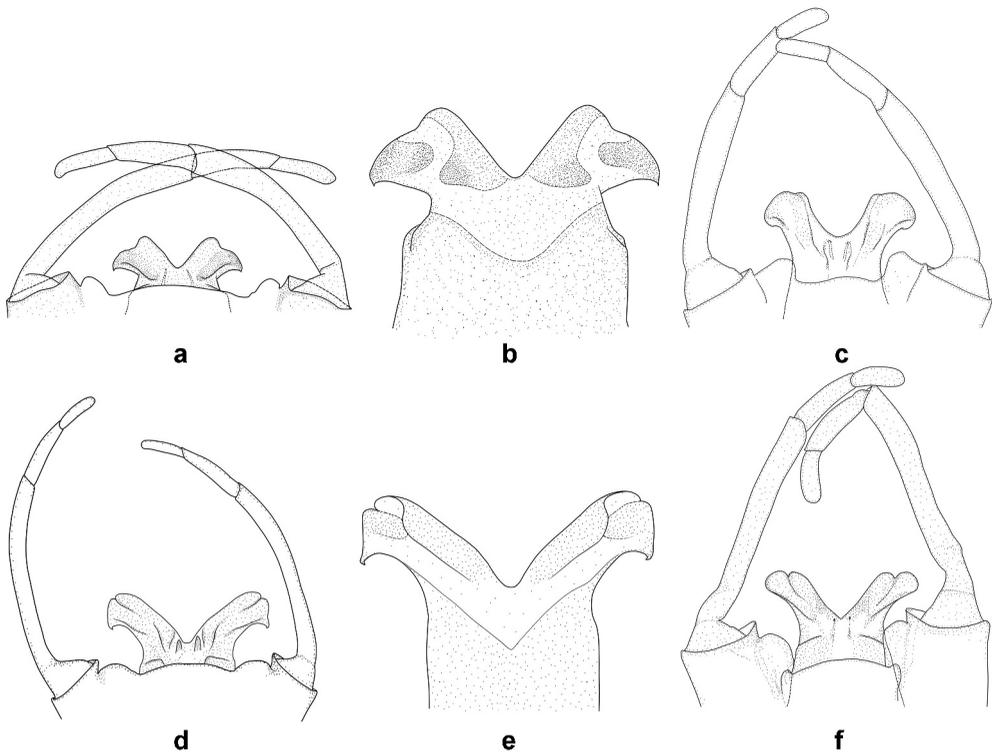


Figure 13. Genitalia of male: (a, b) *Epeorus (Proepeorus) gibbus* **sp. nov.**, (a) Ventral view, (b) Dorsal view; (c) *Epeorus (Proepeorus) nipponicus* (ventral view); (d, e) *Epeorus (Proepeorus) falcatus* **sp. nov.**, (d) Ventral view, (e) Dorsal view; (f) *Epeorus (Proepeorus) aculeatus* (ventral view).

Etymology

The Latin specific name *falcatus* means sickle-shaped, curved or hooked, refers to the sickle-shaped gill I of nymph.

Biology

Nymphs of this species occur in the small-sized mountain streams (1.0–3.0 m wide, 0.1–0.5 m deep, ca. 1000–1300 m a.s.l.), and they are found underneath stones in moderately flowing sections where the substrate is mostly stony. Moulting of the subimago was observed in 7:30 PM, and the process lasts ca. 4 minutes.

Diagnosis and remarks

This species can be recognised by the following diagnosis characters. In the adult: 1) penis lobes with lateral hooked projections and distinct median titillators (Figure 13(d)); 2) subgenital plate of female oval, extended to posterior margin of sternum VIII (Figure 14 (c,d)). In the nymph: 1) lamellae of gill I moderately expanded forward and narrowed apically (Figure 9(i)); 2) abdominal terga with paired small submedian spines and blunt denticle posteriorly (Figure 9(h)).

The nymph of *E. (P.) falcatus* **sp. nov.** is most similar to that of *E. (P.) bifurcatus*. They both have paired small submedian spines and blunt denticles along posterior

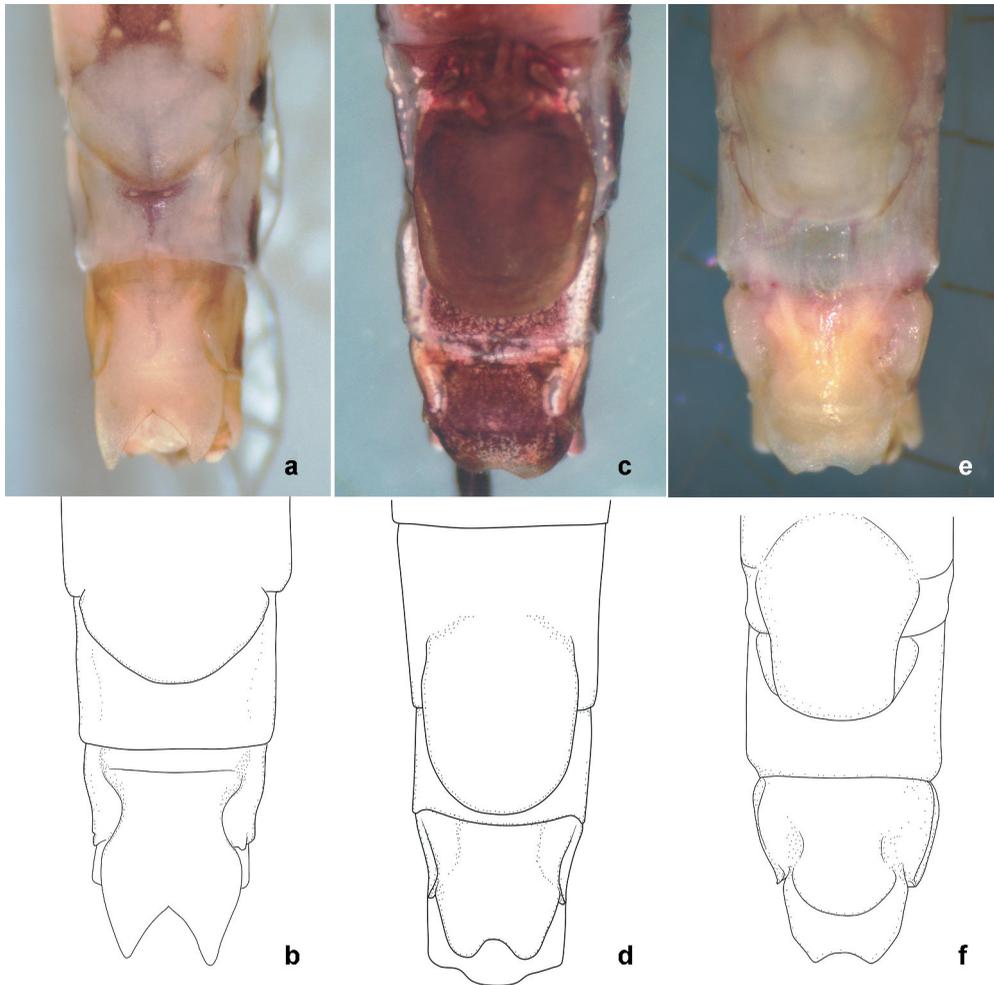


Figure 14. Subgenital plate and sternum IX of female: (a, b) *Epeorus (Proepeorus) gibbus* **sp. nov.**; (c, d) *Epeorus (Proepeorus) falcatus* **sp. nov.**; (e, f) *Epeorus (Proepeorus) nipponicus*.

margin of abdominal terga. But *E. (P.) bifurcatus* can be distinguished by the somewhat expanded gills I (Figure 6(e)), which are moderately expanded in *E. (P.) falcatus* **sp. nov.** In addition, the imaginal characters of *E. (P.) aculeatus* are very similar to *E. (P.) falcatus* **sp. nov.**, especially the colouration pattern of abdomen (see Webb and McCafferty 2006a: Figures 1 and 2). However, the penis of *E. (P.) aculeatus* differs from that of *E. (P.) falcatus* **sp. nov.** by the absence of the lateral hooked projections and the smaller titillators (Figure 13(f)).

As a new species belonging to the 'paired-spines' species in China, *E. (P.) falcatus* **sp. nov.** possess similar imaginal characters as *E. (P.) aculeatus* and its titillators on penes are distinct. Therefore, it is possible that all the male imagoes of 'paired-spines' species may have titillators.

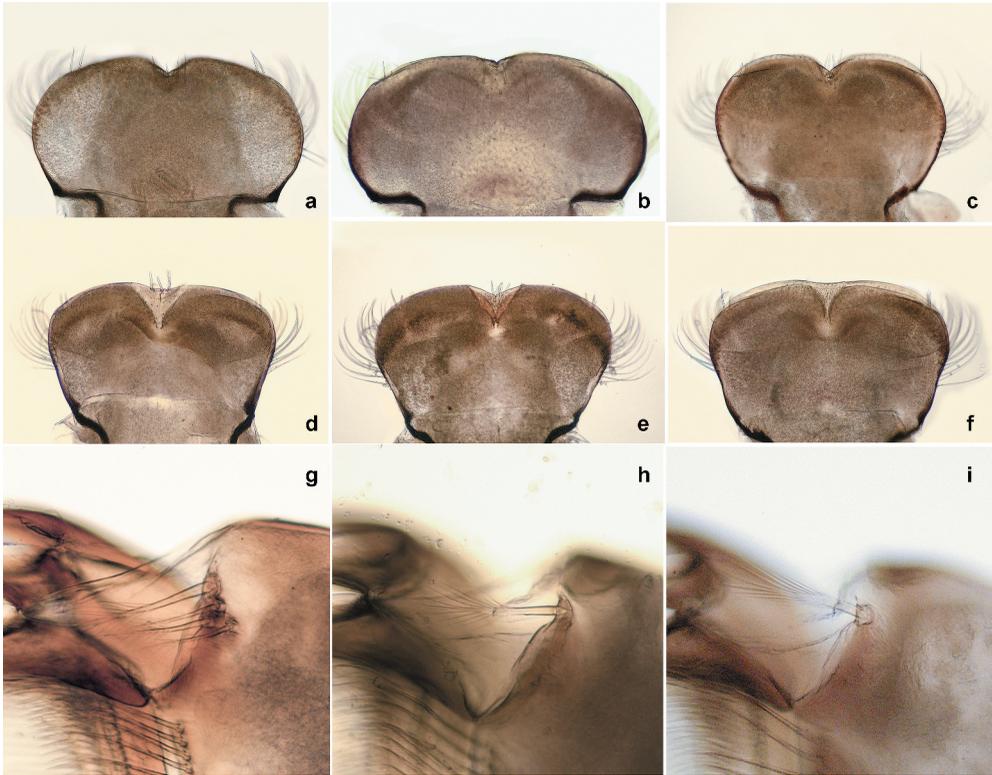


Figure 15. Mouthparts of *Epeorus* (*Proepeorus*) spp.: (a–f) labrum, (a) *E. (P.) nipponicus*; (b) *E. (P.) unispinosus*; (c) *E. (P.) bifurcatus*; (d) *E. (P.) aculeatus*; (e) *E. (P.) rhithralis*; (f) *E. (P.) bispinosus*; (g–i) base of apical tooth complex of maxilla, (g) *E. (P.) gibbus* **sp. nov.**; (h) *E. (P.) falcatus* **sp. nov.**; (i) *E. (P.) nipponicus*.

Distribution

China (Guizhou, Guangxi, Hunan).

Discussion

The ‘paired-spines’ *Proepeorus* species in China, including *E. (P.) falcatus* **sp. nov.**, *E. (P.) aculeatus*, *E. (P.) rhithralis*, *E. (P.) bispinosus* and *E. (P.) bifurcatus*, have common nymphal characters which differ from *E. (P.) nipponicus*, the typical species of this subgenus designed by Kluge (2004): 1) labrum with somewhat straight lateral margins (Figure 15(c,f)) while the counterpart of *E. (P.) nipponicus* with clear convex margins (some species of *Epeorus* s.str. and *Proepeorus* also with similar shape as *E. (P.) nipponicus*, see Figures 6(a–c) and 15(a,b)); 2) paired median spines or tubercles on posterior margins of nymphal terga which absent in *E. (P.) nipponicus* (some *Proepeorus* species in Nearctic region have median protuberances on each tergum, see Webb and McCafferty 2006b); 3) inner incisor on left mandible slender and slightly curved, not expanded distally (Figure 16(h,i)), while that of *E. (P.) nipponicus* (Figure 16(c)) with wider apex (some species in subgenus *Belovius* and *Epeorus* s.str. also have left inner incisor with expanded apices, see Figure 16(a–d)). Meanwhile, *E.*

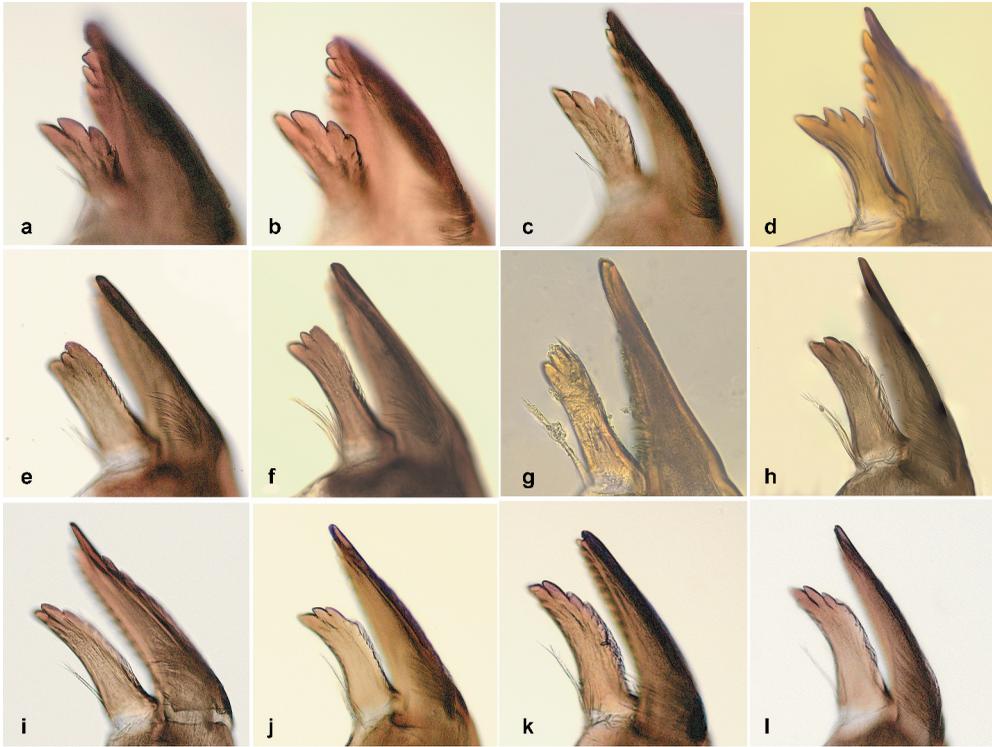


Figure 16. Incisors of left mandible in ventral view: (a) *Epeorus (Epeorus) melli*; (b) *Epeorus nguyenii*; (c) *Epeorus (Proepeorus) nipponicus*; (d) *Epeorus (Belovius) pellucidus*; (e) *Epeorus (Proepeorus) unispinosus*; (f) *Epeorus (Proepeorus) gibbus sp. nov.*; (g) *Epeorus (Iron) alexantri*; (h) *Epeorus (Proepeorus) falcatus sp. nov.*; (i) *Epeorus (Proepeorus) aculeatus*; (j) *Epeorus (Proepeorus) bifurcatus*; (k) *Epeorus (Proepeorus) bispinosus*; (l) *Epeorus (Proepeorus) rhithralis*.

(*P.*) *falcatus sp. nov.* and *E. (P.) aculeatus* possess male imaginal characters different to *E. (P.) nipponicus* too: 1) penis lobes cylindrical, widely divergent (in contrast to rounded and laterally expanded penis lobes in *E. (P.) nipponicus*); 2) in forceps, combined length of segment III–IV subequal to half of segment II (Figure 13(d,f)), while that length is longer than half segment II in *E. (P.) nipponicus* (Figure 13(c)). Those differences seem to indicate that the morphological variation of the subgenus *Proepeorus* is relatively great.

Besides having single tergal spine or ridge, *E. (P.) gibbus sp. nov.* and *E. (P.) unispinosus* can be grouped together and distinguished from all other Chinese *Proepeorus* species by their unique mouthparts: labrum with an additional long bristle near the median tuft of bristle (Figures 4(b), 6(c) and 15(b)) and inner incisor on left mandible slender and nearly straight (Figure 16(e,f)). Similar structures of mouthparts are found in some *Iron* species belonging to group *longimanus* (see Figure 16(g) and Kluge and Tiunova 1989: Figure 2). Furthermore, the penis of *E. (P.) gibbus sp. nov.* is also similar to that of group *longimanus*: penis lobes expanded laterally forming a lateral projection (see Figure 13(a) and Kluge and Tiunova 1989: Figure 1). However, their unfolded gills VII (Figure 2(e)) are totally different from group *longimanus*.

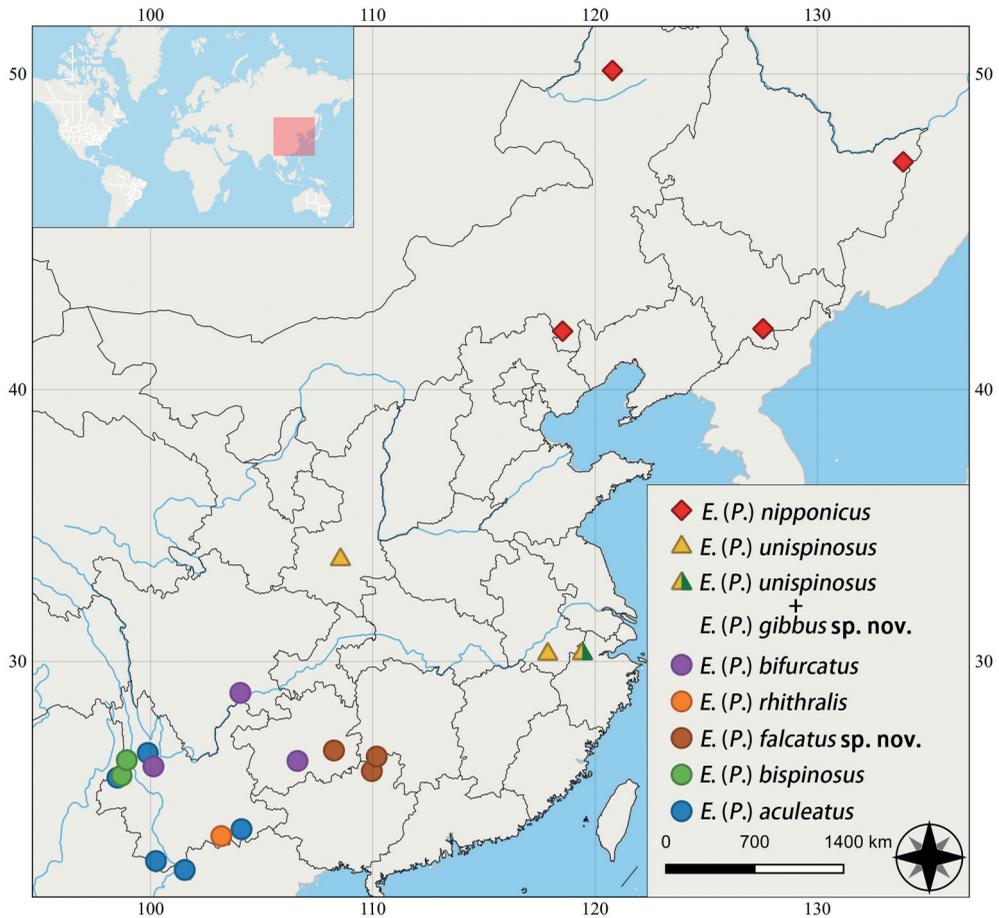


Figure 17. Distribution of Chinese *Epeorus* (*Proepeorus*) species in China (based on sampling sites of specimens examined in this study). Different shapes and colours represent different species.

Using several nymphal characters, Webb and McCafferty (2006b) divided *Epeorus* species in Eastern North America into two groups: one belongs to subgenus *Proepeorus* and the other belongs to subgenus *Iron* (= *Iron/g2 sensu* Kluge, 2004). In that work, the number of fimbriated setae at base of apical tooth complex of maxillae is a significant character: In *Iron*, there are two or more setae, but in *Proepeorus*, there is only one seta. Again, the Chinese species *E. (P.) gibbus sp. nov.* and *E. (P.) unispinosus* have more than two setae at same place of maxillae (all other Chinese *Proepeorus* species have only one seta, see Figure 15(g–i)), which is similar to American *Iron* instead of *Proepeorus*.

From above, we can see the tergal spines, gill, mouthparts and distributions (Figure 17) of Chinese *Proepeorus* species vary greatly (Table 2). When using different character, we can achieve different classification and some species will even be put into the subgenus *Iron*. So, the monophyly of subgenus *Epeorus* (*Proepeorus*), or any subgenus of this genus, needs more research to prove. Hrivniak et al. (2020b) analyzed the phylogeny of most subgenera in *Epeorus* through molecular evidence, and also show that the ‘suction disc’ of gill is a homoplasy and *Ironopsis/g2 sensu* Kluge (2004) is not monophyletic.

Table 2. Comparison of nymphal characteristics of Chinese *Propeorus* species.

Characters	<i>E. (P.) nipponicus</i>	<i>E. (P.) unispinosus</i>	<i>E. (P.) gibbus</i> sp. nov.	<i>E. (P.) aculeatus</i>	<i>E. (P.) rhithralis</i>	<i>E. (P.) bispinosus</i>	<i>E. (P.) bifurcatus</i>	<i>E. (P.) falcatus</i> sp. nov.
Dorsal setae pattern of labrum	Antero-medial notch with 5–6 bristles; anterolateral margin with 2 bristles	With 1 long bristle medially near the 4 antero-medial bristles; anterolateral margin with 2 bristles		Antero-medial notch with 5–7 bristles; anterolateral margin with 2 bristles				
Shape of labrum	Lateral margin evenly convex, not expanded anteriorly							
Shape of left inner incisor	With significantly expanded apex		Slender and nearly straight	Lateral margin nearly straight, widened anteriorly				
Fimbriated setae at base of apical of maxillae	1	4		Slightly curved but not expanded at the apex				
Spines or tubercles on posterior margin of abdominal terga	Without any spine or tubercle	With 1 median spine	With a longitudinal median ridge	With a pair of submedian long spines	With a pair of submedian tubercles	With a pair of submedian sharp and slender spines	With a pair of small submedian spines	
Distribution	Northern China, Japan	Central China, Nepal	Central China	Southern China, Thailand, Vietnam.	Southern China, Nepal	Southern China, Nepal, Tajikistan	Southern China, Vietnam, Thailand.	Southern China

Key to nymphs of Chinese *Propeorus*

1. Maxillae with 3–4 fimbriated setae at base of apexes (Figure 15(g)); dorsum of labrum with 1 long bristle medially near the tuft of antero-medial bristles (Figure 4(b))..... 2
 - Maxillae with 1 fimbriated seta at base of apexes (Figure 15(h,i)); dorsum of labrum without long bristle near the tuft of antero-medial bristles (Figure 6(b)) 3
2. Posterior margin of abdominal terga with 1 median spine (Figure 1(f)); with a pair of distinct spots near anterior margin of head capsule (Figure 1(e)). *E. (P.) unispinosus*
 - Posterior margin of abdominal terga with a median ridge instead of spine (Figure 2(d)); with a pair of indistinct spots near anterior margin of head capsule (Figure 2(c)) *E. (P.) gibbus* **sp. Nov.**
3. Posterior margin of abdominal terga without spine or tubercle (Figure 1(a,c)); labrum with lateral margins evenly convex (Figure 6(b)); head capsule with paired C-shaped markings (Figure 1(b)) *E. (P.) nipponicus*
 - Posterior margin of abdominal terga with submedian paired spines or tubercles (Figure 5); labrum with lateral margins somewhat straight and expanded anteriorly (Figure 15(c–f)); head capsule without paired C-shaped markings (Figure 5(a,c,e,g)) 4
4. Posterior margin of abdominal terga with relatively long paired spines (Figure 5(b)) *E. (P.) aculeatus*
 - Posterior margin of abdominal terga with relatively short paired spines (Figure 5(d,f,h)) 5
5. Paired spines on terga sharp or blunt, with pointed denticles on posterior margin on terga (Figure 6(f,g)) 6
 - Paired spines on terga small, with blunt denticles on posterior margin on terga (Figures 6(h) and 9(h)) 7
6. Paired spines on terga sharp and slender (Figure 5(d))..... *E. (P.) bispinosus*
 - Paired spines on terga undeveloped and blunt (Figure 5(h))..... *E. (P.) rhithralis*
7. Gill lamellae I somewhat expanded anteriorly (Figure 6(e))..... *E. (P.) bifurcatus*
 - Gill lamellae I moderately expanded anteriorly (Figure 9(i))..... *E. (P.) falcatus* **sp. nov.**

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