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The earliest known brood care in insects

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Brood care enhances offspring fitness and survival by providing protection or feeding through parents (commonly by females). It has evolved independently multiple times in animals, e.g. mammals, birds, dinosaurs and arthropods, especially various lineages of insects, and has significant implications for understanding the emergence of sociality of insects. However, few fossil insects document such an ephemeral behaviour directly. New exceptional fossils of the water boatman *Karataviella popovi* from the Middle–Late Jurassic Daohugou biota (*ca* 163.5 Ma, northeastern China), with adult females bearing clutches of eggs on their left mesotibia, provide a unique brooding strategy (asymmetric egg-carrying behaviour) unknown in all extinct and extant insects. Our discovery represents the earliest direct evidence of brood care among insects, pushing back by more than 38 million years, indicating that relevant adaptations associated with maternal investment of insects can be traced back to at least the Middle–Late Jurassic, and highlighting the existence of diverse brooding strategies in Mesozoic insects. In addition, our discovery reveals that a specialized trawl-like filter-capture apparatus of *K. popovi* probably represents preadaptations originally used for trapping coeval anostracan (fairy shrimp) eggs for food.

1. Introduction

Parental care is considered a significant behavioural adaptation in life-history traits in a wide range of animals [1–3]. The forms of parental care are strikingly diverse in nature, ranging from minimal and uniparental care (e.g. oviposition-site selection, nest building and burrowing, egg attendance, egg guarding and egg brooding) [4–6], to provision of elaborate and long-term care, which is widespread in virtually all birds and mammals [2]. Brood care, a form of uniparental care where parents carry eggs or juveniles after oviposition, enhancing offspring fitness and survival by providing protection against egg predators, parasitoids and pathogens, desiccation, and hypoxia, has been observed in many arthropod groups [1,2]. Brood care is an ancient behavioural strategy that has evolved independently several times in marine arthropods, as evidence by bradoriid and waptiid pancrustaceans from the early Cambrian Chengjiang biota of China (*ca* 515 Ma) [7,8] and the middle Cambrian Burgess Shale of Canada (*ca* 508 Ma) [9], and myodocope ostracods from the Late Ordovician of USA (*ca* 450 Ma), and the Silurian of UK (*ca* 425 Ma) [10,11]. Juveniles attached to the tergites of the adult of *Aquilonifer spinosus* from the Herefordshire Lagerstätte, UK, by means of long threads indicate that intricate brood care was considerably diverse in stem-mandibulates by the mid-Silurian (*ca* 430 Ma) [12]. Fossil evidence of brood care in terrestrial arthropods has also been reported mainly in amber inclusions, including, crustaceans (Peracarida) from the Early Cretaceous amber of Spain and France and the Miocene amber of Mexico [13,14], arachnids from mid-Cretaceous amber of Myanmar [15,16], and insects from the Lower Cretaceous Yixian Formation of China and mid-Cretaceous amber of Myanmar [17,18]. Among Mesozoic insects, the only two direct fossil evidence cases of brooding ethology are provided by the Early Cretaceous cockroach *Piniblattella yixianensis* with its

oothecae enclosing eggs for protection and brood care [17]; and the mid-Cretaceous scale insect *Wathondara kotejai*, which preserves eggs within a wax ovisac attached to the body of an adult female [18]. Furthermore, parental care has been hypothesized in the Cretaceous subsocial insects, including thrips [19] and burying beetles [20] based on the presumed morphological adaptations.

The true water bug superfamily Corixoidea (Hemiptera, Heteroptera), commonly known as the water boatman, is the most diverse lineage within the infraorder Nepomorpha with more than 600 extant species in 35 genera [21,22]. Water boatmen occur in various freshwater ecosystems worldwide, including brackish and acidified waters [21,22] and may represent a majority share of aquatic insect biomass in some habitats. The Jurassic water boatman *Karataviella popovi* Zhang, 2010, one of the most abundant aquatic insects in Middle–Late Jurassic Daohugou biota of northeastern China, was originally described based on three specimens: an adult of uncertain gender, a nymph and a hemelytron [23]. In the present paper, we report a peculiar brooding behaviour in *K. popovi* and elaborate on the morphological details of both sexes based on abundant well-preserved specimens from Daohugou.

2. Material and methods

(a) Studied material

The studied material includes a total of 157 specimens (58 males, 96 females and three nymphs) of *K. popovi*, with 30 egg-carrying females. For comparison, we also studied some specimens of another water boatman species *Yanliaocorixa chinensis* (figures in the electronic supplementary material, S22), and anostracan (fairy shrimps) (figures in the electronic supplementary material, S23) for food source analysis, chosen from the thousands of these specimens in the same bedding plane in our collection. All fossils were collected from the Haifanggou Formation at the Xiayingzi quarry (detailed fossil layer figure 4a, red arrow) below the conchostracan *Triglypta haifanggouensis* layers of the Daohugou beds. This fossil layer represents the highest biodiversity of the Daohugou beds, which has yielded many vertebrate fossils (e.g. feathered dinosaurs, pterosaurs, ancient mammals and abundant salamanders), and well-known insects such as giant fleas, *Strashila*, long-proboscid scorpionflies and carrion beetles [24–26]. Water boatman *Y. chinensis*, conchostracan *T. haifanggouensis*, and salamander *Chunerpeton tianyiensis* are representative organisms in the Daohugou biota [24]. As the appearance of *T. haifanggouensis* indicates the beginning of the Late Jurassic [27], the geological age of the studied fossil layer is close to the boundary of the Middle–Late Jurassic (163.5 Ma).

(b) Analytical methods

All specimens examined in this study are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, China. Some specimens were carefully prepared using a sharp knife. Specimens were observed under an OLYMPUS SZX 7 stereomicroscope. Photomicrographs were taken with a digital camera attached to a Zeiss Discovery V16 microscope, and some were moistened with 70% ethanol to show fine details. We used fluorescence microscopy and scanning electron microscopy to obtain images with higher resolutions and sharp external boundaries of the surface structures of the eggs and detailed features of *K. popovi*. Fluorescence image (electronic supplementary material, figure S18b) with

green background was acquired using a Zeiss Axio Imager 2 compound microscope. Backscattered electron images were obtained with TESCAN MAIA 3 GMU FESEM with the accelerating voltage set at 20.0 kV. The EDS elemental maps were done with OXFORD ULTIM MAX 170 EDS (produced by the Oxford Instruments Company) with an accelerating voltage of 20.0 kV and a working distance of 9 mm with approximately 12 000 counts/s and approximately 30% dead time. Brighter areas represent a greater number of elements. The SEM and EDS analyses were performed in NIGPAS. Focus stacking software (Helicon Focus 7.0.2) was used to increase the depth of field. Morphological measurements in the electronic supplementary material, table S1 were conducted using ImageJ software.

3. Results

The Jurassic water boatman *K. popovi* bears a relatively large body, with its body length ranging from 10.9–14.7 mm. The head is armed with two symmetrical, closed foveate depressions between the compound eyes, with their marginal ridges each bearing a row of setae (figure 1g and figure 3b), and the front of face equipped with three patches of elongated elliptically distributed setae (figure 3a). The pronotum is well developed, with a longitudinal and straight median ridge. The scutellum is broad. The foreleg has stout femur and fused tibiotarsus in both sexes (electronic supplementary material, figure S7h); the peculiar protarsi (=pala) possess three longitudinal rows of specialized densely packed palmar setae on the inner side of palm; the mesotibia is greatly elongated, and the left mesotibia thicker in egg-carrying females (figure 2d; electronic supplementary material, figures S13f and S17c); the mesotarsal claw is long, slightly longer than the tarsomere II (figure 1f); the metatarsus is large, oar-like, covered with long hairs (figure 1h). The hemelytron has a rounded apical margin and reduced venation (electronic supplementary material, figure S1h). The abdominal segments IV–VII are symmetrical in both sexes.

Extant water boatmen commonly deposit eggs on various subaquatic substances such as leaves or stems of aquatic vegetation (figure 2i), stones, woody debris, snail shells and even on the exoskeletons of crayfish and carapaces of terrapins [29,30]. The eggs of water boatmen are variable in types of attachment to the substrate and most are, however, supported by short stalks, which are parts of the eggs. The stalks are very long and exceeding the lengths of the eggs in some genera (e.g. *Cymatia*, *Agraptocorixa*, *Heterocorixa* and *Tenagobia*), resembling the stalked eggs of green lacewings, while egg stalks are completely absent in the extant genera *Diaprepocoris* and *Micronecta* [31–33]. Generally, water boatmen females deposit a layer of a waterproof gelatinous substance on underwater substrates before depositing the eggs anchored in the plaque of glue by the expanded base of their stalks [31,33].

Of the 157 examined *K. popovi* fossils, 30 adult females were preserved with a cluster of eggs anchored, without exception, on their left mesotibia (figures 1a,d and 2a,c; electronic supplementary material, figures S15 and S16) by short egg stalks (e.g. figure 2b,e,h,j). The egg clusters are compact, overlapping and arranged in approximately 5–6 staggered rows throughout the left mesotibia, which is reminiscent of eggs laid by extant corixids on aquatic plants (figure 2i). As inferred from the arrangement of the eggs, each row seems to have 6–7 eggs. The number of eggs may
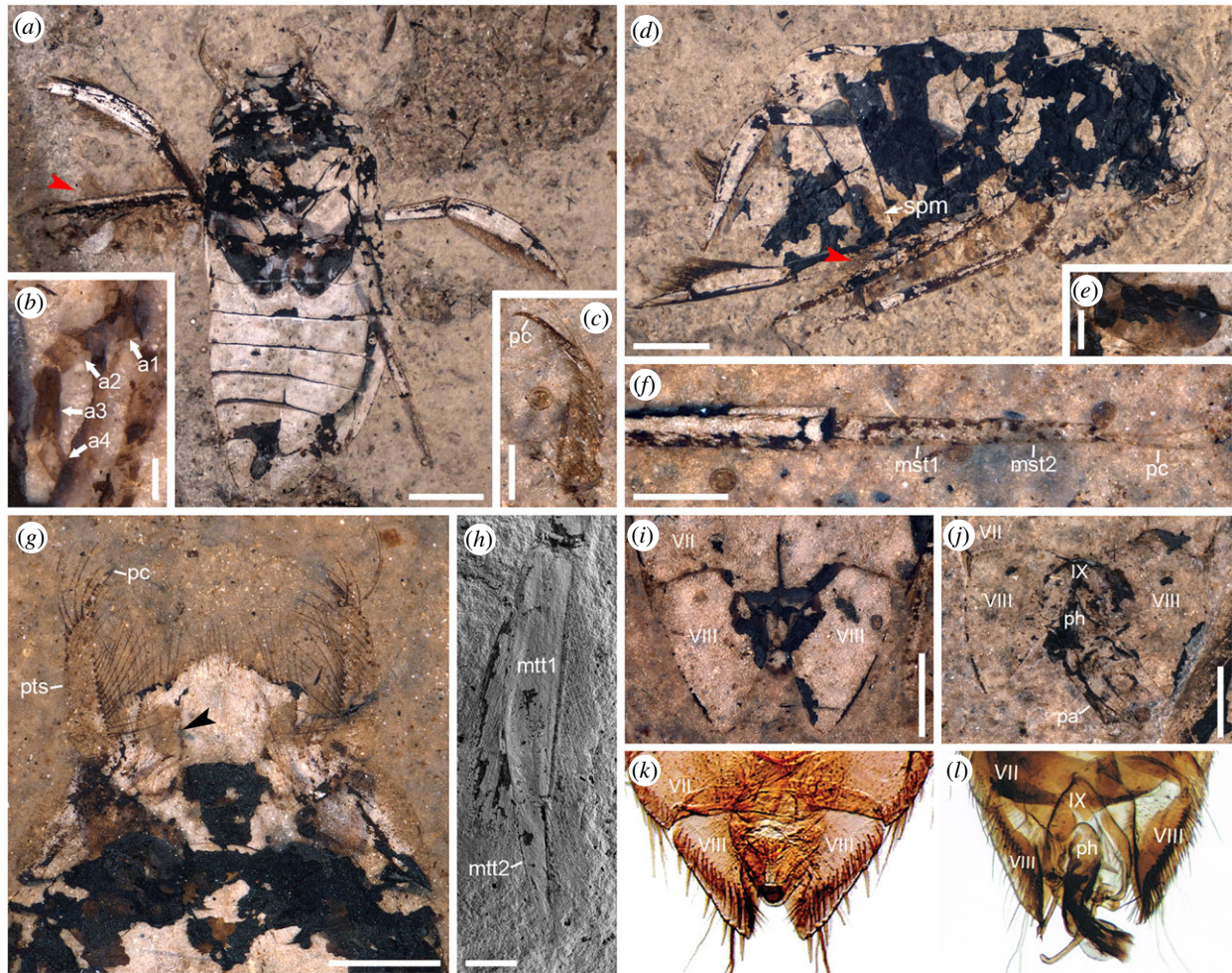
Figure 1. *Karataviella popovi* from the Jurassic Daohugou biota and the genitalia structures of extant *Micronecta* sp. (*a*) General habitus of egg-carrying specimen (NIGP177383), inner view of ventral aspect. (*b*) Antenna (NIGP177450). (*c*) Protarsus (NIGP177386). (*d*) General habitus (NIGP177385). (*e*) Spermathecal (NIGP177385). (*f*) Middle leg (NIGP177387). (*g*) Head structures and forelegs (NIGP177384), black arrow indicates oval foveate depressions with setae. (*h*) SEM image of metatarsus (NIGP177384). (*i–l*) Comparison of abdomen and genitalia structures between *K. popovi* and extant *Micronecta* sp. [28]. (*i*) Female genitalia structures (NIGP177387). (*j*) Male genitalia structures (NIGP177421). (*k*) Female genitalia structures of *Micronecta* sp. (*l*) Male genitalia structures of *Micronecta* sp. Arrows indicate the cluster of eggs on left mesotibia in (*a,d*). Moistened with 70% ethanol in (*a–g,i,j*). Abbreviations: a1–a4, antennomeres I–IV; spm, spermatheca; pts, protarsus; pc, pretarsal claw; mst1–2, mesotarsomeres I–II; mtt1–2, metatarsomeres I–II; ph, phallus; pa, paramere. Scale bars: 2 mm in (*a,d*), 1 mm in (*f,g,j*), 500 μm in (*c,e,h*), 200 μm in (*b*). (Online version in colour.)

be underestimated due to variations in the angle of burial and distortion. Eggs are approximately of the same size, suggesting that each cluster corresponds to a single clutch oviposited within a short time span.

Since water boatmen eggs cannot adhere to new surfaces after being detached from their original place of deposition [34], this suggests that the females first secreted mucous substance and then laid eggs onto their own left mesotibia by specific bending movements of the abdomen, and then carried the brood until hatching. The unoccupied right mesotibia might have been used to maintain balance when swimming and feeding. *Karataviella* possesses unusual modifications of the mesotibia that enable egg-carrying. The mesotibia is elongated, with a length of 4.2–4.5 mm, representing on average about 35% of the insect's total body length, so it is long enough to be extended backwards and reach the tip of the abdomen. It is noteworthy that the left mesotibia of egg-carrying female appears thicker than the non-egg-carrying (right) mesotibia by statistical comparison (figure 2*d*; electronic supplementary material, figures S13f and 17c,d), which represents an important morphological adaptation for the egg-carrying behaviour. By contrast, non-

egg-carrying females and males have slender mesotibiae with the left and right mesotibiae of the same thickness. Besides, the egg-carrying mesotibia becomes gradually tapered apically, while the non-egg-carrying mesotibia is almost evenly thick throughout (e.g. electronic supplementary material, figure S13f). The egg-carrying mesotibia is preserved as a dark structure with a coarse outline (figure 2*e,h,j*; electronic supplementary material, figures S13f, 17c,f,g and 18b,c,h,i,j), while the non-egg-carrying mesotibia appears smooth. The rough outline of the left mesotibia is possibly caused by the remnants of egg stalks attached to the leg by a gelatinous coating.

4. Discussion

Parental care has evolved independently multiple times in diverse heteropteran lineages, and its origin and evolution is of a great significance for understanding emergence of sub-sociality in insects. Heteroptera (true bugs) care for their eggs or offspring is pervasive and with a broad range of strategies [3,35,36].
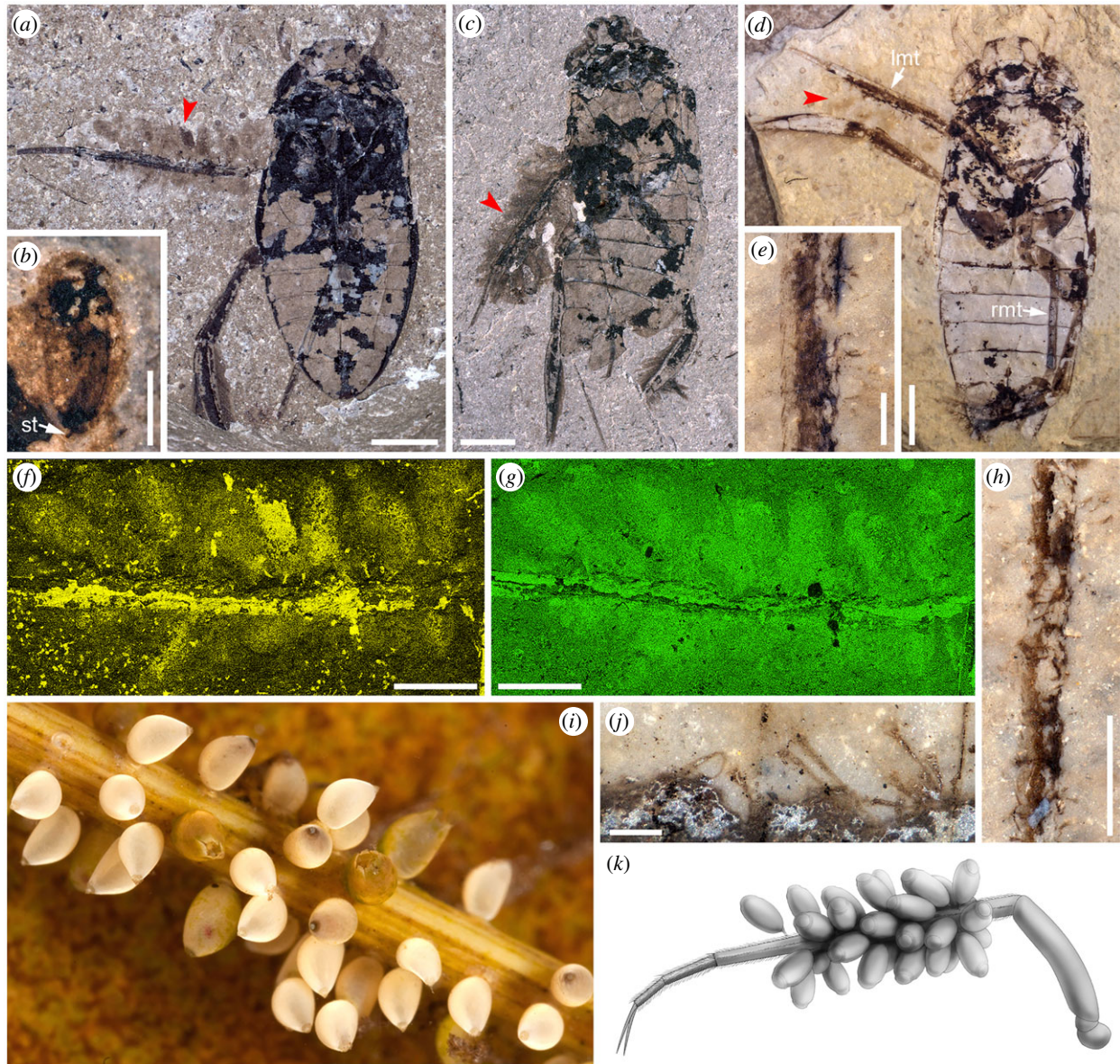
Figure 2. Brooding in *Karataviella popovi*. (*a*) General habitus of egg-carrying specimen (NIGP177390). (*b*) Details of egg (NIGP177447). (*c*) General habitus of egg-carrying specimen (NIGP177445). (*d*) General habitus of egg-carrying specimen (NIGP177391). (*e*) Egg stalks (NIGP177391). (*f*) EDS image (C elemental mapping) of the left mesotibia with eggs. (*g*) EDS image (K elemental mapping) of the left mesotibia with eggs. (*h*) Left mesotibia with egg stalks (NIGP177392). (*i*) The extant corixid eggs on stem of aquatic plant. (*j*) Detail of egg stalks (NIGP177393). (*k*) Reconstruction of left mesotibia with eggs. Inner view of ventral aspect in (*a,c,d*), red arrows indicate the cluster of eggs on left mesotibia. Moistened with 70% ethanol in (*b,d,e,h,j*). Abbreviations: st, stalk; lmt, left middle tibia; rmt, right middle tibia. Scale bars: 2 mm in (*a,c,d*); 1 mm in (*f–h*), 500 μm in (*b,e*), 200 μm in (*j*). (Online version in colour.)

The emergence of different reproductive strategies may be related to internal genetic variability, which results in phenotypic differences in body size [37]. The diameters of *K. popovi* egg (without stalk) range from 1.14 to 1.20 mm (larger than most extant water boatmen), representing on average about 10% of body lengths, one of the highest ratios when compared with those of extant water boatmen [31,38]. A positive correlation exists between the diameters of eggs and body length of adult females in insects because of heritable variation [39], which explains the sizable eggs of *K. popovi*. Large eggs often provide more nutrient reserves for offspring, which is conducive to juvenile survival in harsh environments [39]. However, the cost of laying large eggs is a longer hatching period, and more importantly, surface/volume ratio of large egg is low, which adversely impacts gas exchange between water and eggs, making it more difficult for eggs to obtain adequate oxygen [40,41]. Because water and oxygen are crucial and mutually restrictive

environmental factors for the embryonic development of aquatic arthropods, some aquatic arthropods evolved extraordinary behavioural adaptations for aerating and hydrating eggs might be related to their large eggs that must rely on passive diffusion of oxygen [2,35]. For example, the basal giant water bugs in the lethocerines (emergent-brooders) periodically supply water to the egg mass on the sites of oviposition (commonly emergent aquatic vegetation) [35,41–43]; and belostomatines (back-brooders) even evolved brooding behaviour wherein males carry a clutch of eggs laid by the females on their backs until hatching to prevent them from desiccation and drowning [41,43,44]. The same principle is reflected in some extant water boatman species that lay eggs upon the exoskeletons of freshwater crayfish, especially the gills and first abdominal pleurite where there are the best chances for aeration, relying on the current of flowing water [29,45]. *Karataviella* adopted a strikingly similar brooding (egg-carrying) strategy to most marine and freshwater
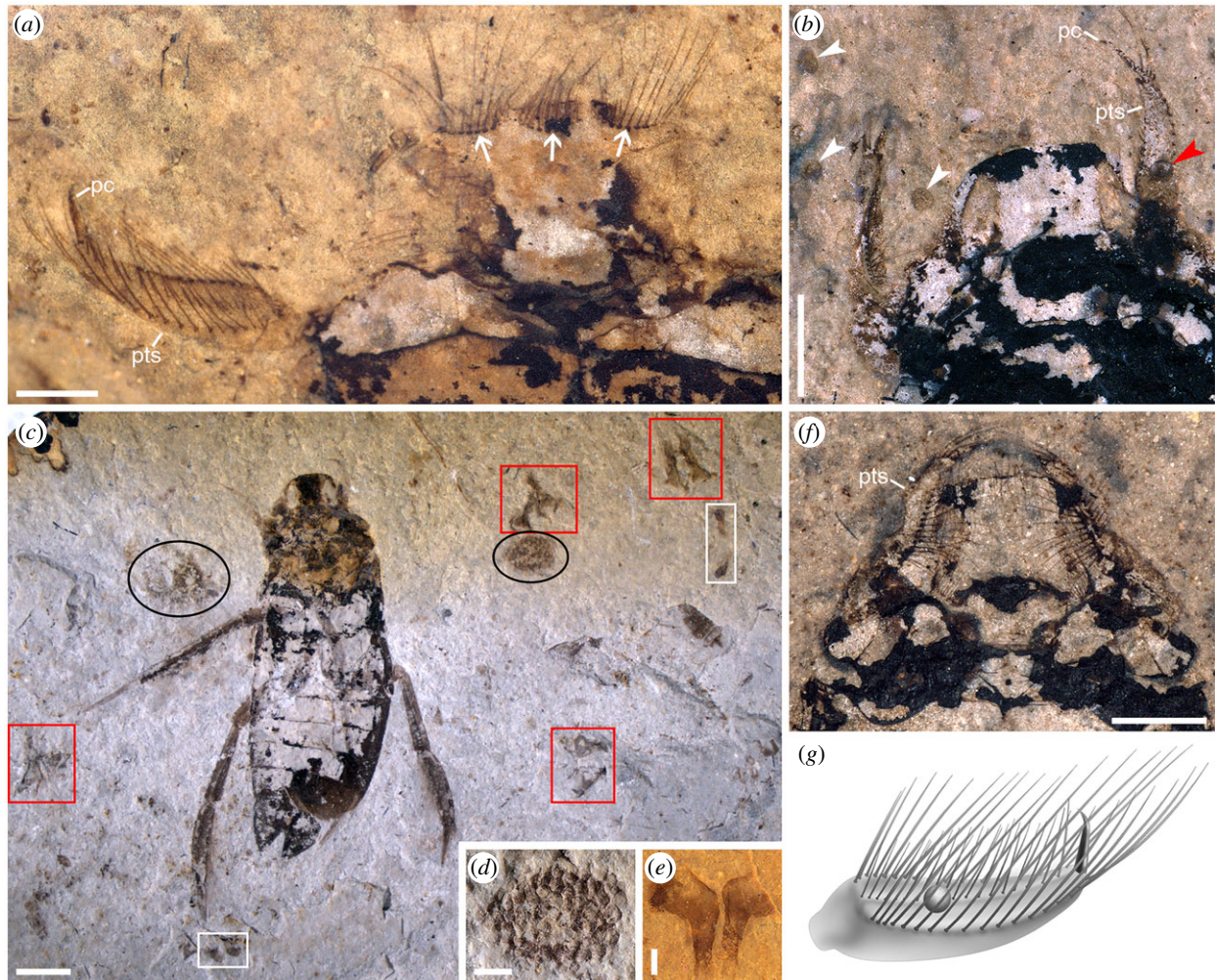
Figure 3. The specialized filter-capture apparatus in *Karataviella popovi* and associated anostracan eggs. (*a*) Head structures and protarsus (NIGP177394), arrows indicate three tufts of setae. (*b*) Head structures and forelegs (NIGP177395), arrows indicate anostracan eggs. (*c*) General habitus (NIGP177484), boxes indicate the second pair of male anostracan antennae and anostracan eyes, and circles indicate anostracan oocyst. (*d*) Anostracan oocyst (NIGP177484). (*e*) Male second pair antennae. (*f*) Head structures and forelegs (NIGP177432). (*g*) Reconstruction of protarsus with a trapped anostracan egg. Moistened with 70% ethanol in (*a,b,e,f*). Abbreviations: pts, protarsus; pc, pretarsal claw. Scale bars: 2 mm in (*c*), 1 mm in (*b,f*), 500 μm in others. (Online version in colour.)

shrimps, lobsters and kin (Pleocyemata), where the females attach eggs to their pleopods using a sticky substance, allowing them to actively and intermittently adjust the position of the eggs in water or air, together with the movement during swimming that generates currents, to ensure ventilation and moistening of the eggs [46]. Moreover, in *K. popovi* and some pleocyematans, a firm but elastic egg stalk is present and may contribute to the aeration of the eggs by facilitating regular shaking motion [33,45,46]. Therefore, we speculate that the particular brooding behaviour of *K. popovi* effectively addresses the problems that large eggs experience relating to hypoxia, drowning and desiccation, resulting in enhanced offspring survival.

As an important part in the food chain of freshwater ecosystem, extant water boatmen are preyed upon by salamanders, fishes and some aquatic insects [47]. The salamander *Chunerpeton tianyiensis* is the most common vertebrate in Daohugou [48], and it appeared in abundance in the same bedding plane with *K. popovi*. Another water boatman species *Y. chinensis* (*ca* 5–6 mm in length) was found in the stomachs of juvenile *C. tianyiensis* in Daohugou [49], proving their predator–prey relationships. The adult *C. tianyiensis* were more likely to prey on the larger adult *K. popovi* (*ca* 11–15 mm in length). Therefore, we speculate

that the *K. popovi* likely faced high predation pressure in the Daohugou palaeolake.

The specialized protarsi of *K. popovi*, combined with the five patches of setae on the head forming a trawl-like structure, seem to be a delicate filtering apparatus for trapping food out of the passing water. By statistical analysis, the variation of spacing between two adjacent rows of setae on the protarsus ranges from 99 to 260 μm, mainly in the 140–250 μm range due to the tarsus becoming narrow from middle to terminal, corresponding in size to the isolated anostracan eggs [50,51]. The diameters of anostracan eggs in brood pouches (oocyst) and isolated eggs range from 137 to 251 μm and 120 to 240 μm, respectively, after analysis of 731 eggs herein (figure 4*b*; electronic supplementary material, table S1). Thus, the isolated anostracan eggs could be trapped between two adjacent rows of long setae on the protarsi of *K. popovi* as evidenced by figure 3*b*. Moreover, the spacing of adjacent setae on the protarsus and head is always less than the diameters of the smallest anostracan eggs (*ca* 103 μm), ensuring that all eggs could be trapped efficiently. Besides, the anostracan and the water boatman *K. popovi* represent the precursors and dominators in the same layer of the Daohugou beds, and they show high consistency with their emergence, radiation, prosperity, decline and
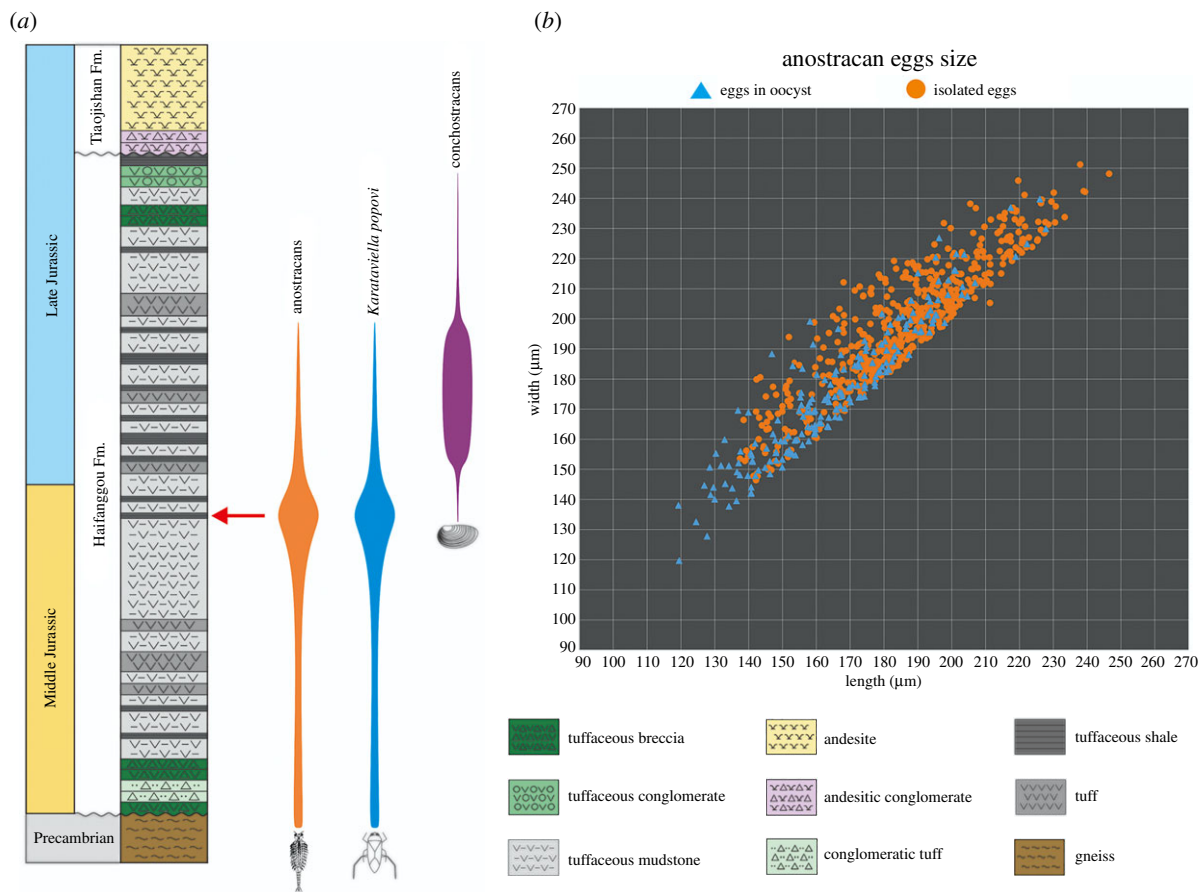
Figure 4. (*a*) The stratigraphic duration and abundance trend of *Karataviella popovi* and anostracans in the Daohugou beds. (*b*) Scatterplots showing the size distribution of anostracan eggs. (Online version in colour.)

Figure 5. Ecological reconstruction of *Karataviella popovi* and anostracans in the Middle–Late Jurassic Daohugou biota. (Online version in colour.)

extinction (figure 4*a*). The conchostracans appeared in the upper layers and reached prosperity in the Daohugou limnic ecosystem probably as ecological competitors for anostracans, while the population of anostracans along with *K. popovi* began to decline significantly. Therefore, we hypothesize that the seasonally produced anostracan eggs in the

Daohugou biota are the potential and optimal food of *K. popovi* (figure 5).

Due to the potential high predation risk and seasonal (ephemeral) food resources, *K. popovi* may have been exposed to fierce ecological pressure in the Daohugou biota. The brooding behaviour developed in *K. popovi* probably reflected

adaptations to habitat or an evolutionary response to ecosystem changes through the Middle–Late Jurassic.

5. Conclusion

Compared to eggs laid on any underwater substances by other water boatmen, *K. popovi* most likely provided effective protection for eggs and helped newly hatched nymphs to enter the water smoothly, largely avoiding the risks of predation, desiccation and hypoxia, which had important effects for its evolution, development and reproductive success. However, the specific factors that have driven the particular brooding behaviour of *K. popovi* remain elusive. This selfless behaviour of *K. popovi* incurred high ecological costs in terms of reduced mobility and increased conspicuousness of egg-carrying individuals, which causes an increased risk of predation.

A recent molecular analysis recovered the superfamily Corixoidea as the basal most clade of Nepomorpha and dated the divergence to the Middle Triassic [52]. Our discovery of egg-carrying behaviour in the Jurassic water boatman *K. popovi* represents the earliest fossil evidence of brood care in Heteroptera, and more widely in insects. To our knowledge, carrying a cluster of eggs on a leg is a unique strategy among insects, but is not unusual in aquatic arthropods, in which this carrying behaviour even can be traced back to the early Cambrian bradoriid arthropod from the Chengjiang biota [7]. The water boatman *K. popovi* could be viewed as a plesiomorphic relic but exceptional advancement in the evolution of brood care, showing peculiar life-history adaptations in the Jurassic aquatic insects. Our finding pushes back the evidence of definitive brooding behaviour in insects by almost 38 million years, which are helpful for understanding the evolution and adaptive significance of brood care in insects.

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