Proceedings of the Geologists' Association 131 (2020) 67–72

Contents lists available at ScienceDirect

Proceedings of the Geologists' Association

journal homepage: www.elsevier.com/locate/pgeola

First Anostraca (Crustacea: Branchiopoda) from the Middle Jurassic of Daohugou, China

Cihang Luo[a], Edmund A. Jarzembowski[b,c], Yan Fang[b], Bo Wang[b], Chuantao Xiao[a,*]

[a] School of GeoSciences, Yangtze University, Wuhan 430100, Hubei, China
[b] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology and Center for Excellence in Life and Paleoenvironment, Chinese Academy of Sciences, 39 East Beijing Road, Nanjing 210008, China
[c] Department of Earth Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK

ARTICLE INFO

Article history:
Received 17 September 2019
Received in revised form 15 November 2019
Accepted 21 November 2019
Available online 6 December 2019

Keywords:
Anostraca
Branchiopoda
New genus
Middle Jurassic
Daohugou

ABSTRACT

A new extinct genus and species of Anostraca (Crustacea, Branchiopoda), *Daohugounaias cheni* gen. et sp. nov. is described based on a well-preserved specimen from the Middle Jurassic of Daohugou, Inner Mongolia, China. The new genus differs from other Anostraca by the short, forward-pointing spines at the joint of the abdomen and brood pouch. Scanning electron microscopy (SEM) shows that eggs are preserved in three-dimension and some ridges and spines remain on their surfaces. Energy dispersive X-ray (EDS) demonstrates that the relatively abundance or depletion of elements vary between different parts of the body. The new discovery fills a stratigraphical gap in the Anostraca and supports the previous palaeoenvironmental reconstruction of the Daohugou area.

1. Introduction

The Anostraca, or fairy shrimps, together with Notostraca, Laevicaudata, and Spinicaudata, are all branchiopods, representing an important component of the diversity of temporary freshwater pools (Rabet et al., 2018). However, because of the delicate nature of their exoskeleton, anostracans do not occur commonly as fossils, most of which have an ambiguous systematic status (Belk and Schram, 2001). Only one known fossil anostracan can be assigned to an extant family (Branchinectidae), *Branchinecta barstowensis* Belk, 2001 from the Miocene of California (USA) (Belk and Schram, 2001; Gueriau et al., 2016). The oldest known anostracan might be *Rehbachiella kinnekullensis* Müller, 1983) from Swedish Cambrian rocks (Lindholm, 2014), or is at least the earliest branchiopod (Gueriau et al., 2016; Olesen, 2009; Walossek, 1993; Walossek and Müller, 1992). In addition, Harvey et al. (2012) reported well-preserved mandibles and filtering appendages in Cambrian branchiopods from Canada, which are quite similar to those of extant Anostraca. Another early species is *Lepidocaris rhyniensis* Scourfield (1926), a Devonian branchiopod from Scotland with anostracan affinities (Scourfield, 1926). Until now, the oldest modern-looking fossil anostracan that has been confirmed is *Haltinnaias serrata* Gueriau et al. (2016), which was discovered in the 365-million-year-old (Late Devonian) Strud locality of Belgium; it was part of an ephemeral-pool branchiopod community closely resembling extant species (Gueriau et al., 2016). *Chirocephalus rasnitsyni*) Trusova (1971) from the Lower Cretaceous Baleisk Formation of eastern Probaikalia, Russia has been considered as the only fossil anostracan from the Mesozoic for a long time (Trusova, 1971) until some authors mentioned Anostraca from the Middle Jurassic of Daohugou, but they did not describe them (e.g., Huang et al., 2006; Shen and Huang, 2008).

2. Material and methods

The unique type is from the Middle Jurassic Jiulongshan Formation of Daohugou (41°18′N, 119°13′E) in Ningcheng County, Chifeng City, Inner Mongolia, China (Fig. 1). During that time, the climate of Daohugou was humid and warm-temperate (Wang et al., 2013; Wang et al., 2019; Yang et al., 2019). These deposits are well-known for yielding a highly diverse array of plants, insects, and vertebrates (e.g., Wang et al., 2019; Zhao et al., 2019).

The specimen was examined dry and under alcohol using a Zeiss Stemi 508 Microscope. The photographs were taken with a Zeiss Stereo Discovery V16 microscope system, and measurements were taken using Zen software (Figs. 2A, B; 3 A, B). The micro-surface information (Figs. 3C, D; 4 A, F, K) was obtained in low voltage mode (1kv) of a TESCAN MAIA3 Triglav (SEM). The elementalmapping was done with OXFORD ULTIM MAX EDS (produced by the Oxford Instruments Company) with an accelerating voltage of 20kv

* Corresponding author.
E-mail address: ctxiao@yangtzeu.edu.cn (C. Xiao).

https://doi.org/10.1016/j.pgeola.2019.11.004
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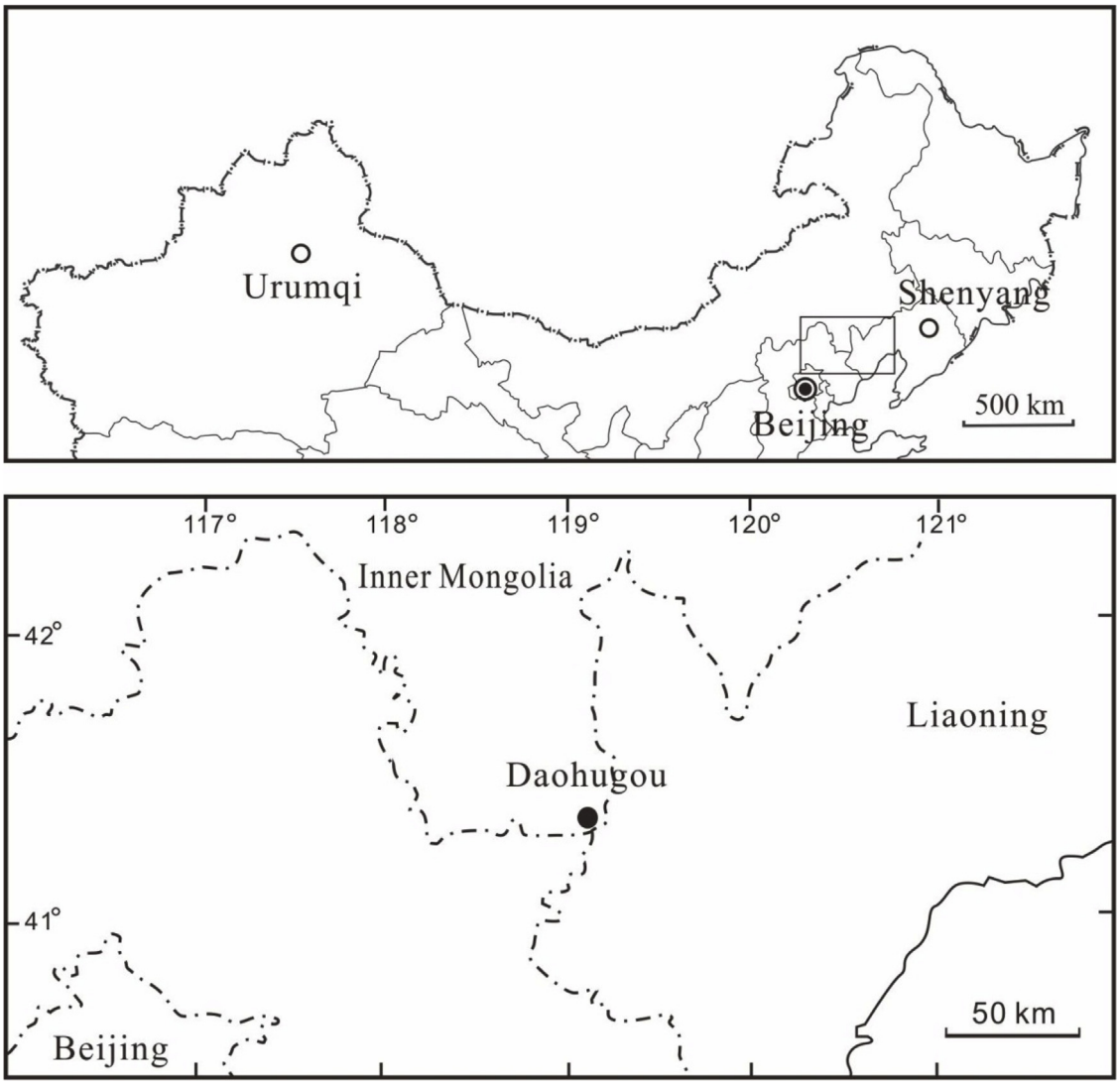

Fig. 1. Map of fossil locality.

(Fig. 4B–E, G–J, L–O). The SEM and EDS analyses were performed in the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). The line drawings were compiled by tracing the photographs using the image-editing software CorelDraw X8. The unique type is deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

3. Systematic paleontology

Order Anostraca) Sars (1867)
*Daohugounaias cheni*gen. et sp. nov.

3.1. Holotype

NIGP171735, female, adult in ventral view with a brood pouch.

3.2. Etymology

The first noun in apposition, 'Daohugou', refers to the locality of Daohugou Village, where the specimen was collected, and 'naias' is a type of water nymph (gender feminine). The species name 'cheni' is after the late Peiji Chen, in honour of his contribution to the Cretaceous stratigraphy of China.

3.3. Diagnosis

Anostraca with a pair of short, forward-pointing abdominal spines at the joint of the abdomen and brood pouch.

3.4. Description

Body length (from anterior margin of the head to posterior margin of telson) 20.0 mm. Distinct head bearing a pair of sub-rounded compound eyes (length 0.95 mm and width 0.72 mm) and short, tapering first antenna (antennula) (length 0.42 mm); the second antenna cannot be recognized; eye peduncle extremely short, expanding distally to compound eye. Oval thorax, length 7.8 mm, width 4.4 mm, with probably 11 pairs of homologous thoracopods, but fine structural detail of thoracopods absent (Figs. 2; 3A). Female with a protruding, irregular marginal brood pouch, length 3.6 mm, width 1.9 mm, with about 80 eggs inside, covering one or two abdominal segments. The joint of the abdomen and brood pouch bearing pair of short, forward-pointing abdominal spines. Eggshells spherical, diameter of eggs ranging

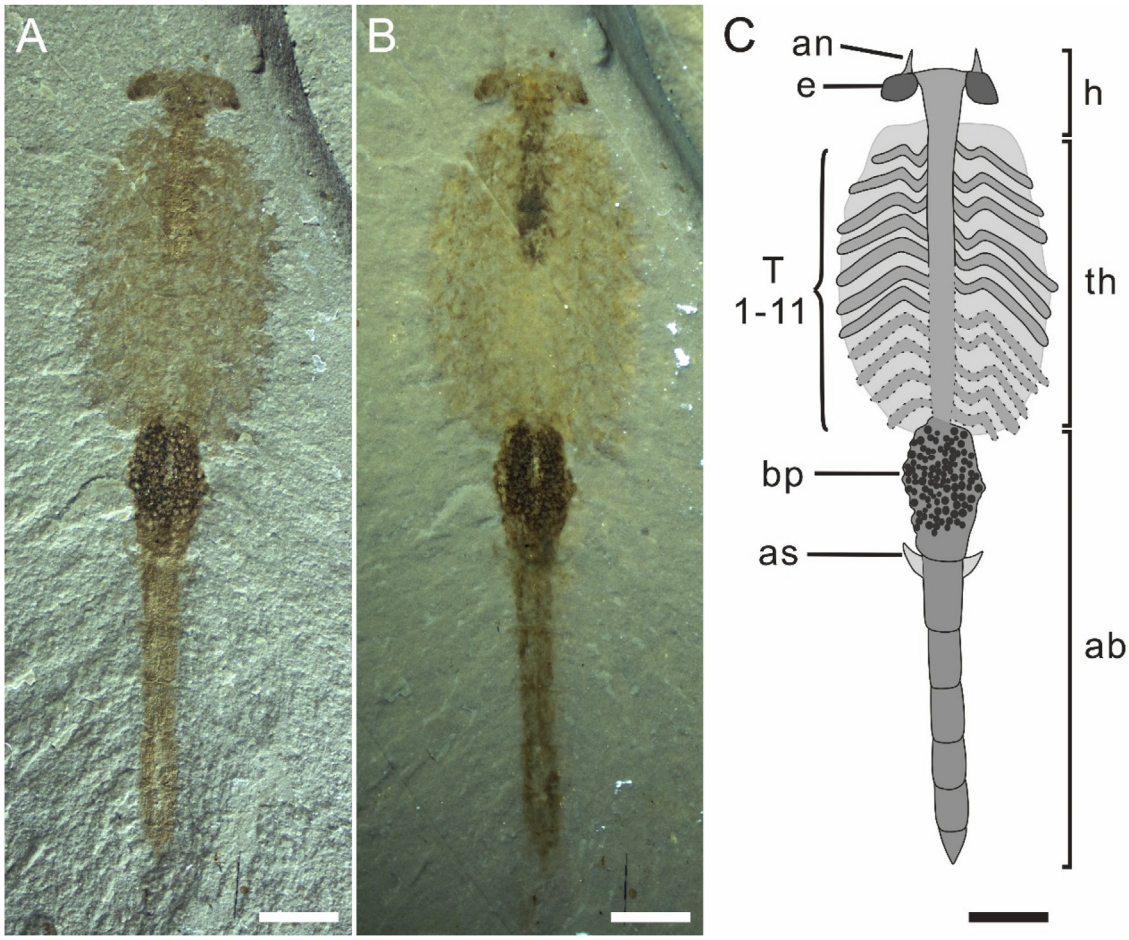

Fig. 2. NIGP171735 b, *Daohugounaias cheni* gen. et sp. nov. A, body (dry); B, body (in alcohol); C, body (line drawing); scale bar represent 2 mm in A, B and C. Abbreviation: ab, abdomen; an, antenna; as, abdominal spines; bp, brood pouch; e, eye; h, head; T, thoracopods; th, thorax.

from 170 μm to 250 μm (Figs. 2; 3A–C). Abdominal length 7.8 mm, width 0.9 mm (without brood pouch); abdomen with at least six apodous segments; telson short and of triangular shape; cercopods probably not preserved.

4. Discussion

Due to amazing morphological stasis (Lindholm, 2014; Gueriau et al., 2016), *Daohugounaias cheni* gen. et sp. nov. is very similar to extant Anostraca. However, the systematics of extant Anostraca are based on the structure and shape of the legs, gonopod, brood pouch, and male head (Linder, 1941; Brtek and Mura, 2000; Rogers, 2002), characters that are rarely preserved in fossils and the Daohugou fossil has not got the microscopic details due to diagenetic alteration (Zhang et al., 2018; Zhao et al., 2019). So it is difficult to assign *D. cheni* to an extant family or determine its phylogenetic relationship within the clade (Gueriau et al., 2016). The most similar species is *Haltinnaias serrata*) Gueriau et al., 2016, with the same character of forward-pointing abdominal spines (Figs. 2; 3A,B), but its diagnostic series of small distal spines on the brood pouch of the female aren't shared with *D. cheni*. Considering the 200-million-year time gap and geographic separation, such differences are not surprising. Furthermore, *D. cheni* is different from *Chirocephalus rasnitsyni* Trusova (1971) from Russia because the latter has the round-triangular brood pouch extending over all seven abdominal segments (Trusova, 1971).

The eggs' three-dimensional preservation, which contrasts with the body's preservation in two dimensions (Fig. 3), indicates that the eggs were decayresistant and tougher, helping them survive seasonal desiccation, and then hatch in ephemeral pools (Gueriau et al., 2016). In addition, the SEM images show that there are some ridges or spines on the surface of the eggshells (Fig. 3C,D) which could provide useful taxonomic characters (Gilchrist, 1978; Mura, 1992,2001; Shen and Huang, 2008; Bruner et al., 2013). Unfortunately, because of diagenetic alteration, it's hard to conclusively compare these ridges or spines with extant species at present.

Our EDS analyses reveal that slight enrichment of Al and depletion of Na can be seen in the body of the holotype (Fig. 4B, E, G, J, L, O). The head is relatively rich in Ca and K (Fig. 4C, D), whereas the brood pouch is characterized by elevated concentrations of Ca, but voided of K (Fig. 4H, I). It indicates that these eggs have been calcified, which may lead to their three-dimensional preservation; the telson has elevated K (Fig. 4N). Al and K elemental maps of the telson have a trident-like configuration, and the median line coincides with the alimentary canal. These differences of elemental distribution reflect the different composition of the minerals that replicated the decaying organism, which were probably controlled by contrasts in tissue chemistry (Orr and Kearns, 1998).

The occurrence of Anostraca together with very abundant clam shrimps (Laevicaudata) indicates that the paleoenvironment of Daohugou comprised small, isolated, shallow ponds and

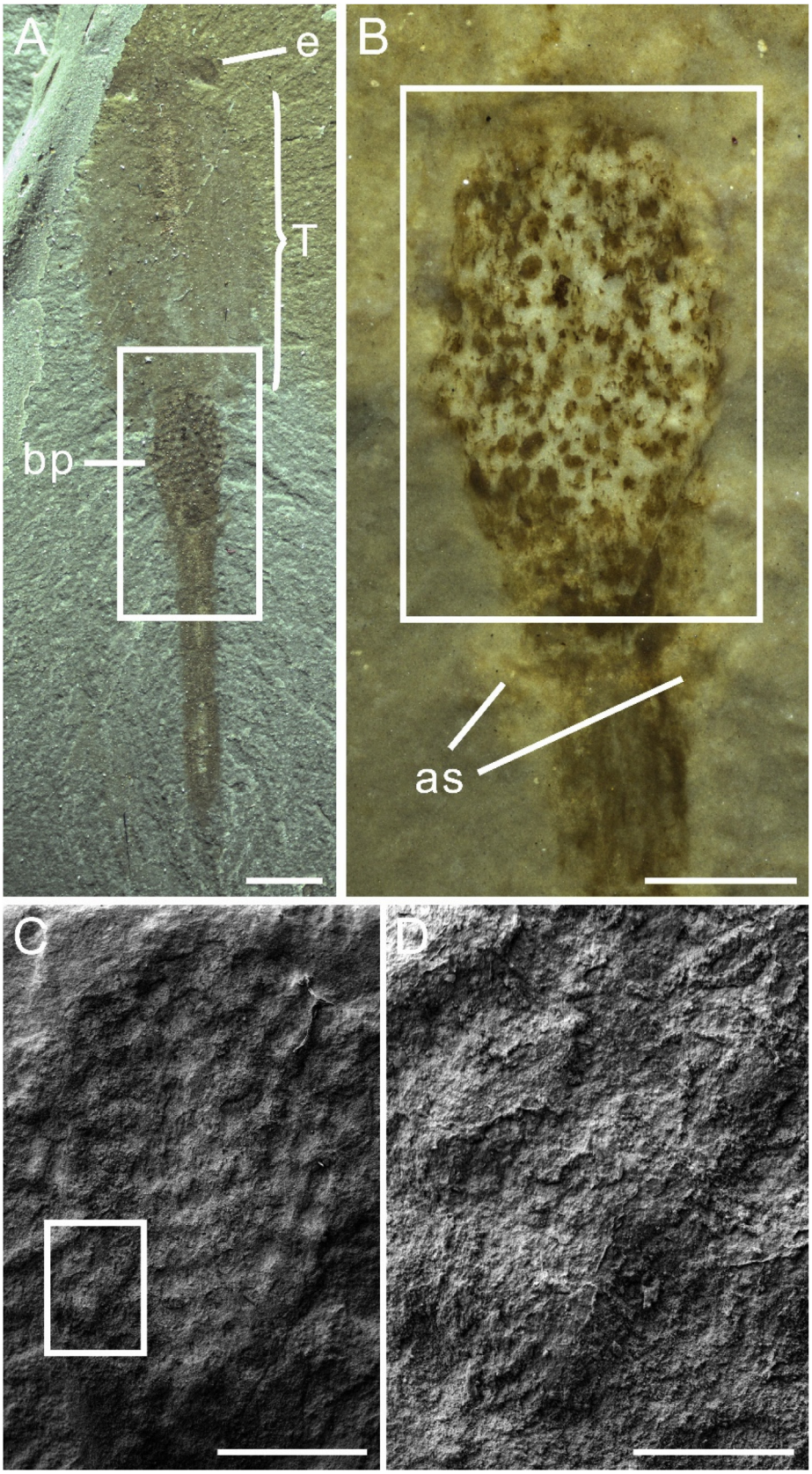

Fig. 3. NIGP171735 a (the counterpart to NIGP171735 b), *Daohugounaias cheni* gen. et sp. nov. A, body (dry); B, brood pouch (in alcohol), higher magnification of area shown by white square in A; C, brood pouch (dry), SEM magnification of area shown by white square in B, showing three-dimensionally preserved resting eggs; D, eggs (dry), SEM magnification of area shown by white square in C, with some ridges or spines on their surface; scale bars represent 2 mm in A, 1 mm in B and C, and 200 μm in D. Abbreviation: as, abdominal spines; bp, brood pouch; e, eye; T, thoracopods.

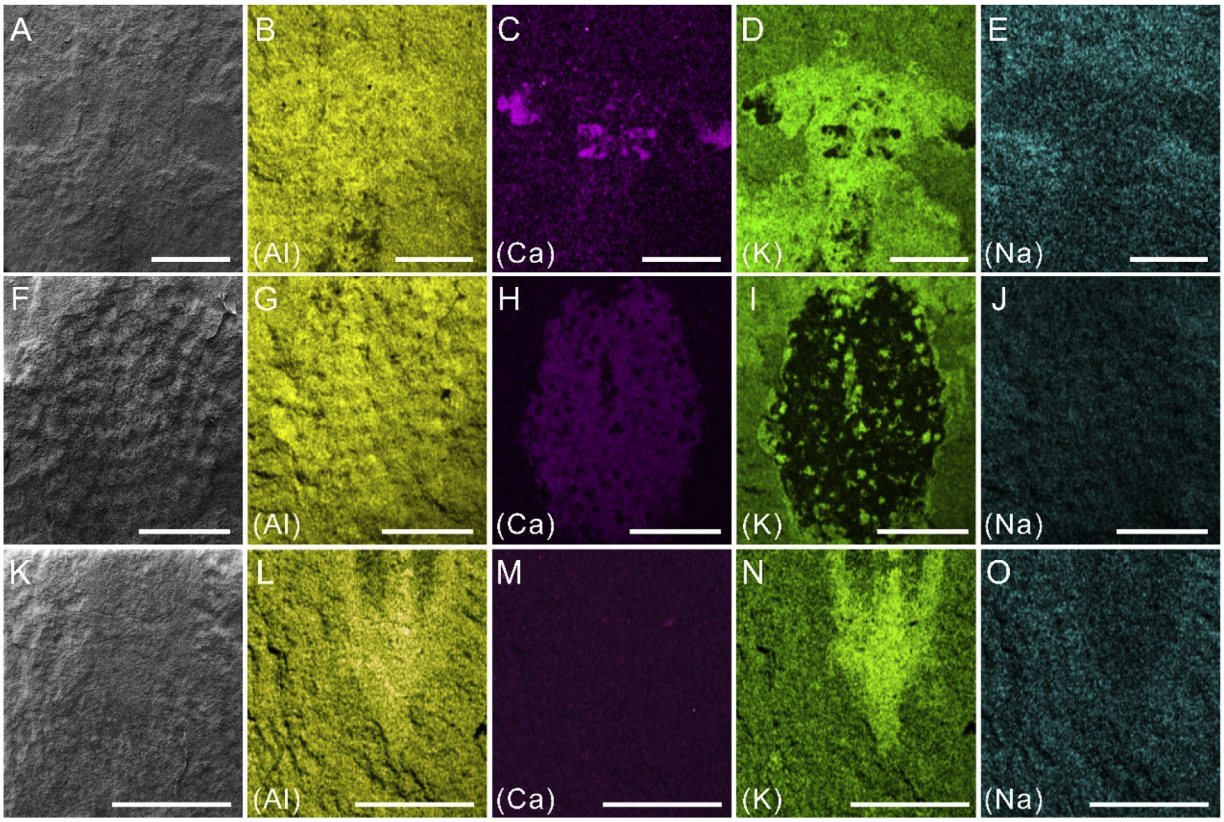

Fig. 4. NIGP171735 a (the counterpart to NIGP171735 b), *Daohugounaias cheni* gen. et sp. nov. A, SEM image of head; B–E, EDS image, Al, Ca, K and Na elemental maps of A; F, SEM image of brood pouch; G–J, EDS image, Al, Ca, K and Na elemental maps of F; K, SEM image of telson; L–O, EDS image, Al, Ca, K and Na elemental maps of K. Scale bars represent 1 mm in.A–O.

ephemeral pools, all devoid of fish (Lindholm, 2014; Yang et al., 2019). Moreover, the delicate nature of Anostraca suggests that burial was extremely rapid or that the environment was not suitable for such scavengers, consistent with previous research (Wang et al., 2019; Yang et al., 2019).

5. Conclusion

A new extinct genus and species of Anostraca, *Daohugounaias cheni* gen. et sp. nov. is described from the Middle Jurassic Daohugou deposits. The new genus differs from other Anostraca by the short, forward-pointing spines at the joint of the abdomen and brood pouch. The eggs' three-dimensional preservation indicates that they were decayresistant. The occurrence of Anostraca supports the previous palaeoenvironmental reconstruction and enhances the ecological diversity of the Daohugou area.

Declaration of Competing Interest

Here, we declare no competing interests.

Acknowledgements

This research was supported by the Strategic Priority Research Program (B) of the Chinese Academy of Sciences (XDB26000000 and XDA19050101), the National Natural Science Foundation of China (41572010, 41622201,41688103), and the State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) (No. 183101). This is a Leverhulme Emeritus Fellowship contribution for EAJ.

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