A New Fossil of Necrotauliidae (Insecta: Trichoptera) from the Jiulongshan Formation of China and Its Taxonomic Significance

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Abstract

Background: Acisarcuatus variradius gen. et sp. nov., an extinct new species representing a new genus, is described from the Middle Jurassic Jiulongshan Formation in Daohugou Village, Inner Mongolia, China.

Methodology/Principal Findings: In this paper, we revised the diagnosis of Necrotauliidae Handlirsch, 1906. One new genus and species of Necrotauliidae is described. An analysis based on the fossil morphological characters clarified the taxonomic status of the new taxa.

Conclusions/Significance: New fossil evidence supports the viewpoint that the family Necrotauliidae belongs to the Integripalpia.

Introduction

The Amphiesmenoptera, comprising two distinctive insect orders: the Trichoptera and the Lepidoptera [1]. Trichoptera, or caddisflies, are holometabolous insects. Their bodies and wings are covered by bushy hairs, and the adults resemble moths in appearance. They are among the largest group of aquatic insects [1, 2] and one of the most diverse groups of insects overall with more than 14,000 extant species and more than 680 fossil species [3]. Trichoptera include three living suborders: Annulipalpia, Integripalpia, and Spicipalpia [4], but the monophyly of Spicipalpia is disputable [2, 5]. Species of the Permian suborder Protomeropina Sukatcheva (1980) [6] are sometimes placed in Trichoptera [7, 8] and sometimes are considered representatives of the Amphiesmenoptera stem group or more distant lineages [9, 10].
The Necrotauliidae Handlirsch, 1906, an extinct caddisflies family, has been considered as representatives of the Amphiesmenoptera stem-group [1, 11–16]. Since the original description definition imprecise, at one time the family was deemed to “primitive” Trichoptera-like Mesozoic insects [12, 17–21]. However, the stem-group of Trichoptera is exactly similar to that of Lepidoptera. This ambiguity has augmented the heterogeneity of the Necrotauliidae [22]. Necrotauliidae have been described in the Late Triassic of Western Europe and the Late Mesozoic of Asia. Most fossil specimens of Necrotauliidae collected from Germany, Russia, China, and United Kingdom [13, 14, 16, 23, 24]. In China four Mesozoic Necrotauliidae, including *Necropsis paludis* Hong, 1983, *Necrotaulius fascialatus* Hong, 1983, *N. kritus* Lin, 1986, and *N. qingshilaense* Hong, 1984 have been described [13, 25].

Here, we describe a new and unique male adult fossil specimen collected from the Daohugou beds. The beds consist of 100–150 m thick succession of grey-white or locally reddish, thinly bedded claystones, shales, siltstones and sandy mudstones with intercalated ash-fall tuffs and ignimbrites. It was radiometrically dated by $^{40}\text{K}/^{40}\text{Ar}$ at 164–165 Ma [26], which accorded with the Callovian–Oxfordian boundary interval of the latest Middle Jurassic, using the latest standard international time scale [27]. Although there has been controversial to the precise age and stratigraphic position [28, 29]. The well-preserved fossils of insects and other animals also prove that the Daohugou fauna assemblages may correlate with the Middle Jurassic Yan-Liao biota [30]. This new fossil specimen is significant because of its well-preserved head, maxillary palps, fore- and hind wings, abdomen, and male genitalia. Most previously described representatives of the family were based only on fragmentary remnants and/or isolated wings [23, 31–33]. Thus, this new fossil is an important supplement to Necrotauliidae records and provides new evidence for studying their origin and evolution. The complete preservation of the new specimen enables us to determine the phylogenetic status of Necrotauliidae.

**Materials and Methods**

**Material**

The part and counterpart of the fossil specimen (CNU-TRI-NN2013001pc) are deposited in the Key Lab of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China. No specific permits were required for the described field studies.

**Nomenclatural Acts**

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Methods

The fossil specimen was examined using a Leica MZ12.5 dissecting microscope (Wetzlar, Germany) and illustrated with the aid of a drawing tube attachment. When observing the details, the specimen was put under pure alcohol. Line drawings were made by Photoshop 9.0 graphic software (Adobe Systems, San Jose, CA, USA). Photographs were taken with a Nikon Digital Camera DXM 1200C (Tokyo, Japan).

Body length was measured from the apex of the head to the apex of the abdomen. The wing length was measured from the base to the apex of the wing. The length of antennae was measured from the base to the apex.

Interpretation and terminology used herein follow Holzenthal et al. [5]: C, costa; Sc, subcosta; R, radius; R1, branches of anterior radius; Rs, posterior branch of radius (composed of R2, R3, R4, and R5); M, media; M1+2, anterior branch of media, composed of M1 and M2; M3+4, posterior branch of media, composed of M3 and M4; Cu, cubitus; Cu1, anterior branch of cubitus (composed of Cu1a and Cu1b); Cu2, posterior branch of cubitus; 1A, 2A, and 3A, first, second, and third branches of anal vein; the forks giving rise to R2 and R3, R4 and R5, M1 and M2, M3 and M4, CuA1a and CuA1b, are referred to as F1, F2, F3, F4, and F5, respectively; the discoidal cell (Dc) is the cell formed by the branching of Rs into R2+3 and R4+5 and is closed apically by the sectorial crossvein (s); the medial cell (Mc) is formed by the branching of M into M1+2 and M3+4; the anal cells delimited by 1A, 2A, and 3A.

Results

Systematic Paleontology

Family Necrotauliidae Handlirsch, 1906.

Type genus

Necrotaulusi Handlirsch, 1906.
Revised diagnosis
Head with setal warts. Antennae filiform. Maxillary palps five-segmented, segment V terminal, invisibly annulated, not covered densely hair or scales. Pronotum with one pair of setal warts. Mesothorax with triquetrous scutellum. Tibial spur formula: 0: 2: 3 or 4?. Forewing with vein Sc long, extending into pterostigma region; pterostigma variously developed; Rs with 4 branches; M usually with 4, rarely 3 branches, crossveins weakly developed or absent. Hind wing, Sc long; Rs with 4 branches; M with 3 or 4 branches; anal veins not joined.

Remark
According to the new fossil, we added the characters on head, antennae, maxillary palps and tibial spur formula. On hind wing, M with only 3 branches on the previously reported specimens, but our specimen has M four-branched, thus we revised this character.

Genera included. Acisarcuatus gen. nov.; Cretotaulius Sukacheva, 1982 [19]; Karatauliodes Sukacheva, 1968 [34]; Karataulius Sukacheva, 1968 [34]; Mesotrichopteridium Handlirsch, 1906 [12]; Necropsis Hong, 1983 [35]; Necrotaulius Handlirsch, 1906 [12]; Pteromixanum Sukatcheva and Jarzembowski, 2001 [23]; Scyphindusia Sukacheva, 1985 [36].
Acisarcuatus gen. nov.
urn:lsid:zoobank.org:act:85FB6752-52E4-4BFE-8549-9D43976642BB.

Type Species
Acisarcuatus variradius gen. et sp. nov.

Diagnosis
Warts present on head. Forewing with 5 forks (I–V); Sc forked, Sc2 straight and long, extending into pterostigma region; anal veins form a typical anal loop; discoidal cell short and closed, median cell and thyridial cell very long and open. Male genitalia harpagoness regularly curving mesad, narrowing at apex; median phallic apparatus seems to be spicular and arcuate.

Etymology
The generic name is a combination of the Latin word acis (tip) and arcuatus (arc, curve), describing the peculiar curving of R1; gender masculine.

Distribution
China.

Remark
We assigned Acisarcuatus variradius gen. et sp. nov. to the Necrotauliidae on the basis of the following characters: head with anterior and posterior setal warts; maxillary palps five-segmented, first segment stout; tibial spur formula: 0: 2: 3 or 4?; forewing Sc long, extending into pterostigma region; Rs with 4 branches; M with 4 branches; crossvein rare; hind wing Sc extending about 2/3 length of hind
wing, Rs and M with 4 branches; anal veins not joined; male genitalia inferior appendages two-segmented gonopods, with dense hairs around margin.

This new specimen shows affinity on vein characters with some other genera of Necrotauliidae. *Acisarcuatus* share several characters with *Necrotaulius* Handlirsch, 1906 [12] such as warts on the head are present, forks I–V long and slender, and crossvein m-cu₁ present. However, *Acisarcuatus* differs from *Necrotaulius* in: 1) Sc forked (vs. Sc unforked); 2) R₁ unforked, straight in basal part but curved in pterostigma area (vs. R₁ forked and straight in pterostigma area); 3) Dc short and closed by r₃–r₄ (vs. Dc open); 4) Rs₁₊₂ furcation before Rs₁₊₂ furcation (vs. Rs₁₊₂ furcation beyond Rs₁₊₂ furcation).

*Acisarcuatus* differs from *Mesotrichopteridium* Handlirsch, 1906 [12] in the following characters: 1) forewing length 0.9 mm (vs. forewing length 3.5–4.5 mm); 2) forewing without crossvein sc-r (vs. crossvein sc-r present); 3) M four-branched on the hind wing, (vs. M₄ reduced).

*Acisarcuatus* differs from *Pteromixanum* Sukatcheva and Jarzembowski, 2001 [23] in the following characters: 1) body size relatively large, length 0.9 mm (vs. length 0.5 mm); 2) Sc forked (vs. Sc unforked); 3) forewing with forks I–V (vs. forewing with forks I, II, III, V); 4) M forking before Rs forking (vs. M forking beyond Rs forking).

*Acisarcuatus variradius* gen. et sp. nov. (Figs. 1–3).

urn:lsid:zoobank.org:act:D1107F5B-EAB9-4C76-B0F2-89CF7264A77F.

**Type Material**

Holotype, male: CNU-TRI-NN2013001pc (part and counterpart, dorsoventrally compressed). Antennae, maxillary palps, setal warts on head and thorax, tibial spurs, forewing, hind wing and male genitalia are well-preserved.

**Locality and horizon**

Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China (N41°18.979′, E119°14.318′), Jiulongshan Formation, Middle Jurassic.

Etymology. Specific name is a combination of the Latin word *vari* (different) and *radius*, indicating peculiar R₁; gender masculine.

**Diagnosis**

Body small; Sc 2-branched; R₁ unforked, straight basally and curved in pterostigma area, R₁ closed to Rs₁ terminally.

**Description**

Head with saponaceous triangle, compound eye at head sides, oval. Anterior setal warts and posterior setal warts present surrounding compound eye, irregularly oval. Antennae filiform but not well-preserved, scape slightly thicker than pedicel and flagellum, pedicel cylindrical, flagellum slender, length of segments equal to their diameter. Maxillary palps five-segmented; segment I swollen, segment II longest, segment III subequal to IV, segment V indistinct.

Thorax: Pronotum with one pair of setal warts, symmetrically drop-shaped. Mesothorax with triquetrous scutellum. Legs well-preserved. Foretibial spur
Fig. 1. Photographs of the holotype of *Acisarcuatus variradius* gen. et sp. nov. CNU-TRI-NN2013001pc. A, ventral view, B, dorsal view.

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Fig. 2. Line drawings of *Acisarcuatus variradius* gen. et sp. nov. CNU-TRI-NN2013001pc.

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Fig. 3. Photographs of *Acisarcuatus variradius* gen. et sp. nov. CNU-TRI-NN2013001pc. A, head, antennae, maxillary palps, fore leg, and mid leg in alcohol. B, head, antennae, maxillary palps, fore leg, and mid leg. C, forewing and hind wing. D, male genitalia in alcohol.

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invisible, mesotibia with two apical spurs; metatibia with two preapical spurs and one or two apical spurs; tibial spur formula: 0: 2: 3 or 4. Fore tarsus five-segmented, slender, segment I longest, II-IV subequal in length; mesotarsus five-segmented, all tarsal segments with terminal spinules. Tarsal claw visible. Forewings elongated elliptic; Rs₄ terminating slightly below apex of forewing. Forewing with forks I–V; Sc forked, Sc₂ slightly bend terminally and ending into C at about 2/3 the length of forewing, Sc₁ terminating into C at about 2/3 length of Sc; R₁ unforked distally, straight in basal part and curved in pterostigma area; Rs forked at mid-length of the forewing; Dc short and closed by r₃–r₄; F₁ forks before than F₂; Rs₁ slight bent towards R₁ at terminus; M originating from base of R; M forking before Rs forks; F₃ and F₄ longer than their stems; F₃ forks later than F₄; Mc very long and apparently open; Cₚ₁ bifurcated into Cₚ₁a and Cₚ₁b, and then F₅ forks as same level as Rs fork; crossvein m-cu₁ present; Tc open; Cₚ₂ straight and simple; anal veins visible, 1A straight, 2A reaches the median of 1A, 3A strongly curved and reaches median of 2A. Hind wing narrower and shorter than forewing. Hind wing with forks I–V; Dc, Mc, and Tc open; Sc simple; R₁ straight and simple; F₁ forks later than F₂, F₃ forks slightly before F₄, F₅ forks earliest.

Abdomen: In dorsal view, eight sternites visible and male genitalia prominent, bearing pair of two-segmented gonopods; coxopodite broad at base and shorter than harpago. Harpagones regularly curving mesad, narrowing at apex. Coxopodites and harpagos with dense hairs around margin. Middle preanal appendage and periphallus visible, median phallic apparatus seems to be spicular and arcuate. External structural details of male genitalia indistinct in fossil.

**Remark**

In our specimen, only one apical spur is visible, but the presence of another apical spur cannot be excluded (i.e. absent due to incomplete preservation).

**Measurements (in mm)**

Body length 9.92, width 1.74. Head length 0.91, width 1.43. Interocular space 0.75. Maxillary palp segments I–IV: 0.15, 0.52, 0.30, 0.30. Scutellum length 0.42, width 0.57. Forewing length 9.36, width 3.40. Hind wing length 6.79, width 3.02. Fore leg length: femur 1.09, tibia 0.79, tarsus I–V: 0.38, 0.30, 0.23, 0.23, 0.23; middle leg length: tarsus I–V: 0.52, 0.34, 0.30, 0.26, 0.26; hind leg length: tibia 2.38, tarsus I–V: 0.64, 0.42, 0.42, 0.42, 0.49.

**Discussion**

Kristensen provided a summary of 21 apomorphies supporting the monophyletic group of Amphiesmenoptera, with both Trichoptera and Lepidoptera certain features (e.g. forewing the terminal of the anal vein fusion) [37]. Furthermore, the monophylies of Trichoptera and Lepidoptera are also generally accepted [9]. Insect fossil caddisflies are generally preserved incompletely or indistinctly, and often only forewing is visible on the fossil [32, 33]. Many paleontologists considered Necrotauliidae to be a representative of the amphiesmenopteran stem...
group, and proximal to the common ancestor of trichopterans and lepidopterans that survived after the Triassic [1, 11–14, 17–21, 38]. This viewpoint is mainly based on the characteristics of forewing.

Our specimen possesses very clear male genitalia with harpagones (coxopodite broad at base and shorter than harpago), middle preanal appendage, spicular and arcuate median phallic apparatus. The harpgones is a synapomorphy of Trichoptera [5, 24]. Beside that, maxillary palps of the new fossil specimen correspond to the apomorphy of Integripalpia [39, 40]: maxillary palps upturned, with segment I swollen, densely hairs or scales invisible, segment II longest, segment III subequal to IV. The character that crossvein m absent is also similar to suborder Integripalpia [40]. On the basis of these characters, we believe Necrotauliidae is belongs to Integripalpia (Trichoptera).

Meanwhile A. variradius gen. et sp. nov. has some plesiomorphies of Integripalpia: Sc forked; forewing with five forks; crossveins very rare on both forewing and hind wing; only two crossveins, r and m-cu, present. These characters also can be found in the extinct suborder Protomeropina [6, 41–43]. It is interesting to speculate that necrotauliids are representatives of the Integripalpia stem-group rather than the amphiesmenopteran.

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Author Contributions
Conceived and designed the experiments: YJL YZY DR. Performed the experiments: YJL WTZ YZY DR. Analyzed the data: YJL WTZ YZY DR. Contributed reagents/materials/analysis tools: YJL WTZ YZY DR. Wrote the paper: YJL WTZ YZY DR. Photographs: YJL YZY. Line drawings: YJL.

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