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A new *Potamanthodes* Ulmer, 1920 species from central China (Ephemeroptera: Potamanthidae)

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Abstract

In June 2025, a mayfly survey in central China revealed a new *Potamanthodes* species, which shares relatively big compound eyes with other two congeners (*P. macrophthalmus* You, 1984 and *P. yooni* (Bae & McCafferty, 1991)). In contrast, its nymphs have larger mandibular tusks and its male imagos have more wing pigmentation and more strongly curved forceps than those species. Therefore, it is herein named *P. curvativus* **sp. nov.** This discovery provides new insights into the evolution of nymphal eyes, mandibular tusks and the venation of imagos within the genus *Potamanthodes*.

Key words: Asia, China, taxonomy, morphology, *Potamanthodes yooni*, species diversity

Introduction

The taxon *Potamanthodes* Ulmer, 1920 is currently treated as an independent genus within the family Potamanthidae because it shows distinct imaginal and nymphal differences from the genus *Potamanthus* Pictet, 1843 (Li & Zhou 2023). At present, the genus comprises nine species out of a total of 26 species in the family (Bae & McCafferty 1991; Zhou *et al.* 2015; Li & Zhou 2023), some of them have been re-described in recent years (Kwanboon *et al.* 2021; Li *et al.* 2022; Li & Zhou 2023). All those previous studies provide a good base for further research on the genus.

The species *P. macrophthalmus* You, 1984 and *P. yooni* (Bae & McCafferty, 1991) show some uniqueness in the genus: both having relatively larger male compound eyes and more divergent penes but shorter nymphal mandibular tusks than others (Bae & McCafferty 1991; Li & Zhou 2023). In contrast, the other congeners usually have smaller eyes, parallel penes, and large mandibular tusks. This morphological gap within the genus requires further investigation.

The distributions of these two species are disjunct: *P. macrophthalmus* occurs in western China while the *P. yooni* is distributed in northeastern China to the Korean peninsula. The region between these areas remains poorly sampled and requires additional collecting efforts.

In June 2025, we collected mayflies from Qinglin Mt., Shaanxi Province, located in the central part of China. In our collection, both imagos and nymphs of a *Potamanthodes* species were gathered. With careful examination, they showed clear morphological differences from known congeners, and its COI sequence has more than 15% genetic distance from other registered species. So a new species is described herein, and its key diagnostic characters are illustrated and compared with those of the two closely related species.

Material and methods

Specimen collection and photography documentation

Nymphs were collected by hand net, and adults were attracted by collecting light and by rearing mature nymphs indoors. Associations between nymphs and adults were confirmed through rearing and morphological matching. All

examined materials are stored in ethanol ($\geq 80\%$) and deposited in the Mayfly Collection, College of Life Sciences, Nanjing Normal University (NNU), China.

The morphological characters of specimens were documented through multiple imaging techniques. Whole-body images of nymphs and adults were obtained using a Canon EOS 90D camera. For intermediate-sized structures like male genitalia and hindwing, a Sony a7R II camera equipped with a 90 mm macro lens was used. Eggs extracted from female imagos were examined using a Thermo Fisher Scientific Apreo 2S scanning electron microscope.

Gene sequence acquisition

Sequences of the mitochondrial Cytochrome C Oxidase subunit I (COI) gene were obtained using the following procedure: muscle tissue was extracted from the thorax and legs of female adults, and the DNA was isolated using the Animal Genomic DNA Kit (TsingKe, Beijing, China). COI sequence was amplified through polymerase chain reaction (PCR). The PCR protocol consisted of an initial denaturation step at 94 °C for 3 minutes, followed by 36 cycles of denaturation at 94 °C for 30 seconds, annealing at 48 °C for 40 seconds, and extension at 72 °C for 40 seconds, with a final extension at 72 °C for 10 minutes. The PCR amplification was carried out using Premix Taq (Takara Bio Inc., Beijing, China) and the universal primers LCO1490-JJ and HCO2198-JJ (Astrin & Stüben 2008). The sequence utilized in this study has been submitted to GenBank.

We obtained three COI sequences in our present study and additional four from the National Center for Biotechnology Information (NCBI) (Table 1). These sequences enable analyses of intra- and interspecific genetic distances.

The genetic distances of those seven sequences were calculated and performed with the Kimura 2-parameter model (Kimura 1980) in the MEGA 11 software (Tamura *et al.* 2021).

Table 1. COI sequences obtained in this study and their GenBank Accession Number.

Species name	GenBank Accession Number	Provider
<i>Potamanthodes curvativus</i> sp. nov.	PX752070	This study
<i>Potamanthodes yooni</i>	PX752071	This study
<i>Potamanthodes macrophthalmus</i>	PX734132	This study
<i>Potamanthodes longitibius</i>	PQ723066.1	Direct Submission
<i>Potamanthodes formosus</i> (1)	LC797307.1	Hayashi <i>et al.</i> 2022
<i>Potamanthodes formosus</i> (2)	LC805097.1	Direct Submission
<i>Potamanthus luteus</i>	PP473795.1	Guo <i>et al.</i> 2024

Results

Potamanthodes yooni (Bae & McCafferty, 1991)

(Figs 5B, 5E, 6B, 6E, 7B, 7E, 7H)

Materials Examined: 2 ♂ subimagos, 2 ♀ subimagos, 5 nymphs, Jojong stream, Cheongpyeong-myeon, Gapyeong-gun, Gyeonggi Prov., South Korea, 37.734194°N, 127.41420°E, 2021-IV-12, leg. A. Mayorga. 1 nymph, Ming-Xing civil square, Len-Jiang city, Hei-Long-Jiang province, 49.185764°N, 125.212151°E, alt. 386 m, 2023-VI-2, leg. Ya-Weng Zhu and Xiao Yang; 2 ♂ imagos, 6 ♀ imagos, Wu-Dao-Gou village, Xing-Bing county, Liaoning Province, 125.1961°E, 41.5312°N, alt. 413 m, 2023-VII-29, leg. Xin-Yu Ge and Xin-He Qiang; 1 ♀ imago, Hun-He river, Liaoning Province, 124.99140257°E, 41.28444348°N alt. 493 m, 2023-VII-29, leg. Xin-He Qiang; 1 nymph, Tang-Wang river, Heilongjiang Province, 129.62886°E, 46.721669°N, alt. 109.23 m, 2024-V-4, leg. Xin-He Qiang, Mu-He Deng, Meng-Yao Li.

Potamanthodes macrophthalmus You, 1984

(Figs 5A, 5D, 6A, 6D, 7A, 7D, 7G)

Material Examined: Holotype (♂ imago) and Paratypes (2 ♂ imagos and 3 ♀ imagos), Guankou Town, Ankang County, Shaanxi Province, 34.20038°N, 110.29040°E, 1982-VII-25, leg. Hong Gui and Xing-Yong Wu; 2 ♂ imagos, 2 ♂ subimagos, 10 nymphs, Guiyang County, Guizhou Province, 26.38048°N, 106.37041°E, 2021-VII-11, leg. Peng-Xu Mu.

***Potamanthodes curvativus* sp. nov.**

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(Figs 1–4, 5C, 5F, 6C, 6F, 7C, 7F, 7I)

Material Examined: Holotype (♂ imago), Feng-Jia-Ping village, Zhouzhi county, Shaanxi Province, China, 33.799277°N, 107.982618°E, alt. 1215 m, 2025-VI-23–24, leg. Gong De-Wen and Xu-Hong-Yi Zheng. Paratypes: 1 ♂ 1 ♀ imagos and 2 exuviae (reared from nymphs), 15 ♀ imagos, 5 nymphs, same as the holotype.

Other materials: 1 ♂ imago and 4 ♀ imagos, Hua-Er-Ping village, Zhouzhi county, Shaanxi Province, China, 33.827956°N, 107.822577°E, alt. 1325 m, 2025-VI-25–29, leg. Gong De-Wen and Xu-Hong-Yi Zheng. 2 ♀ imagos, Hei-He village, Zhouzhi county, Shaanxi Province, China, 33.848066°N, 107.834504°E, alt. 1280 m, 2025-VI-24–28, leg. Gong De-Wen and Xu-Hong-Yi Zheng.

Mature nymph (in alcohol, Figs 1–2, 5C, 5F): Body length 16.0–17.0 mm, cerci 6.0–7.0 mm, terminal filament slightly shorter than cerci (Fig. 1A). Body brown to dark brown, gills reddish brown, vertex deep brown, ocelli apex pale, occiput with two pale dots (Fig. 1A). Antennae 2.5 mm, pedicel ca. 2x scape (Fig. 1B); a spine-like projection between antenna and compound eye (Fig. 5C). Clypeus with a transverse row of dense hair-like setae dorsally (Fig. 2D).



Figure 1. Nymphal characters of *Potamanthodes curvativus* sp. nov.. A, habitus (dorsal view); B, base of antenna; C, foreleg; D, apex of forefemur; E, midleg; F, tarsus and claw of midleg enlarged; G, hindleg; H, Gill I; I, Gill II; J, Gill VII. Scale bar in A=2mm, others 0.5 mm.

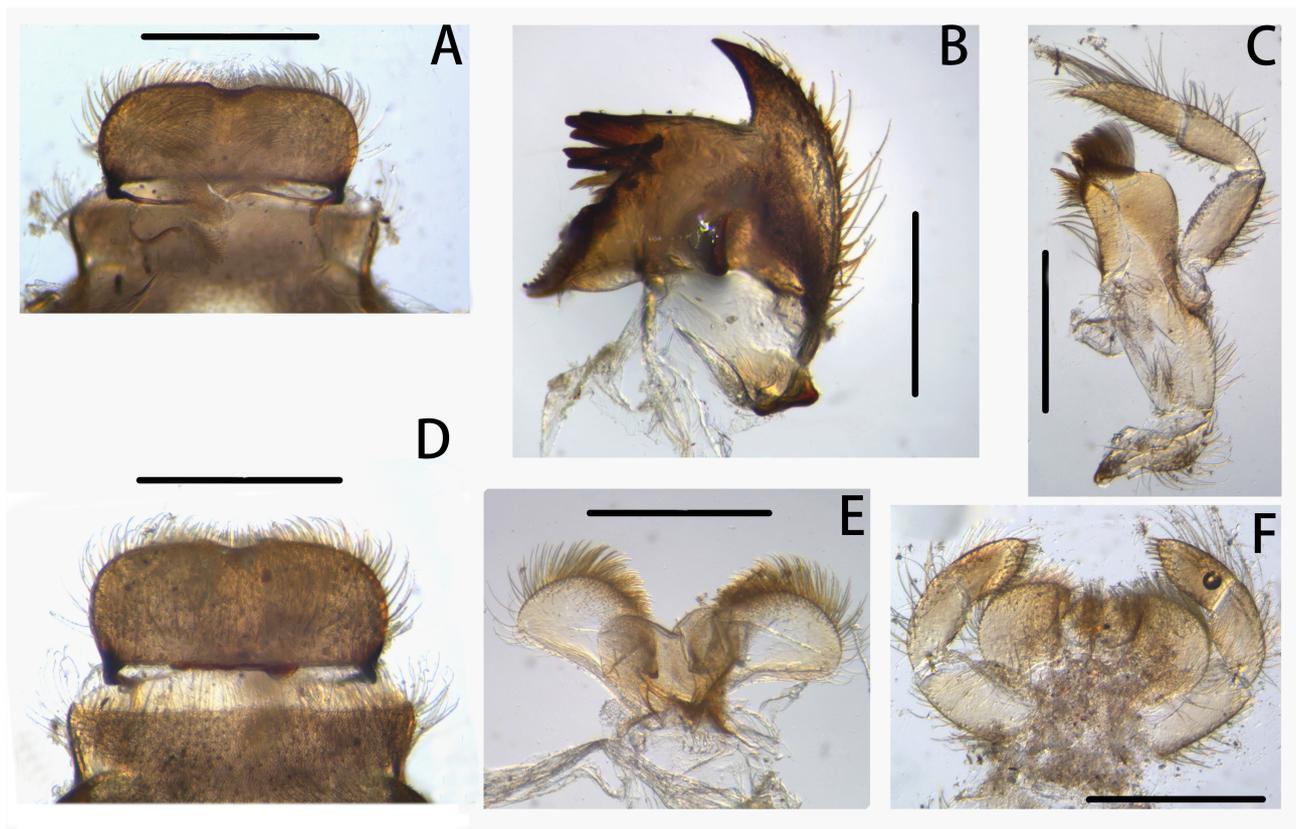


Figure 2. Nymphal mouthparts of *Potamanthodes curvativus* sp. nov.. **A**, labrum (ventral view); **B**, right mandible (dorsal view); **C**, maxilla (ventral view); **D**, labrum and clypeus (dorsal view); **E**, lingua and superlinguae (ventral view); **F**, labium (dorsal view). Scale bar= 0.5 mm.

Mouthparts (Fig. 2): both dorsal and ventral surfaces of labrum with hair-like setae, those of dorsal surface longer than ventral ones (Fig. 2A, 2D); setae on ventral surface basically forming two sub-median tufts; anterior margin with a very shallow median notch; width ca. 2x length (Fig. 2A). Surfaces of mandibles with both hair-like and spine-like setae; mandibular tusks curved significantly, horn-like, only slightly lower than outer incisors, distinctly visible in dorsal view of head (Figs 1A, 5F). Prosthema very close to inner incisor, with a spur and a tuft of spines on apex (Figs 2B, 5F). Both dorsal and ventral surfaces of maxillae with a column of hair-like setae, those setae on crown denser, forming brush-like tuft, two dentisetae distinct (Fig. 2C); length ratio of three segments of maxillary palp =1.0: 0.75: 1.0; outer margin of segment I and surface of segments II and III with hair-like setae, those of segment III longer than others (Fig. 2C). Lingua of hypopharynx smooth, superlinguae with dense hair-like setae (Fig. 2E). Two sides of labium with dense hair-like setae; length ratio of three segments of labial palp =1: 0.8: 0.6, both sides of palp with hair-like setae, segment III with additional spine-like setae on inner margin (Fig. 2F).

Pronotum brown but with two pale submedian stripes, lateral extensions pale; anterolateral angles blunt. Mesonotum with three pairs of pale dots nearby wingpads and pale middle line (Fig. 1A). Femora of all legs with a brown subapical marking dorsally, other parts of legs pale yellowish (Fig. 1C–G). Coxa and trochanter of foreleg with sparse hair-like and spine-like setae; dorsal surface and both margins of femur with spine-like setae along with very sparse hair-like setae, sometimes invisible (Fig. 1C); subapical spine-row from anterior margin to midline of femur (Fig. 1D). Inner margin of tibia with hair-like setae, apex with more and longer setae, an additional spine-like setal tuft at apex. Surface of tarsus with hair-like setae, inner margin and apex with spine-like setae, thicker than those of tibia (Fig. 1C). Setal pattern of midleg similar to foreleg but tarsus with less hair-like setae while more spine-like setae at apex (Fig. 1E–F). Margins of hindfemur with hair-like and spine-like setae but surface without visible setae, a subapical setal tuft at inner margin; proximal half inner margin of hindtibia with a setal tuft, other part with very sparse hair-like and spine-like setae; setal pattern of hind tarsus similar to midtarsus (Fig. 1G); claws of all legs similar, with reddish brown curved apex but smooth base (Fig. 1C, E–G). Length ratio of forefemur: tibia: tarsus=1.7: 1.4: 1.0 (Fig. 1C); that ratio of midleg=2.2: 1.4: 1.0 (Fig. 1E); hindleg=2.6: 1.1: 1.0 (Fig. 1G). Both mid and hindtibiae with patellar-tibial fusion sutures (Fig. 1E, 1G).

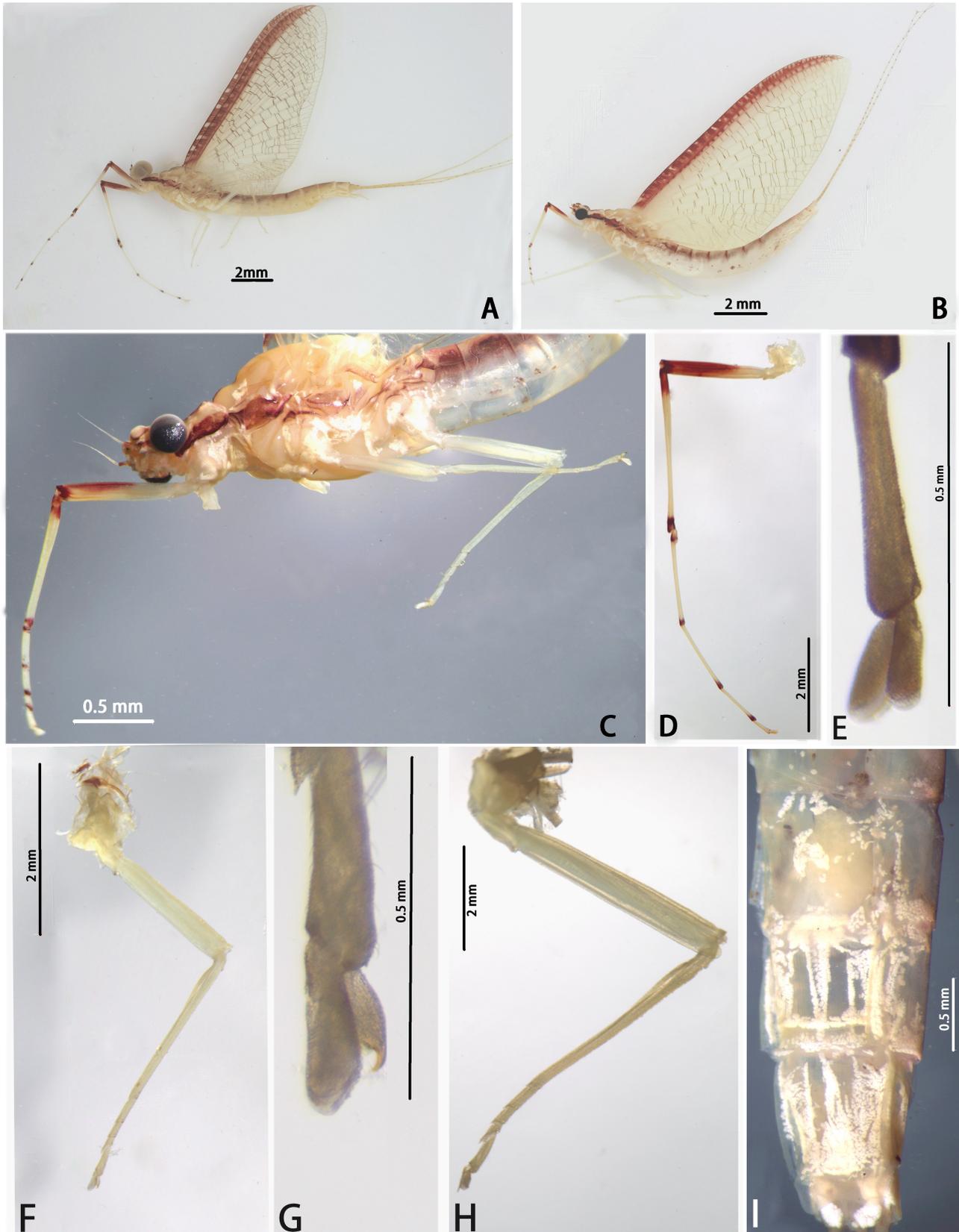


Figure 3. Imaginal characters of *Potamanthodes curvativus* sp. nov.. **A**, male imago (lateral view); **B**, female imago (lateral view); **C**, anterior part of female imago; **D**, foreleg of male; **E**, foreclaw of male; **F**, midleg of male; **G**, midclaw of male; **H**, hindleg of male; **I**, posterior part of female (ventral view).

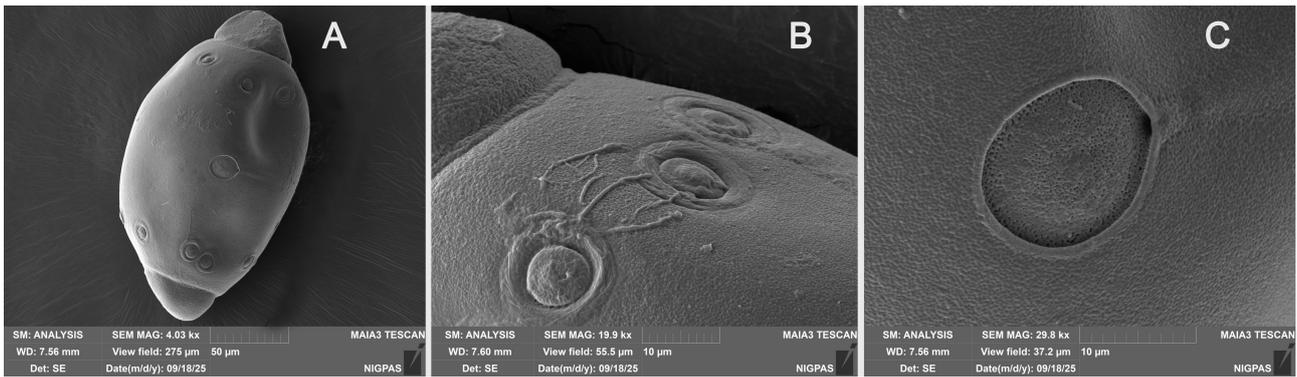


Figure 4. Egg of *Potamanthodes curvativus* sp. nov.. (SEM pictures). **A**, whole view; **B**, KCTs enlarged; **C**, micropyle enlarged.

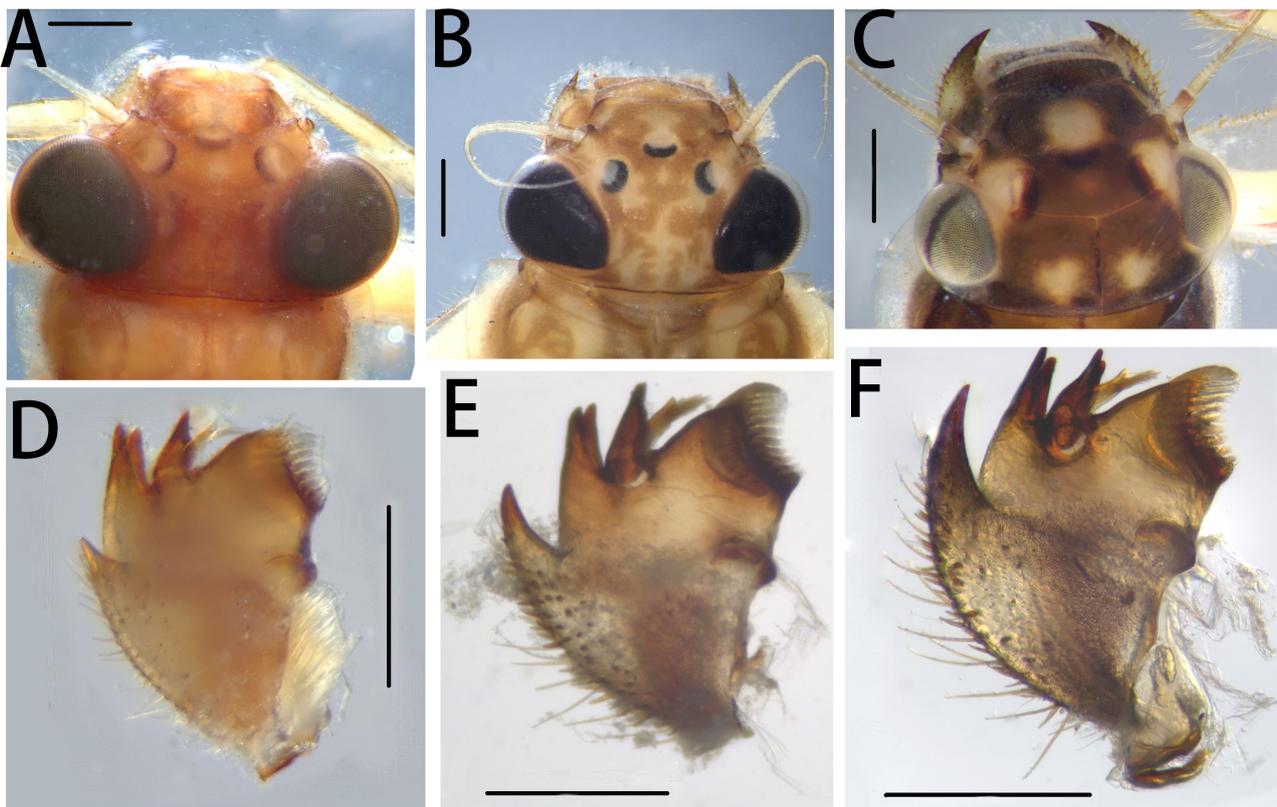


Figure 5. Nymphal head and left mandible of three *Potamanthodes* species. **A–C**, head (dorsal view); **A**, *P. macrophthalmus*; **B**, *P. yooni*; **C**, *P. curvativus* sp. nov.; **D–F**, left mandible (dorsal view): **D**, *P. macrophthalmus*; **E**, *P. yooni*; **F**, *P. curvativus* sp. nov.. Scale bar= 0.5 mm.

Abdomen dark brown, midline and lateral portion pale. Posterolateral angles of terga I–VIII slightly extended into small spine-like structure, spine of tergum IX slightly larger than others (Fig. 1A). Gills I two-segmented, thread-like, surface with hair-like setae (Fig. 1H); gills II–VII similar to each other, forked into very base, tracheae reddish brown (Fig. 1I–J). Cerci with mesal setae while terminal filament with setae on both lateral margins (Fig. 1A).

Male imago (in alcohol, Figs 3A, 3D–H, 6C, 6F, 7C, 7F, 7I): body length 12.0–13.0 mm, forewing 12.0–13.0 mm, cerci 27.0–28.0 mm, terminal filament 17.0–18.0 mm, foreleg 11.0–12.0 mm, hindwing 5.0–6.0 mm (Fig. 3A). Body pale yellowish, with reddish stripes at lateral sides, markings on pronotum, foreleg and forewings more distinct than other part (Fig. 3A). Base and scape of antennae with reddish pigments on outer side, apical half of pedicel reddish, flagella pale (Fig. 6C). Upper portion of compound eye gray while lower portion black; shortest distance between two eyes ca. 3x width of median ocellus (Fig. 6C). Basal half of ocelli reddish, apical half pale (Fig. 6C).

Lateral parts and midline of pronotum reddish, other part pale (Fig. 6C); counterparts of meso- and metanota with pigments but paler. Femur, base and apex of tibia, apex of all segment of tarsus of foreleg reddish, other part pale or yellowish (Fig. 3D). Mid- and hindleg pale (Fig. 3F–H). Two claws of foreleg similar, blunt (Fig. 3E); claws of mid-

and hindleg similar to each other, one blunt one acute (Fig. 3G). Length ratio of femur: tibia: tarsus of foreleg=1: 0: 1.6: 2.3, length ratio of tarsal segment=1.0: 8.0: 7.6: 4.4: 2 (Fig. 3D). Length ratio of midleg=1.0: 1.2: 0.6, ratio of tarsal segment = 1.0: 0.6: 0.3: 1.2 (Fig. 3F). Those two ratios of hindleg=1.0: 0.9: 0.4, 1.0: 0.6: 0.4: 1.4 (Fig. 3H). All longitudinal veins of forewings pale yellowish, crossveins dark brown, those crossveins between C, Sc and R₁ darker than others, and washed with reddish cloud, making area between C, Sc and R₁ almost reddish (Figs 3A, 7C). MA forked at middle, MP₂ fused with CuA at base (Fig. 7C). Crossveins of hindwings brown, slightly paler than forewings; costal projection sharp; MP₂ fused with CuA at base (Fig. 7F). Lateral portions of abdominal terga with reddish to brown pigments, others pale (Fig. 3A). Posterolateral tergite IX extended into sharp spine. Genitalia (Fig. 7I): subgenital plate with deeply V-shaped to smooth curved median notch; segment I of forceps significantly bent inward at middle; length of segments II and III subequal. Two penes forked beyond posterior margin of subgenital plate, forming V-shaped cleft between two penes; penes bent outwards, with almost uniform width from base to apex; apex blunt. Cerci with reddish articulations, others of caudal filaments pale yellowish (Fig. 3A).

Female imago (in alcohol, Fig. 3B–C, I, 4): Body length 12.0–13.0 mm, cerci 18.0–19.0 mm, terminal filament 16.0–17.0 mm, forewings 13.0–14.0 mm, hindwings 7.0–8.0 mm (Fig. 3B). Color pattern similar to male imago, including those of legs (Fig. 3B–C). Compound eyes on lateral sides of head, shortest distance between two eyes ca. 5x width of median ocellus (Fig. 6F). Length ratio of forefemur: tibia: tarsus=1.0: 1.1: 1.0, ratio of tarsal segments=1: 0: 3.0: 2.5: 1.5: 2.0; length ratio of midleg=1.0: 1.1: 0.6, ratio of hindleg=1.0: 1.0: 0.5; length arrangements of mid- and hind tarsal segments=4>1>2>3 (Fig. 3C). Posterior margin of sternum VII extended slightly, forming a narrow rectangular lobe (Fig. 3I), posterior half of sternum VIII projected ventrally, forming a shallow hump (Fig. 3I). Subanal plate with V-shaped median notch (Fig. 3I). Pigments of cerci less than male (Fig. 3B).

Subimago: Unknown.

Egg: Spindle-shaped, both poles with cap; a circle of distinct KCTs (knob-terminated coiled threads) near pole or cap; micropyle oval, near equator of egg (Fig. 4).

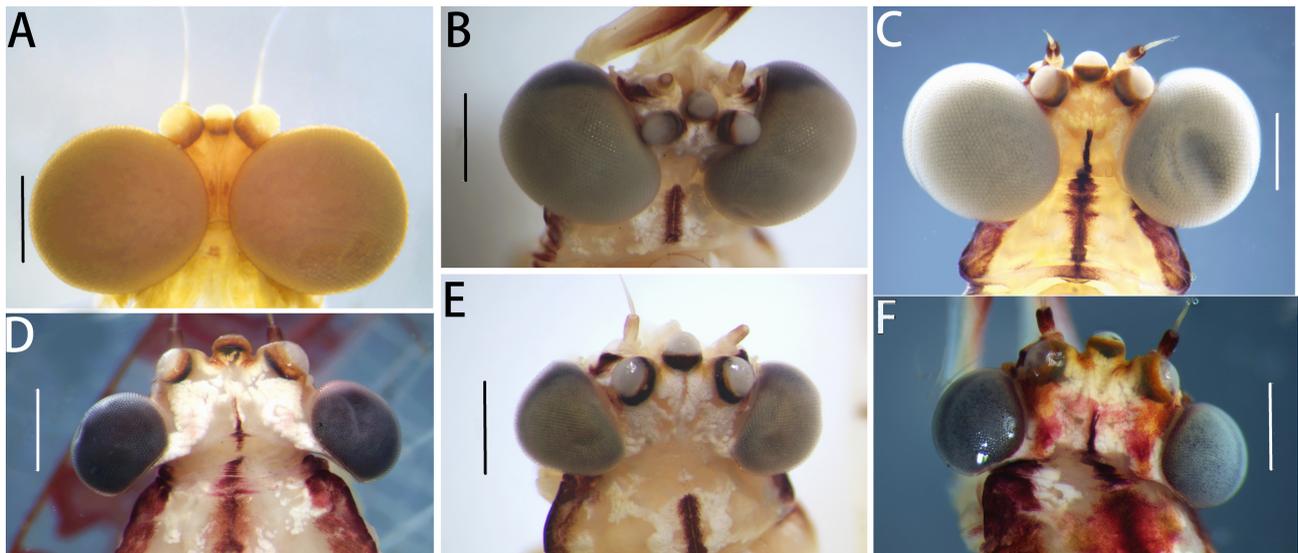


Figure 6. Head of imagos of three *Potamanthodes* species (dorsal view), (A–C) male. **A**, *P. macrophthalmus*; **B**, *P. yooni*; **C**, *P. curvativus* sp. nov.; **D–F**, female: **D**, *P. macrophthalmus*; **E**, *P. yooni*; **F**, *P. curvativus* sp. nov.. Scale bar= 0.5 mm.

Etymology

The specific epithet *curvativus* is a Latin word, means curve or curved, indicating the shape of forceps of the new species.

Diagnosis

The nymphs of *Potamanthodes curvativus* sp. nov. can be identified by: (1) brown body, without distinct colorful marking or stripes on abdomen (Fig. 1A); (2) relatively large compound eyes (Fig. 5C); (3) distinct mandibular tusks in dorsal view (Figs 1A, 5F); (4) legs, especially forelegs, have less and smaller hair-like setae than others (Fig. 1C–D); (5) setal row on subapical forefemur has less setae than others (Fig. 1D). Male imago of the new species *Potamanthodes curvativus* sp. nov. can be recognized by: (1) relatively large compound eyes (Fig. 6C); (2) wings with pigmented crossveins but without other markings except reddish costal and subcostal portions (Figs 3A, 7C); (3)

strongly curved forceps (Fig. 7I); (4) penes forked outside the subgenital plate (Fig. 7I); (5) tubular penis with blunt apex (Fig. 7I). Female imago has been diagnosed by the similar color pattern of the male (Fig. 3B–C) and by its eye size (Fig. 6F) and wing color (Fig. 3B–C).

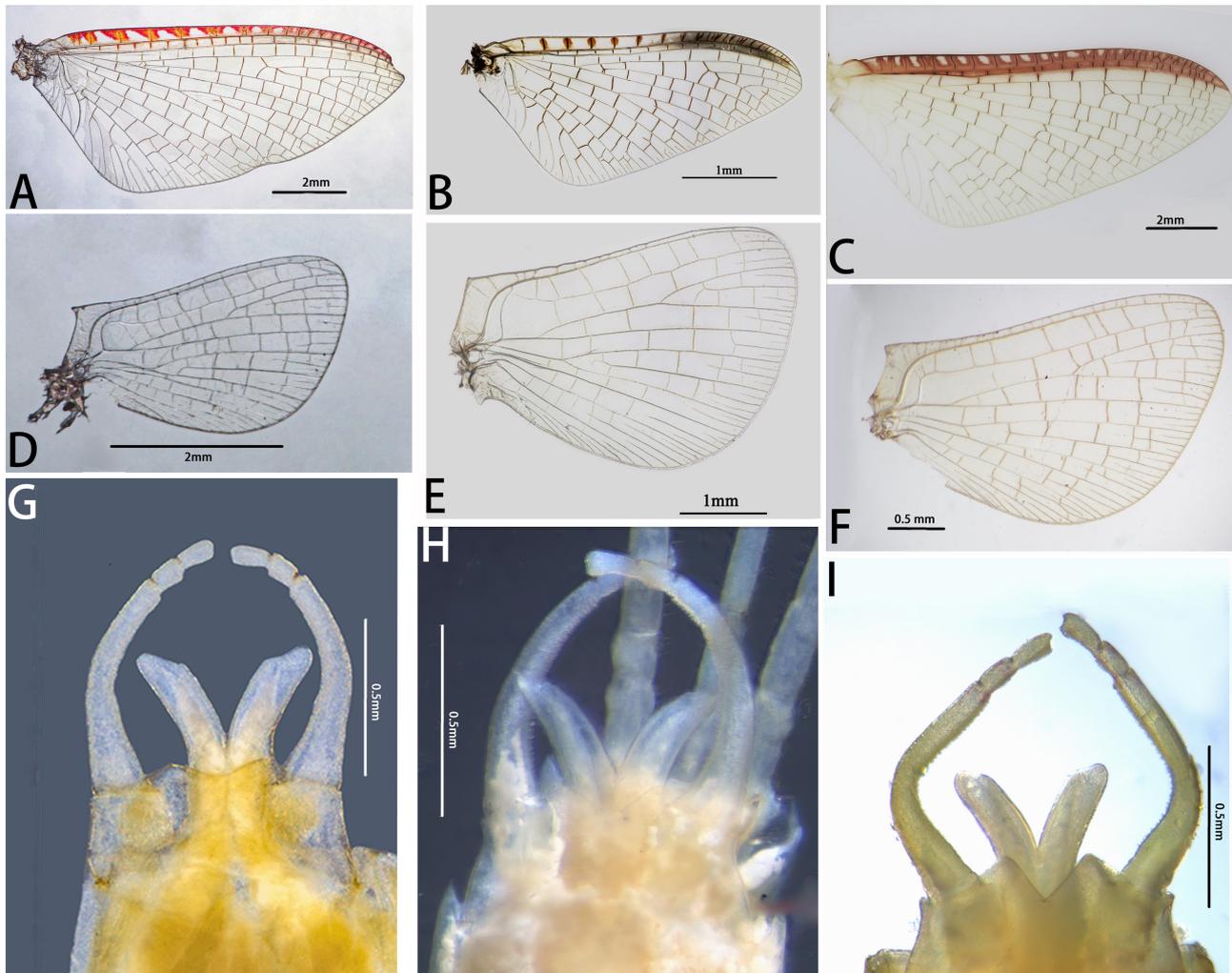


Figure 7. Wings and genitalia of three *Potamanthodes* species (male imago), (A–C) forewing. **A**, *P. macrophthalmus*; **B**, *P. yooni*; **C**, *P. curvativus* sp. nov.; (D–F) hindwing: **D**, *P. macrophthalmus*; **E**, *P. yooni*; **F**, *P. curvativus* sp. nov.; **G–I**, genitalia (ventral view): **G**, *P. macrophthalmus*; **H**, *P. yooni*; **I**, *P. curvativus* sp. nov..

Comparison

In the genus *Potamanthodes*, three species (*P. curvativus* sp. nov., *P. macrophthalmus* and *P. yooni*) have bigger compound eyes. Amongst them, the species *P. macrophthalmus* has the biggest eyes in both nymphal and imaginal stages (Figs 5A, 6A). Additionally, its male has the longest penes, the penal apex extended into blunt lobe (Fig. 7G), and the area between subcostal and R_1 has less pigments than *P. curvativus* sp. nov. (Fig. 7A). In nymphal stage, besides the biggest eyes, the mandibular tusks are tiny, spine-like, which almost invisible in dorsal view of head (Fig. 5A, 5D).

The nymphal compound eyes of *P. yooni* are smaller than *P. macrophthalmus* but bigger than *P. curvativus* sp. nov. (Fig. 5B), same as its nymphal mandibular tusks (Fig. 5E). Besides, the adults of *P. yooni* have pigmented clouds surrounding the crossveins of C and Sc area of forewings, but those clouds or markings are usually independent patches, without merging into connected stripes (Fig. 7B). The male penes of this species are sharp (Fig. 7H). Geographically, this species distributes in northeastern China and Korea peninsula, the other two species are in central to western China.

Compared to *P. yooni* and *P. macrophthalmus*, the new species *P. curvativus* sp. nov. has the smallest nymphal compound eyes (Fig. 5C) but largest mandibular tusks (Fig. 5F). In addition, the nymphs of this new species are more uniform than *P. macrophthalmus* and *P. yooni* (Fig. 1A), nymphs of latter two are usually with distinct marking on legs and abdomen (see Li *et al.* 2022; Li & Zhou 2023). The male genitalia of this new species has the shortest penes and

curved forceps (Fig. 7I). Its forewings have more pigments on crossveins, especially those of C and Sc, making those two areas almost totally reddish (Fig. 7C). Unlike the other two species, the hindwings of this new species have less curved base of longitudinal vein R_1 (with slightly larger distance between Sc and R_1) and fused bases of MP_2 and CuA (Fig. 7F), those two veins of *P. macrophthalmus* and *P. yooni* are independent although very close (Fig. 7D–E).

Eggs of this new species *P. curvativus* **sp. nov.** are typical of *Potamanthodes*.

Molecular similarity

The Kimura 2-parameter (K2P) distances between the three *Potamanthodes* COI sequences obtained in this study and other four potamanthid species are listed in table 2. The results show that the new species *Potamanthodes curvativus* **sp. nov.** differs by more than 17% from all other examined species, except *P. yooni*, supporting its status as a distinct species. The genetic distance between *P. curvativus* **sp. nov.** and *P. yooni* is 15.78%, which is slightly larger than that between *P. macrophthalmus* and *P. formosus* (15.76%).

The data in table 2 also show that intraspecific COI distances within the genus *Potamanthodes* (around 17%) are slightly lower than those observed between the two genera *Potamanthus* and *Potamanthodes* (approximately 18%).

Table 2. COI distance of some *Potamanthus* and *Potamanthodes* species in the GenBank (K2P %).

	<i>P. curvativus</i> sp. nov.	<i>P. formosus</i> (1)	<i>P. formosus</i> (2)	<i>P. longitibius</i>	<i>P. macrophthalmus</i>	<i>P. yooni</i>
<i>Potamanthodes formosus</i> (1)	17.67					
<i>Potamanthodes formosus</i> (2)	17.28	1.08				
<i>Potamanthodes longitibius</i>	17.15	16.54	15.76			
<i>Potamanthodes macrophthalmus</i>	17.15	17.14	16.35	1.23		
<i>Potamanthodes yooni</i>	15.78	16.86	16.46	17.74	17.34	
<i>Potamanthus luteus</i>	18.11	18.35	17.54	19.51	18.89	20.36

Discussion

The genus *Potamanthodes* currently includes ten species: *P. curvativus* **sp. nov.**, *P. formosus* (Eaton, 1892), *P. idiocerus* (Bae & McCafferty, 1991), *P. kwangsiensis* (Hsu, 1937), *P. longitibius* (Bae & McCafferty, 1991), *P. macrophthalmus*, *P. nanchangi* Hsu, 1936, *P. sangangensis* You, 1984, *P. yooni*, *P. yunnanensis* You *et al.*, 1982. Among them, the imaginal stage of *P. longitibius* and the nymphal stage of *P. yunnanensis* remain unknown. We are looking for them right now and aim to clarify the true diversity and character states of the genus in the near future.

The nymphal eyes and mandibular tusks of three species (*P. curvativus* **sp. nov.**, *P. macrophthalmus* and *P. yooni*) show some relevance pattern (Fig. 5). The species with biggest eyes (*P. macrophthalmus*) has the smallest mandibular tusks whereas *P. curvativus* **sp. nov.** has the smallest eyes but the longest tusks; *P. yooni* exhibits intermediate conditions (Fig. 5). If large eyes are regarded as a plesiomorphic condition, given that species in other genera such as *Potamanthus* Pictet, 1843 and *Rhoenanthus* Eaton, 1881 also possess this characters and it appears that mandibular tusks increase in size as the eyes become reduced.

With reduction of size, the venation of mayfly hindwings usually deformed, which in turns lost their original pattern or venation. However, the new species *P. curvativus* **sp. nov.** has fused MP_2 and CuA at the base in both forewings and hindwings (Fig. 7C, 7F). This character first supports the hypothesis that the ancestral mayfly condition included similar venation patterns in the forewings and hindwings. Second, it implies that this new species is more plesiomorphic than its congeners because it keeps the original pattern of wings, just like the forewings. This interpretation is further supported by its relatively colorful wings and simple tubular penes.

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