

High-resolution taphonomic and palaeoecological analyses of the Jurassic Yanliao Biota of the Daohugou area, northeastern China

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ARTICLE INFO

Keywords:

Quantitative analysis
Biostratigraphy
Palaeoenvironment
Mass mortality
Volcanism

ABSTRACT

The Yanliao Biota contains numerous exceptionally preserved fossils of evolutionary importance. However, the palaeoenvironment of this biota has not been fully studied. Here we present the first taphonomic and palaeoecological analysis of fossil abundance data from two newly excavated sites in the Daohugou area. In our study we have investigated the taxonomic composition, specimen abundance and size distribution patterns of invertebrate palaeocommunities, and corresponding taphonomic features, such as completeness, articulation and fossil orientation. Our results show that abundant aquatic and terrestrial organisms from various ecological niches are preserved in very thinly planar-laminated mudstone. Aquatic organisms of the two excavations are represented by low-diversity but high-density assemblages containing four species: the clam shrimp *Triglypta haifanggouensis*, the mayfly nymphs *Fuyous gregarius* and *Shantous lacustris*, and the water boatman *Daohugocorixa vulcanica*. *Triglypta haifanggouensis* dominates the fauna with carapace lengths ranging from 1.34 mm to 5.62 mm. Size distributions of different bedding planes vary between normal, bimodal and polymodal, implying multiple causes of death: reproductive senescence, and mass mortality events related to active volcanism or to rapid environmental fluctuations within the lake. Generally calm depositional conditions were repeatedly interrupted by weak currents, indicated by preferred plan-view orientations of aquatic insects on four out of nine investigated bedding planes. Changes in the community composition of aquatic arthropods relate to varying lake depth through time, or to different dispersal strategies after community breakdown. Terrestrial insects are highly diverse but less abundant. As a result of rapid burial, 49.8% of which are almost complete and articulated. The flora surrounding the comparatively shallow lake was rich, picturing a thriving forest-like ecosystem with moisture relation in a warm-temperate climate.

1. Introduction

Numerous exceptionally preserved fossils, such as Spinicaudata (one of the three groups that were formerly combined into the paraphyletic taxon ‘Conchostraca’; Olesen, 2009; Olesen and Richter, 2013), bivalves, insects, spiders, salamanders, dinosaurs, pterosaurs, mammaliaformes, bennettites, ginkgophytes and conifers, have been reported from the Middle to Late Jurassic Yanliao Biota (synonymous with “Daohugou Biota”) in western Liaoning, southeastern Inner Mongolia and northern Hebei, NE China (Fig. 1) (Huang et al., 2006; Sullivan et al., 2014; Na et al., 2015; Huang, 2016; Xu et al., 2016). Many of these fossils have added, significantly, to our understanding of the evolution of birds, mammals, and of Mesozoic continental ecosystems.

Some of the most renowned fossils discovered in the Daohugou area include the haired pterosaur *Jeholopterus ningchengensis* (Wang et al., 2002), the earliest filter-feeding pterosaur *Liaodactylus primus* (Zhou et al., 2017), the feathered dinosaurs *Pedopenna daohugouensis* (Xu and Zhang, 2005), *Epidexipteryx hui* (Zhang et al., 2008) and *Epidendrosaurus ningchengensis* (Zhang et al., 2002), the swimming mammaliaform *Castorocauda lutrasimilis* (Ji et al., 2006), the gliding mammal *Volaticotherium antiquus* (Meng et al., 2006) and mammaliaform *Megaconus mammaliaformis* (Zhou et al., 2013), the early pollinating scorpionfly *Lichnomesopsyche gloriae* (Ren et al., 2009; Ren et al., 2010), the amphibious fly *Strashila daohugouensis* (Huang et al., 2013b), and the ectoparasitic insect *Hadropsylla sinica* (Huang et al., 2013a).

In contrast to great advancements in studies on the palaeontology

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<https://doi.org/10.1016/j.palaeo.2019.05.028>

Received 14 December 2018; Received in revised form 7 May 2019; Accepted 16 May 2019

Available online 20 May 2019

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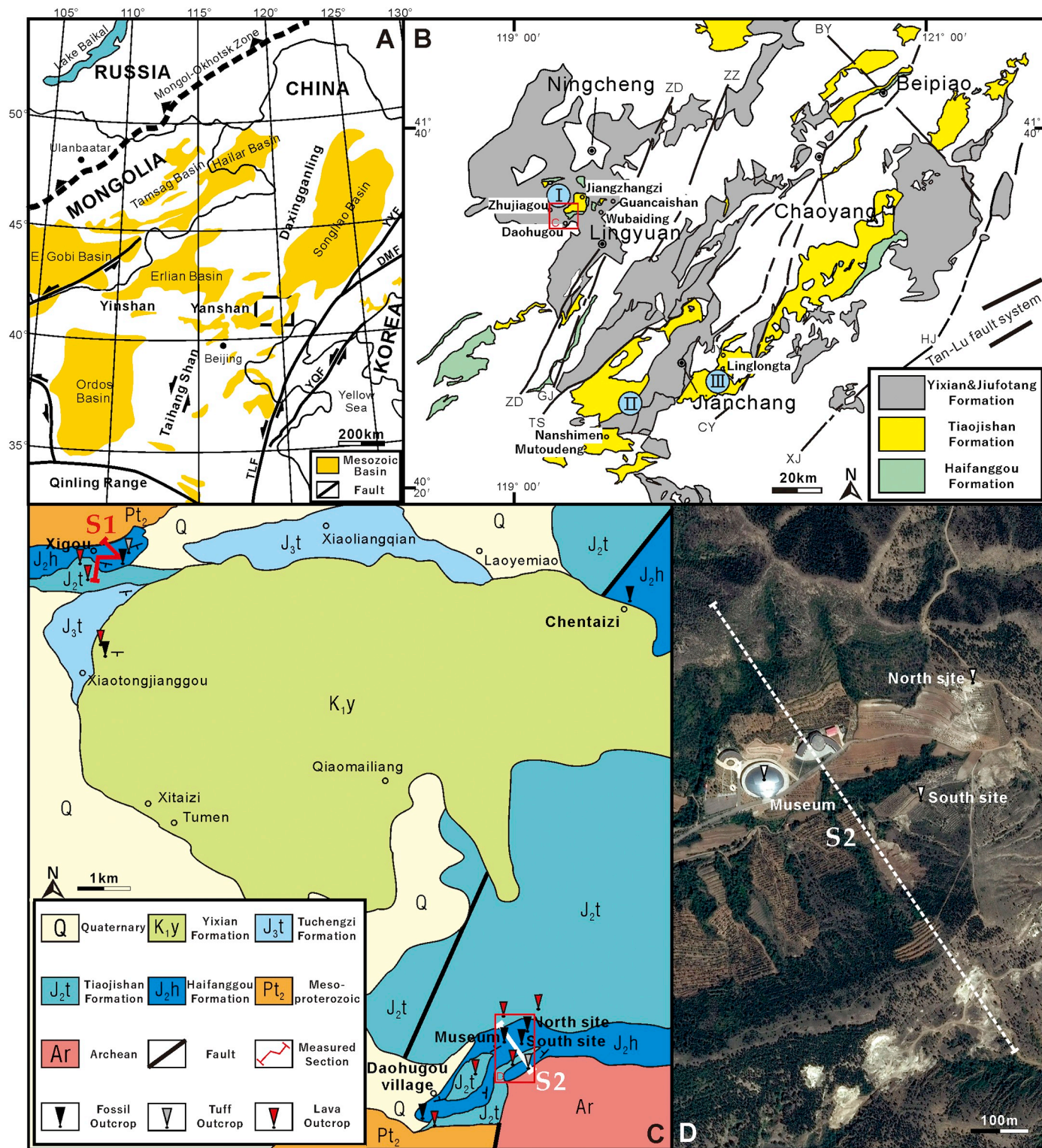


Fig. 1. Geological and geographic setting of the studied area (modified from Yang et al., 2019). A. Tectonic framework and distribution of the Mesozoic basins in the Yinshan–Yanshan tectonic belt (modified from Meng, 2003, and Y. Zhang et al., 2008); DMF, Dunhua–Mishan Fault; TLF, Tan–Lu Fault; YQF, Yalvjiang–Qingdao Fault; YTF, Yilan–Yitong Fault. B. Distribution of the Haifanggou, Tiaojishan, and Yixian/Jiufotang formations in a series of northeast-oriented basins (modified from Jiang and Sha, 2006); I, Lingyuan–Sanshijiazhi Basin; II, Jianchang Basin; III, Jinlingsi–Yangshan Basin; BY, Beipiao–Yixian Fault; CY, Chaoyang–Yaowangmiao Fault; GJ, Western Guojiadian Basin Fault; HJ, Hartao–Jinzhou Fault; TS, Western Tangshenmiao Basin Fault; XJ, Xipingpo–Jinxi Fault; ZD, Zhangjiayingzi–Daoerdeng Fault; ZZ, Zhuluke–Zhongsanjia Fault. C–D. Geological sketch map (C) and Google Earth satellite image (D) showing the studied outcrops and sections (modified from Liu et al., 2004).

and evolutionary biology of vertebrates and insects, there have been few studies on palaeoecological communities and the taphonomy of the major fossil sites (Tan and Ren, 2002; Wang et al., 2008; Wang et al., 2013). Many of the reported fossils have been discovered by local farmers, so exact stratigraphic positions of respective fossil slabs cannot always be reconstructed. Hence, data concerning diversity, size frequency, fossil abundance and biostratigraphy, including fossil completeness, articulation and plan-view orientation, have been unavailable so far.

To understand the taphonomic processes underlining the remarkable fossil preservation of the Middle to Late Jurassic Yanliao Biota – in particular causes of mass mortalities, transportation and burial of organismal remains – we collected key quantitative data from two high-resolution excavations at the Daohugou locality (Fig. 1), where the biota was first discovered and the geological setting is best studied

(Huang et al., 2006; Sullivan et al., 2014; Xu et al., 2016; Yang et al., 2019). Compared to other important fossil localities of the Yanliao Biota, such as the Jianchang and Qinglong areas (Lü, 2009; Lü et al., 2012; Luo et al., 2017; Meng et al., 2017), the Daohugou area yields a much higher diversity and abundance of invertebrate fossils and a more extensive exposure of fossiliferous horizons, rendering the Daohugou site an excellent research area for taphonomic and palaeoecological studies.

2. Geological setting

The strata that yield the Yanliao Biota in the Daohugou area, sometimes referred to as the “Daohugou Bed”, correspond to the Haifanggou Formation, which consists of three units, in ascending order (Fig. 2; Yang et al., 2019): 1) massive tuff-breccia with rare laminated

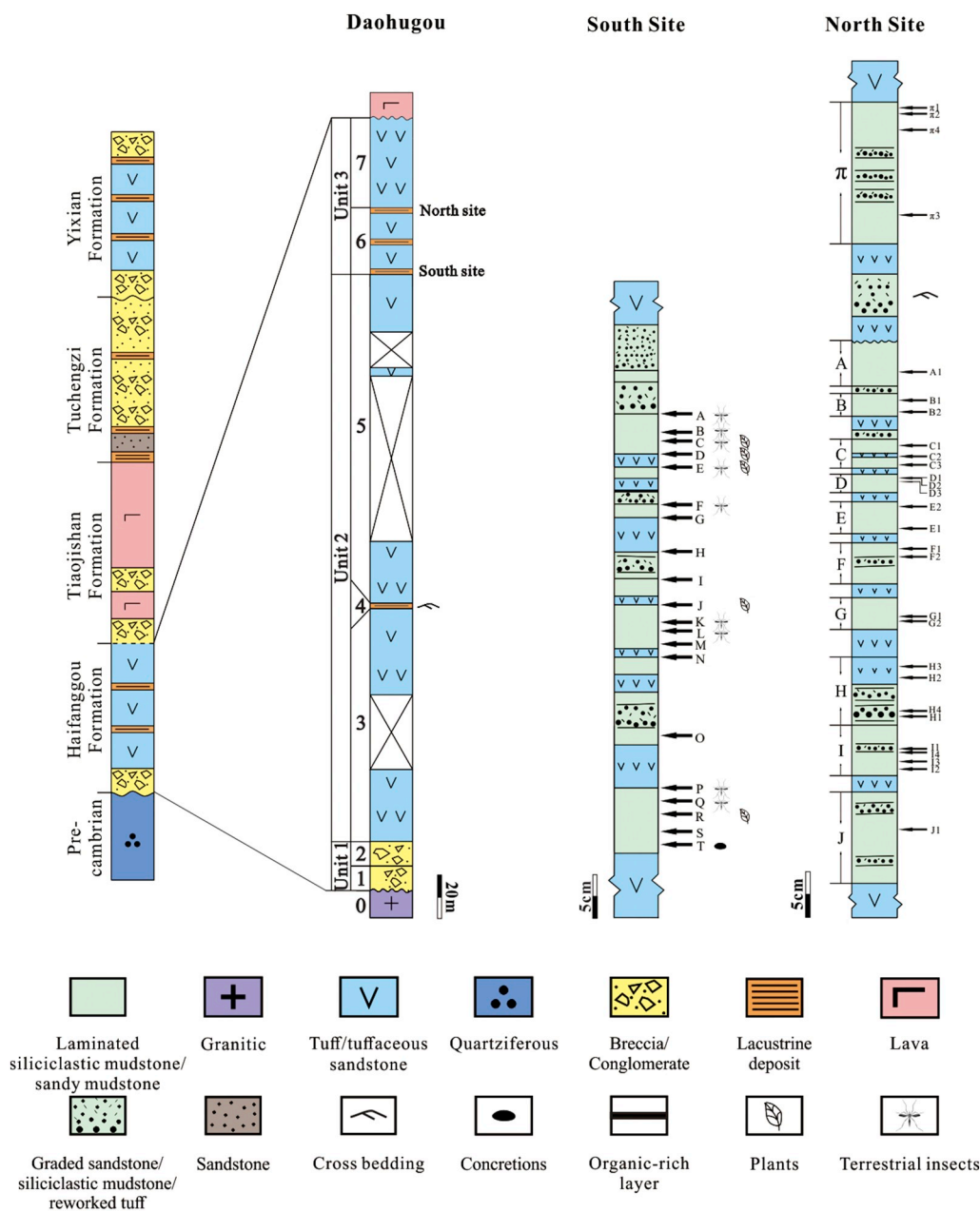


Fig. 2. Lithologies of the two excavation sites from the Daohugou area (modified from Yang et al., 2019).

mudstone intercalations, 2) crudely bedded to massive tuff intercalated with tuffaceous sandstones, siltstone and laminated mudstones, and 3) crudely bedded to massive tuff alternating with laminated to horizontally bedded lacustrine deposits, yielding abundant insects, clam shrimp, plants and rare vertebrates.

Most of the Yanliao vertebrate fossils derive from the laminated lake deposits of Unit 3. In addition, a limited number of fossils, although poorly preserved, have been reported from planar-laminated mudstone intercalations into the tuff-breccia of Unit 1, including bivalves, clam shrimp, insects, and plants (Huang et al., 2015).

Radiometric ages of volcanic rocks overlying the fossil-bearing strata in the Daohugou region include 165–164 Ma (Chen et al., 2004), 159.8 Ma (He et al., 2004), 164–158 Ma (Liu et al., 2006) and 166–153 Ma (Yang and Li, 2008), indicating a largely Bathonian to Callovian age for the Haifanggou Formation, which corresponds to the older Daohugou phase of the Yanliao Biota (Xu et al., 2016).

3. Material and methods

3.1. Field work

Two excavations were carried out in the laminated deposits of the Haifanggou Formation adjacent to the “Paleontology Fossil Museum”

near Daohugou village, Inner Mongolia (Figs. 1, 3). Both excavation sites were about 15–20 m² in area and 3–4 m deep. The strata exposed in the south and north sites stratigraphically belong to the lower and middle parts of Unit 3 (Fig. 2), respectively. Freshly exposed rock was hard to split, so particularly tough rock slabs were frozen in refrigerating cabinets for at least 24 h and then exposed to sunshine until they were ready for splitting. Slab thicknesses ranged from 20 mm (level D in north site) to 155 mm (level π in north site). Layer by layer, we searched the slabs (called ‘levels’ in this publication) for bedding planes containing fossils. How well fossil beds were exposed was dependent on how readily the rock slabs could be split. But regardless of the uneven intervals, we exposed a total of 49 bedding planes that were closely spaced through the geological section (Fig. 2): 20 bedding planes from a 60 cm interval in the south excavation site, and 29 bedding planes from a 90 cm interval in the north excavation site, respectively. In our high-resolution stratigraphy, we recorded taxonomic diversity and specimen abundance for each bedding plane. As most of the rock was thinly laminated (adjacent fossiliferous bedding planes were often < 1 mm apart), close attention was paid to exposing the same bedding plane across the respective excavation area. Representative, well-preserved samples of clam shrimp, aquatic insects, plants and all terrestrial insects were collected for further investigation in the laboratory.



Fig. 3. A, B. South and north excavation sites, respectively. C. The excavated section in the north site shows lacustrine deposits and crudely bedded tuffs (arrowed). D. Clam shrimp cluster on the bedding plane π 3.

Table 1

Taphonomic grades of the preserved specimens of terrestrial insects.

Taphonomic grade	Preservation
a	> 90% preserved. Body articulated, wing veins visible and almost complete
b	80–90% preserved. Body almost complete, including head, thorax, abdomen and thoracic appendages, details such as antennae or cerci lost
c	60–80% preserved. Body deformed, at least one of six legs lost
d	30–60% preserved. Wings disarticulated, remains of head, thorax and abdomen preserved
e	< 30% preserved. Fully disarticulated body, isolated structures such as single legs, abdomina and/or wings preserved

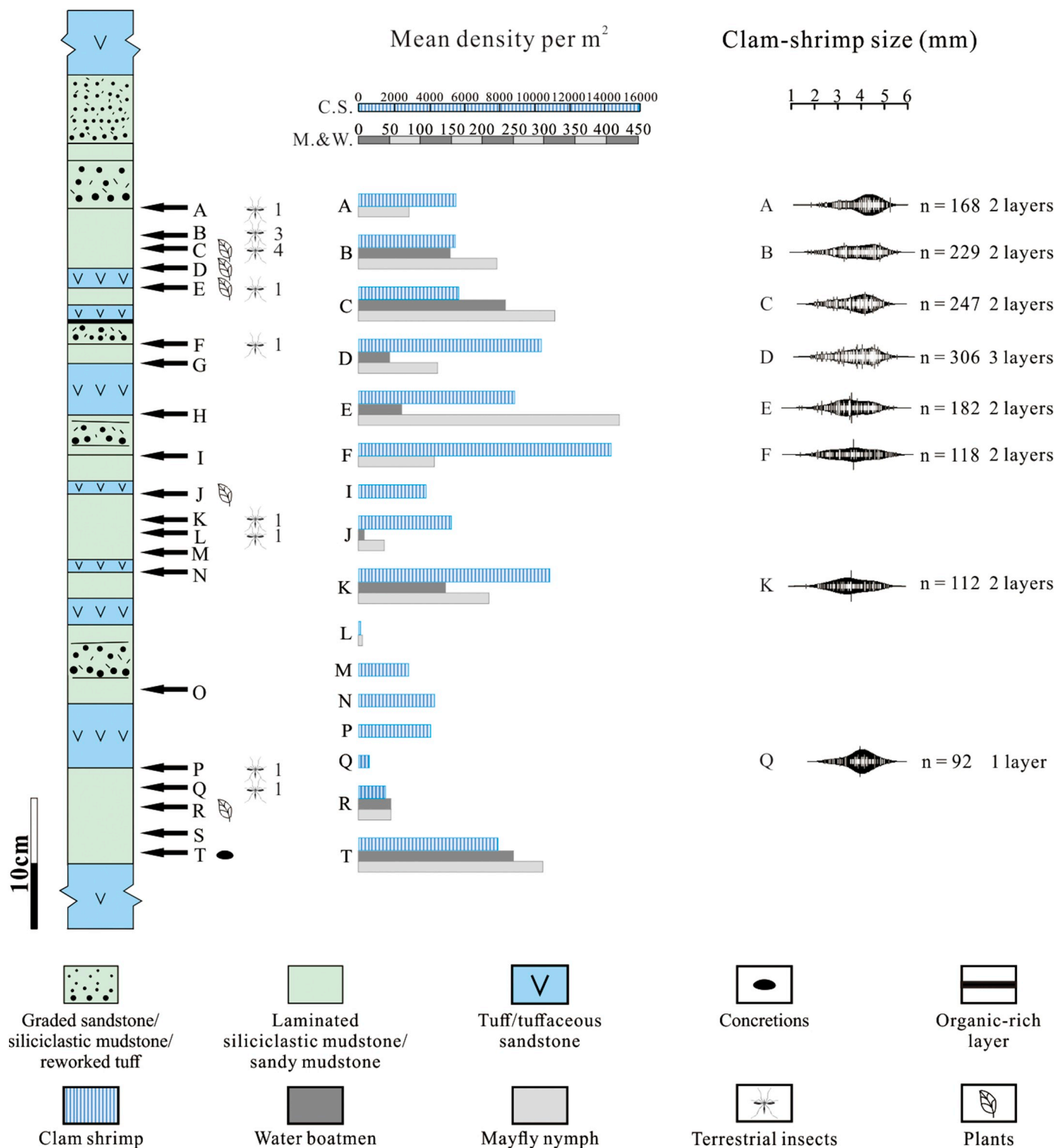


Fig. 4. Specimen abundance of arthropods and body size distribution of clam shrimp through the lithological section of the south excavation site (Daohugou). Left column: Lithological succession of the south excavation site with positions of investigated bedding planes (labeled in capital letters), occurrences of plants and terrestrial insects (indicated by symbols), and the number of insect specimens per bedding plane. Middle column: Specimen abundance on bedding planes (mean densities per square metre for the main aquatic taxa). Right column: Carapace size frequency (beanplots) of clam shrimp on bedding planes. Abbreviations: C.S. = clam shrimp; M. & W. = mayfly nymphs and water boatmen.

3.2. Community and morphometric data

For most bedding planes, we designated counting areas and recorded species abundance and corresponding taphonomic features (articulation and completeness, see below). Levels G, H, O, S of the

south site and level D of the north site have not been considered for the analyses of the present study, as bedding planes within those levels were either poorly exposed (part of lake turbidites) or associated with tuff layers, resulting in poor preservation and the possible loss of community information. Population densities of aquatic taxa (i.e.

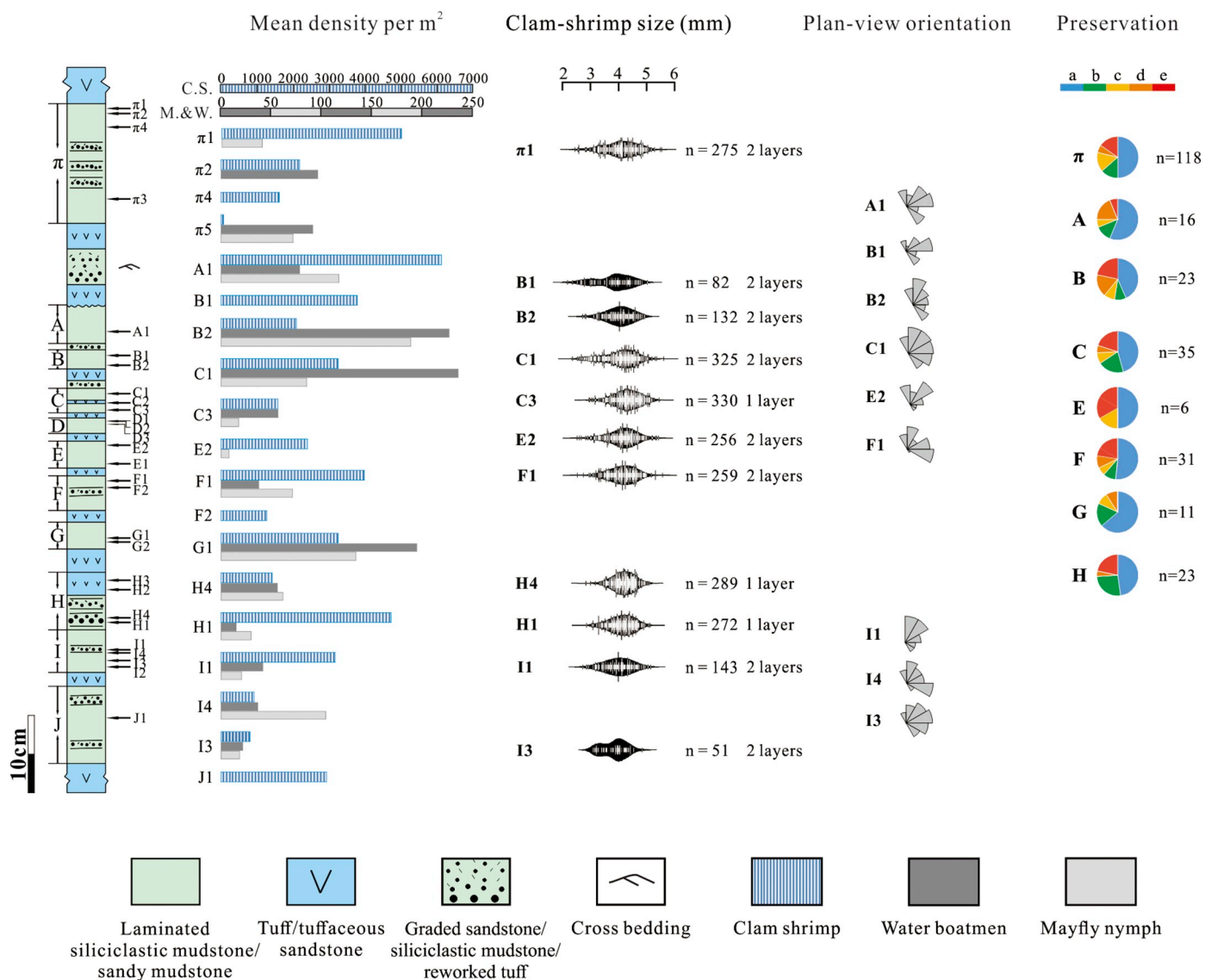


Fig. 5. Specimen abundance of arthropods, body size distribution of clam shrimp, plan-view orientation of aquatic insects, and preservation of terrestrial insects through the lithological section of the north excavation site (Daohugou). Left column: Lithological succession of the north excavation site with positions of investigated levels (labeled in capital letters) and bedding planes. Second column: Specimen abundance on bedding planes (mean densities per square metre for the main aquatic taxa). Third column: Carapace size frequency (beanplots) of clam shrimp on bedding planes. Fourth column: Plan-view orientation of aquatic insects. Fifth column: Proportions of preservational grades of terrestrial insects. The exact position of bedding plane π 5 is uncertain but it belongs to level π . Abbreviations: C.S. = clam shrimp; M. & W. = mayfly nymphs and water boatmen.

Spinicaudata, Ephemeroptera and Corixidae) were standardized to units of square metres, while the density of terrestrial insects, which were less abundant, was calculated per cubic metre. Fossil diversity on bedding planes was measured based on a combination of species richness and evenness (Simpson 1-D) as implemented by the PAST software (version 3.08; folk.uio.no/ohammer/past/; Hammer et al., 2001). Evenness values range between 0 and 1, indicating dominance of a single species and equal species distribution, respectively.

Size data of the clam shrimp *Triglypta haifanggouensis*, the most common species in the studied sections, were obtained from 19 bedding planes (8 from the south site and 11 from the north site) by measuring the distance between the most anterior and posterior points of the valves (Hethke et al., 2018). While counting specimens and measuring the size of individuals, we also recorded the total number of laminae belonging to a particular bedding plane. Size distributions were visualized using beanplots (Kampstra, 2008). In addition, we recorded

the presence of growth-band crowding for 106 individuals from bedding planes C1, C2 (north site) and C, K (south site), to investigate the relationship between carapace size and maturity. The relationship between growth-band crowding and maturity is a hypothesis that is currently being examined by members of our working group.

To further assess the surrounding terrestrial palaeoenvironment, insects were categorized into four ecological groups (following Liu et al., 2010): hydrophytic (H), edaphic (E), silvan (S) and alpine (A). Hydrophytic insects live in water, silvan insects live in woodland at low altitudes and alpine insects inhabit altitudes of > 800 m. Edaphic insects spend the whole or a portion of their life cycle in soil, including epedaphic (living on the soil surface or in litter), euedaphic (inhabiting the voids of mineral horizons beneath the litter layer), and hemiedaphic (a temporary life form for epedaphic and atmobiocytic arthropods from higher strata such as herbaceous, shrub and tree layers) insects (Villani et al., 1999; Eisenbeis and Wichard, 2012).

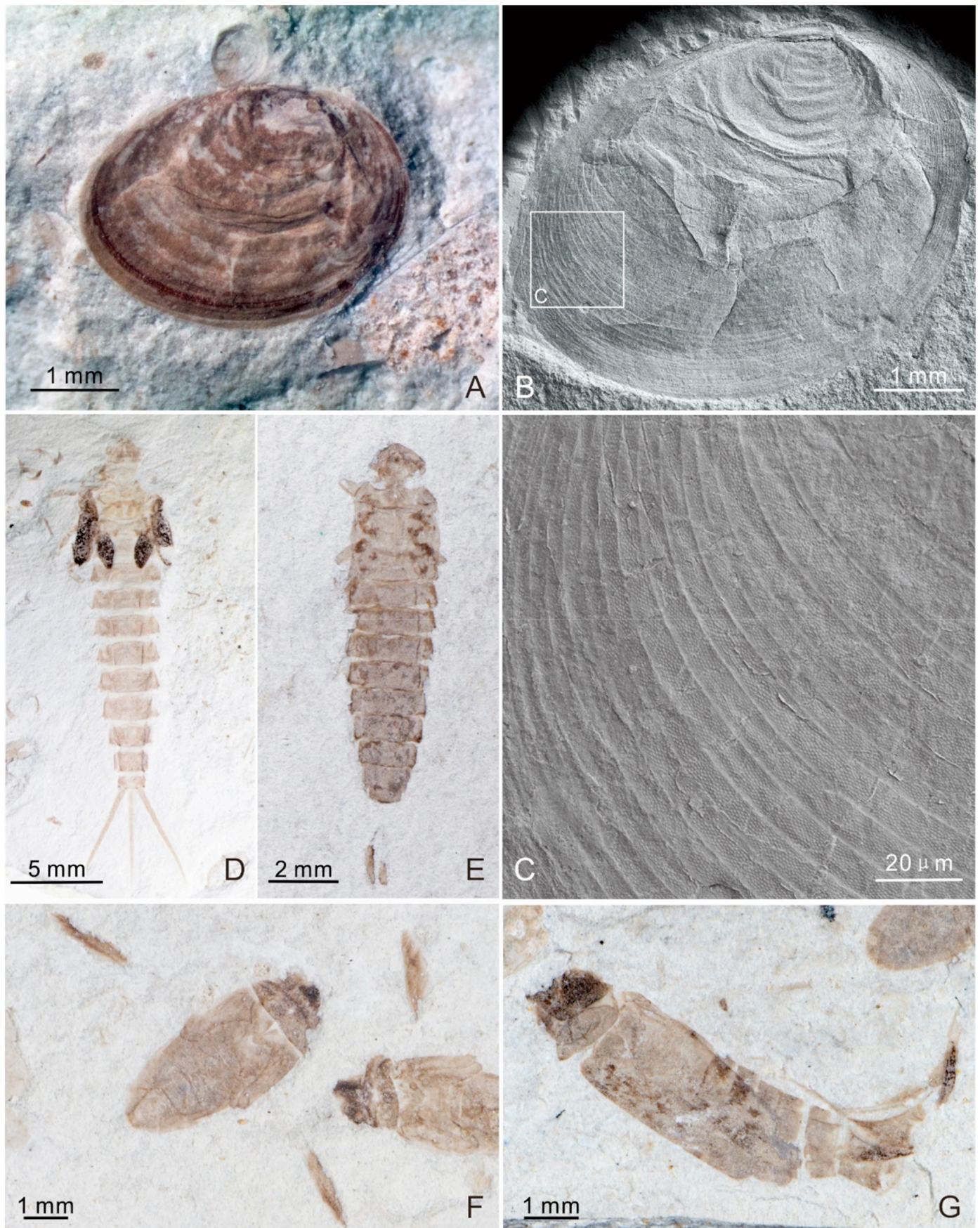


Fig. 6. Major taxa of the aquatic arthropod fauna. A–C. Clam shrimp *Triglypta haifanggouensis*. A. Left valve, mostly external mould. B–C. Left valve, external mould, growth bands crowded at the carapace margin. D. Mayfly nymph *Fuyous gregarius*, ventral view. E. Mayfly nymph *Shantous lacustris*, ventral view. F–G. Water boatman *Daohugocorixa vulcanica*. F. Dorsal view. G. Lateral view.

3.3. Taphonomic observations

Plan-view orientations of the aquatic insects *Fuyous gregarious*, *Shantous lacustris* (Ephemeroptera), and *Daohugocorixa vulcanica* (Corixidae) were obtained from nine bedding planes by subdividing a circle into 12 segments and counting the orientation of each individual. Insect heads pointing in opposite directions were regarded to indicate the same orientation, which is why segments 7 to 12 were subsequently mirrored. The remaining six segments (0–180°) were then tested for preferred orientations by carrying out Rayleigh's test and the Chi-square test using PAST, and the results were interpreted following table 4.1 in Hammer and Harper (2006). Rayleigh's test is based on data drawn from a population with a von Mises distribution (Davis, 1986) and a null hypothesis of uniform distribution of aquatic insects.

The preservation quality of terrestrial insects was evaluated based on anatomic details and the degree of remaining joint articulation, a method that has been widely used in taphonomic analyses (Smith and Moe-Hoffman, 2007; McNamara et al., 2012). Experiments show that most insects have a characteristic pattern of body disarticulation: the abdomen will swell and rupture first, subsequently appendages begin to disarticulate from the body, then the abdomen disintegrates and, prior to complete disintegration, the head and thorax will disarticulate (Duncan, 1997). According to the disarticulation pattern, preservation quality was subdivided into five grades (Table 1; modified from Wang et al., 2013). Individuals preserved on a slab and its counterpart were evaluated based on the combined features of both slabs. Taphonomic grades were allocated only to specimens that were fully recovered from the rock.

4. Results

4.1. Lithofacies and depositional environment

The stratigraphic succession exposed in the two excavation sites consists of alternated dark grey, laminated siliciclastic mudstone and grey, graded sandstone, siltstone and reworked tuff, with numerous intercalations of greenish to pinkish, laminated to thinly bedded tuff (Figs. 4, 5). The planar-laminated siliciclastic mudstone (lithofacies 4 in Yang et al., 2019) exhibits two types of lamination. Type 1 lamination is composed of normally graded siltstone, claystone and reworked tuff with sharp non-erosive bases and uneven top surfaces. The laminae are usually 100 μm–3 mm thick, but thicknesses can vary laterally. Type 1 lamination forms thin intervals (ca. 7–28 mm thick) intercalated by graded sandstone, siltstone and tuff. Type 2 lamination consists of laterally persistent couplets of clay-poor (dark) and clay-rich (light) laminae (ca. 30–700 μm thick) with clear bimodal grain size distributions.

Although aquatic fossils may occur scattered in graded sandstone, siliciclastic mudstone and laminated to thinly bedded tuff (e.g. south site E), most excavated fossils are preserved in planar-laminated mudstone. Aquatic fossils are abundant in both lamination types, while terrestrial fossils were mostly uncovered from Type 1. In addition, terrestrial fossils occur in many laminae associated with abundant aquatic organisms, but are particularly abundant in laminae that are directly underlying the tuff of volcanic fallout origin. With rare exceptions of clam shrimp preserved in three-dimensions in graded sandstone, mudstone and reworked tuff (Fig. 3D), most fossils are preserved in two dimensions, parallel to bedding.

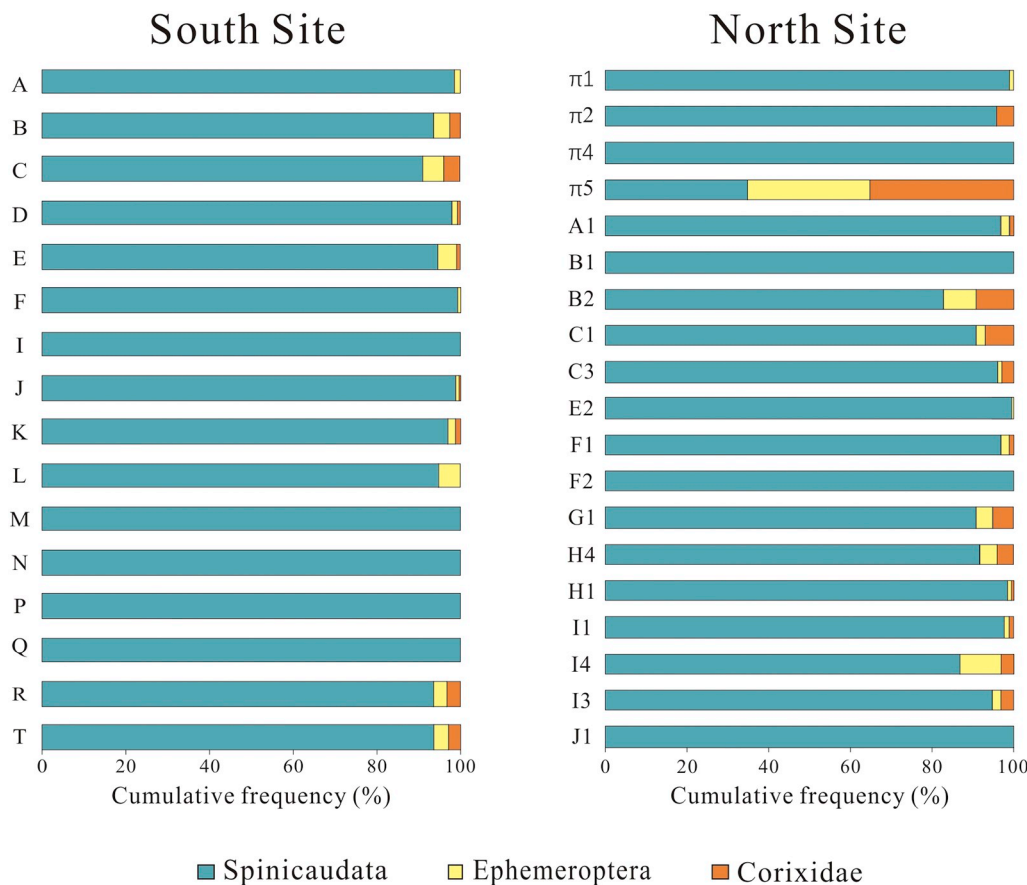


Fig. 7. Relative abundances of clam shrimp, mayfly nymphs and water boatmen on 35 bedding planes (π1–J1 in north site and A–T in south site).

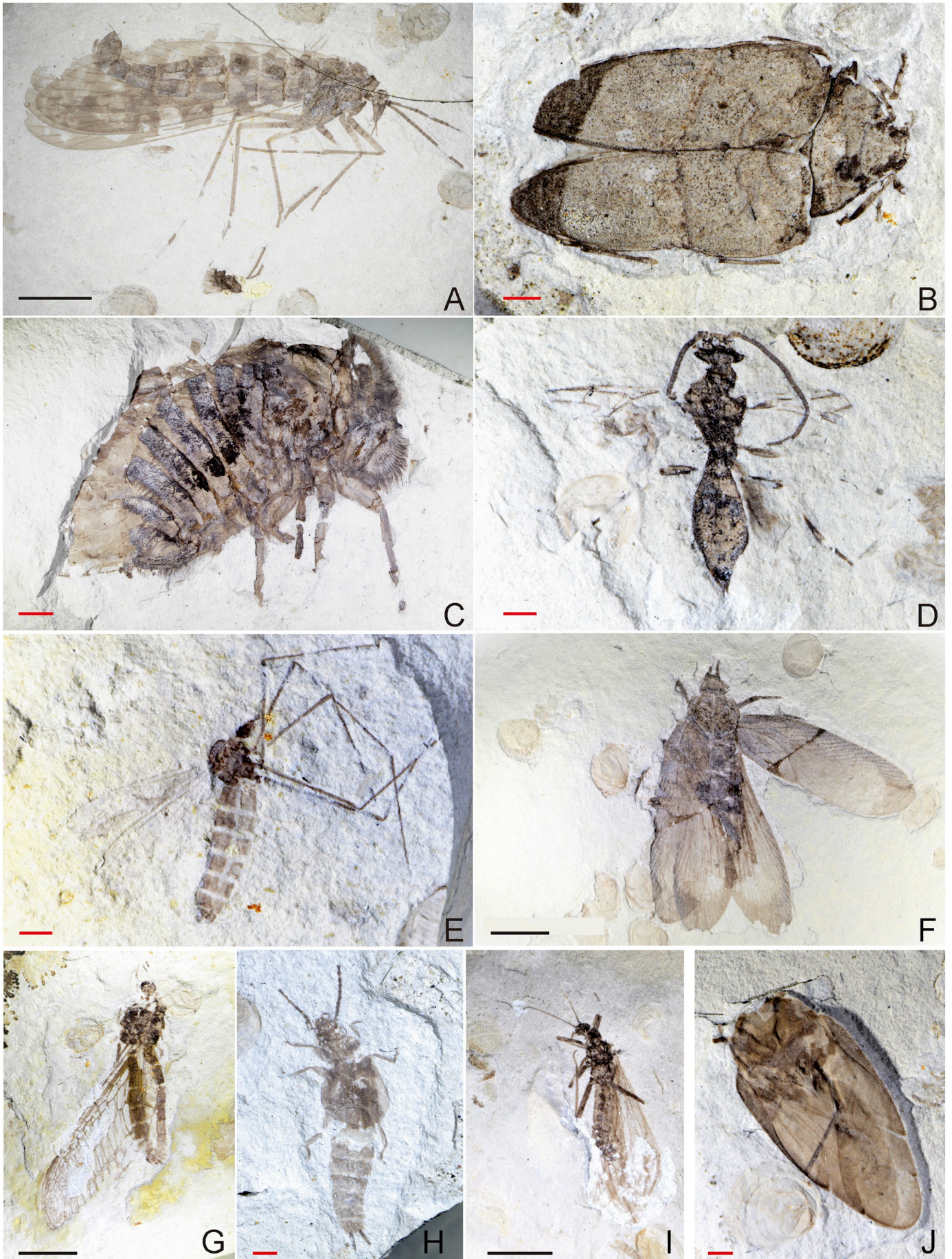


Fig. 8. Exemplary taxa of terrestrial insects. Species belong to the insect groups: A. Mecoptera. B. Coleoptera. C. Cicadomorpha (Hemiptera). D. Hymenoptera. E. Diptera. F. Blattaria. G. Neuroptera. H. Dermaptera. I. Plecoptera. J. Heteroptera (Hemiptera). A, B, C, F represent taphonomic grade a, D, E, G–J represent taphonomic grade b. Red scale bars represent 1 mm. Black scale bars represent 5 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

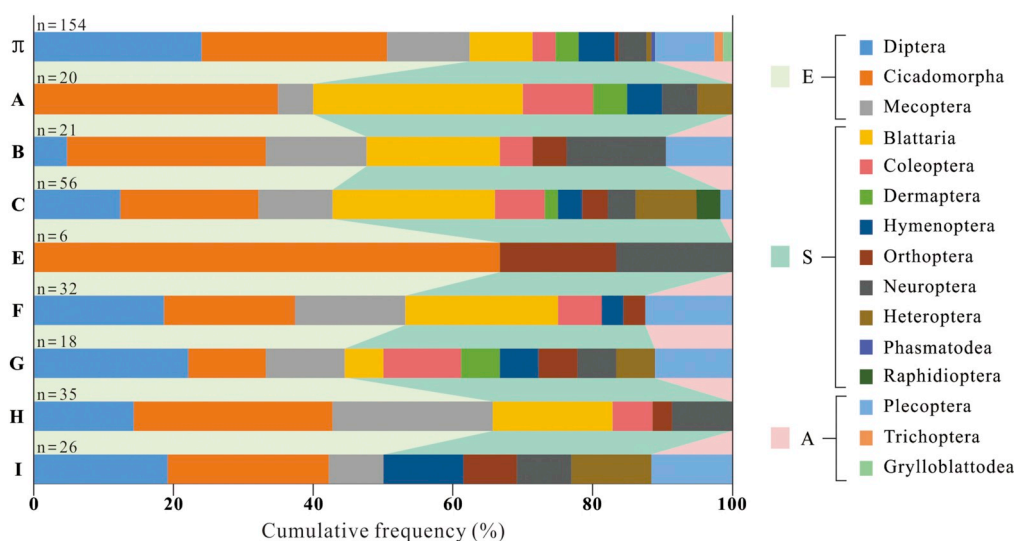


Fig. 9. Compositional proportion of terrestrial insects by taxon and habitat type in each level of the north site. Levels D and J are not shown due to their small sample size (one orthopteran in both levels). A: alpine, E: edaphic, S: silvan.

4.2. Faunal composition

Aquatic organisms in the studied sites are represented by low-diversity, medium to high-density assemblages (Figs. 4, 5), including four arthropod species: *Triglypta haifanggouensis* (Spinicaudata), *Fuyous gregarious* and *Shantous lacustris* (Ephemeroptera), and *Daohugocorixa vulcanica* (Corixidae) (Fig. 6). Clam shrimp individuals are scattered on all fossiliferous bedding planes and occasionally form pavements of up to 14,487 individuals per m² (bedding plane F, south site). Locally, carapaces are clustered into clumps (Kidwell et al., 1986) marked by three-dimensional carapace preservation (bedding plane π 3; Fig. 3D). Aquatic insects are less common than clam shrimp. Mayfly nymphs occur in 25 out of 35 quantitatively studied bedding planes and reach densities of up to 421 individuals per m² (bedding plane E, south site), and water boatmen occur in 21 bedding planes with densities of up to 251 individuals per m² (bedding plane T, south site).

The aquatic community was dominated by clam shrimp, accounting for 90–100% of individuals on most bedding planes. The proportions of mayfly nymphs and water boatmen are comparable, mostly accounting for 0–10% of the individuals on a particular bedding plane (Fig. 7). The only exception forms bedding plane π 5 (north site), which yields similar abundances of clam shrimp and water boatmen.

In comparison, we collected a low-density but diverse fauna of terrestrial insects (Fig. 8). With 370 specimens and densities ranging from 25 individuals/m³ (level D) to 87.8 individuals/m³ (level C), the fauna was particularly rich in the north site. The south site yielded only 14 specimens on nine different bedding planes (Fig. 4). These terrestrial insects have been assigned to > 60 species in 15 orders and suborders (Fig. 9). The evenness value for each level ranges from 0.765 (level A) to 0.8827 (level G; Table 2). Among them, edaphic insects are the most abundant; a total of 203 specimens (65 dipterans, 93 cicadomorphans and 45 mecopterans) have been collected from nine levels, accounting for 57.5% of all terrestrial insects. Silvan insects represent the most diverse but a numerically less abundant ecological group. A total of 138 specimens (49 blattarians, 18 coleopterans, 8 dermapterans, 16 hymenopterans, 12 orthopterans, 19 neuropterans, 11 heteropterans, 1

Table 2

Diversity indices for terrestrial insects from eight levels of the north excavation site. Levels D, E and J are not listed due to their small sample size.

Level	Taxa	Individuals	Evenness	Shannon index
π	14	154	0.8356	2.086
A	8	20	0.765	1.708
B	8	21	0.8254	1.889
C	12	56	0.861	2.173
F	8	32	0.8359	1.9
G	11	18	0.8827	2.274
H	7	35	0.8049	1.751
I	8	26	0.8521	1.995

phasmatodea and 2 raphidiopteran) have been identified from 11 levels, accounting for 37.3% of all terrestrial insects. Only 29 alpine insects (25 plecopterans, 2 trichopterans and 2 grylloblattodeans) have been collected from nine levels. Within each level, terrestrial insects occur on many bedding planes with maximum abundances of 11 but commonly 1–3 individuals per bedding plane.

We collected 114 terrestrial plant fossils from the north site, while only five specimens were collected from the south site. Most of the major plant groups that thrived during the Middle to Late Jurassic have been identified (25 species), including ferns, Caytoniales, ginkgophytes, Czekanowskiales, cycads, bennettites, and conifers. The flora was dominated by conifers (60 specimens), bennettites (33 specimens) and ginkgophytes (11 specimens). Water-bound plants such as ferns are only represented by a few fragmentary remains (Pott and Jiang, 2017).

4.3. Fossil preservation

Most of the aquatic fossils remain articulated with little fragmentation or breakage. Clam shrimp lack soft parts and their valves are articulated near the umbo and slightly rotated against each other. Valves preserved in butterfly position are rare. Mayfly nymphs and water boatmen are mostly well preserved and articulated. Specimens of

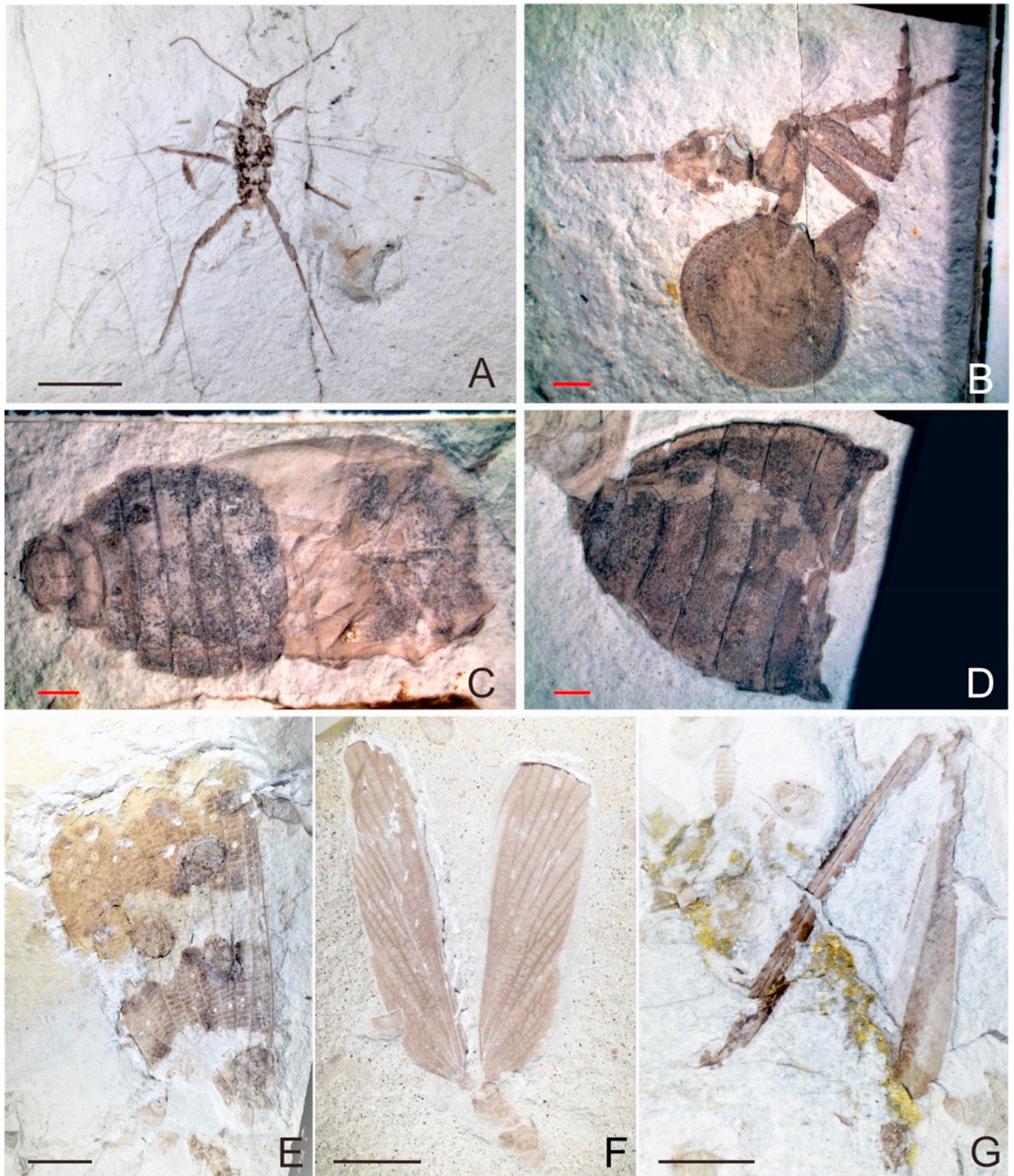


Fig. 10. Examples of preservational grades. A. Grade c: Plecoptera without abdomen. B. Grade e: Part of thorax and legs (Cicadomorpha). C. Grade d: Remains of thorax and abdomen (Heteroptera). D. Grade e: Isolated abdomen (Heteroptera). E–F. Grade e: Isolated wings (Neuroptera and Grylloblattodea). G. Grade e: Isolated leg (Orthoptera). For grades a and b see Fig. 8. Red scale bars represent 1 mm. Black scale bars represent 5 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

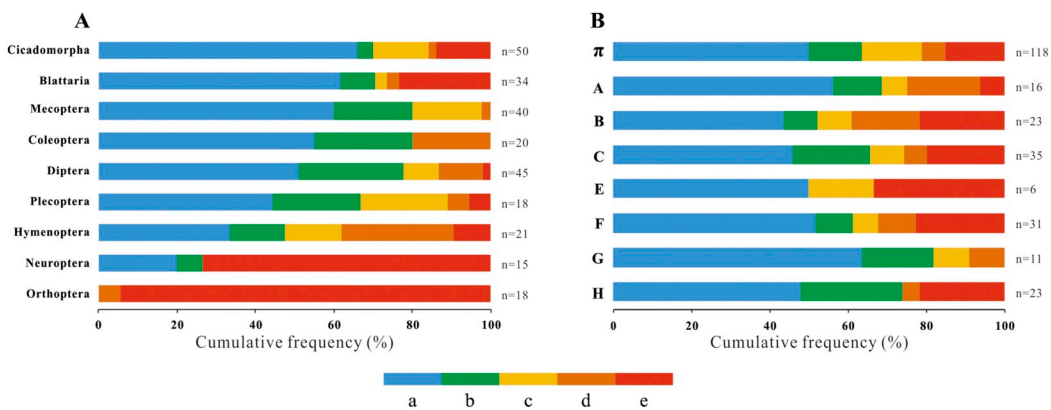


Fig. 11. Proportion of taphonomic grades of terrestrial insects from the north excavation site by taxon (A) and by level (B).

Table 3

Results of Rayleigh's test and the Chi-square test for preferred orientations of aquatic insects on nine bedding planes.

Bedding plane	n	Mean	R	p(rand)	Chi ²	p(rand)
A1	16	83.05	0.2253	0.45	6.5	0.26
B1	16	96.95	0.2253	0.45	5	0.42
B2	77	27.64	0.1368	0.24	39.96	1.52E-07
C1	103	68.74	0.112	0.28	33.49	3.01E-06
E2	13	45	0.2665	0.41	8.69	0.122
F1	27	83.05	0.1335	0.62	16.33	0.006
I1	17	60	0.3529	0.12	6.65	0.25
I3	110	86.39	0.1879	0.02	26.58	6.88E-05
I4	24	80.45	0.1102	0.75	10	0.075

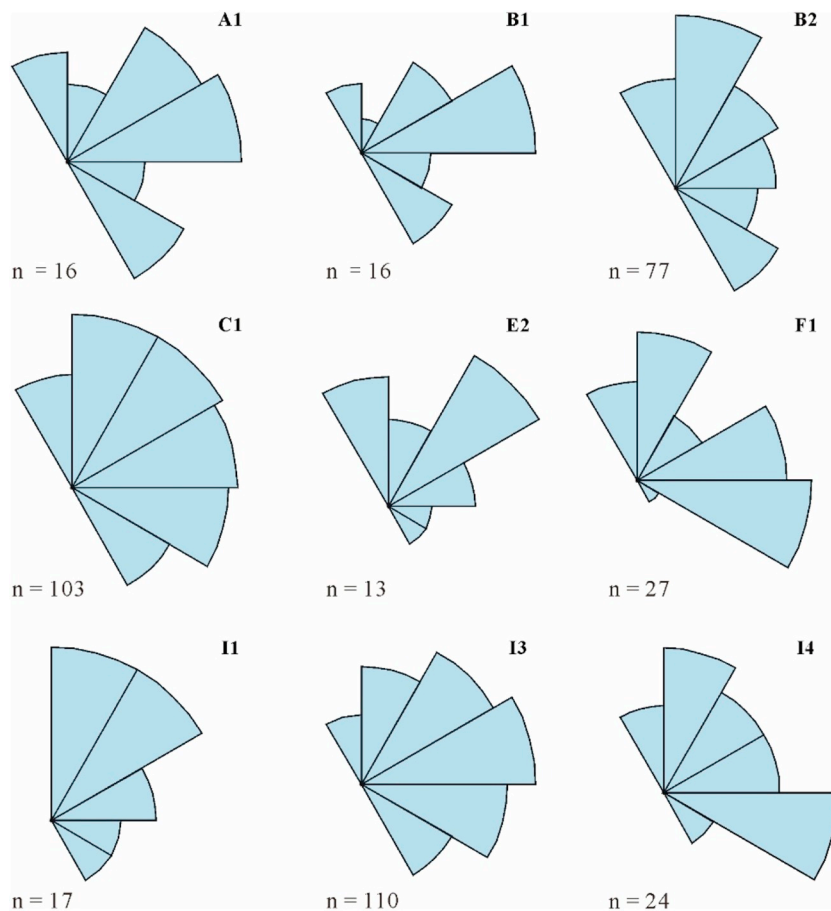


Fig. 12. Rose plots of plan-view orientation of aquatic insects on bedding planes of the north excavation site.

Table 4
Results of normality test for clam shrimp size on eight bedding planes of the south excavation site.

Bedding plane	n	Shapiro-Wilk W	p(normal)
A	168	0.9409	1.917E-06
B	229	0.9748	0.0004196
C	247	0.9615	3.505E-06
D	306	0.9733	0.00001814
E	182	0.9889	0.1673
F	118	0.9863	0.2786
K	112	0.9872	0.3707
Q	91	0.9739	0.06459

Table 5
Results of normality test for clam shrimp size on eleven bedding planes of the north excavation site.

Bedding plane	n	Shapiro-Wilk W	p(normal)
π1	275	0.988	0.02151
B1	82	0.9625	0.01707
B2	132	0.985	0.1574
C1	325	0.9679	1.294E-06
C3	330	0.9907	0.03495
E2	256	0.9831	0.003981
F1	259	0.9926	0.2273
H1	269	0.9894	0.04696
H4	294	0.9863	0.006776
I1	143	0.9938	0.7955
I3	51	0.9606	0.08811

Fuyous gregarius are better preserved than those of *Shantous lacustris*. Subtle anatomic structures, such as tergalium and cerci, are preserved in most *Fuyous gregarius*, but missing in most *Shantous lacustris*. The water boatman *Daohugocorixa vulcanica* is clearly preserved with oar-like hind tarsi fringed with fine hairs, other legs are hard to discern (Fig. 6).

The overall preservation quality of terrestrial insects is high (Figs. 8, 10). It is best in level G, in which 63.6%, 18.2%, 9.1%, 9.1% of the specimens fall into grades a, b, c, d, respectively (Fig. 11). By taxon,

Mecoptera, Coleoptera, Diptera, Blattaria, Cicadomorpha (Hemiptera), and Plecoptera are well preserved, with 80%, 80%, 77.8%, 70.6%, 70%, and 66.7% of the specimens falling into grades a and b, respectively. In contrast, Hymenoptera, Neuroptera, and Orthoptera are relatively poorly preserved; 47.6%, 26.7% and 0% of the specimens belong to grades a and b, respectively (Fig. 11A). By habitat, edaphic insects yield the best preservation quality. 59.3% and 5.9% of edaphic specimens fall into grades a and e, respectively. Second to edaphic insects, 44.4% and 5.6% of alpine insects belong to grades a and e. Silvan insects are comparatively poorly preserved, 38.5% and 35.8% of the silvan specimens fall into grades a and e respectively.

4.4. Plan-view orientation

The orientation of aquatic insects was measured on nine bedding planes from the north site (Table 3; Fig. 12). Among them, one bedding plane (I3) exhibits a single preferred orientation (NE-SW) and three bedding planes (B2, C1 and F1) exhibit two or more preferred orientations. The null hypothesis of randomly distributed aquatic insects could not be rejected for five bedding planes (A1, B1, E2, I1, I4). Smaller sample sizes (13–24) may have affected the statistic results of the latter.

4.5. Clam shrimp size

All clam shrimp individuals have been assigned to *Triglypta haifanggouensis*, which is the only species reported from the Daohugou area (Liao et al., 2017). Specimen length from the south site ranges from 1.34 mm to 5.53 mm, while it ranges from 2.18 mm to 5.62 mm in the north site. Hence, the overall size of individuals from the south site (average of 3.80 mm) is smaller than that of the north site (average of 4.07 mm).

Beanplots (Figs. 4, 5) show different size distribution patterns on different bedding planes, from approximately normal, bimodal (e.g. south site A) to polymodal (e.g. south site D). Statistics indicate that clam shrimp sizes on eight bedding planes are normally distributed (E, F, K, Q, south site; B2, F1, I1, I3, north site; Tables 4 and 5). Also, growth-band crowding has been identified in specimens as small as 2.48 mm in length (Fig. 13).

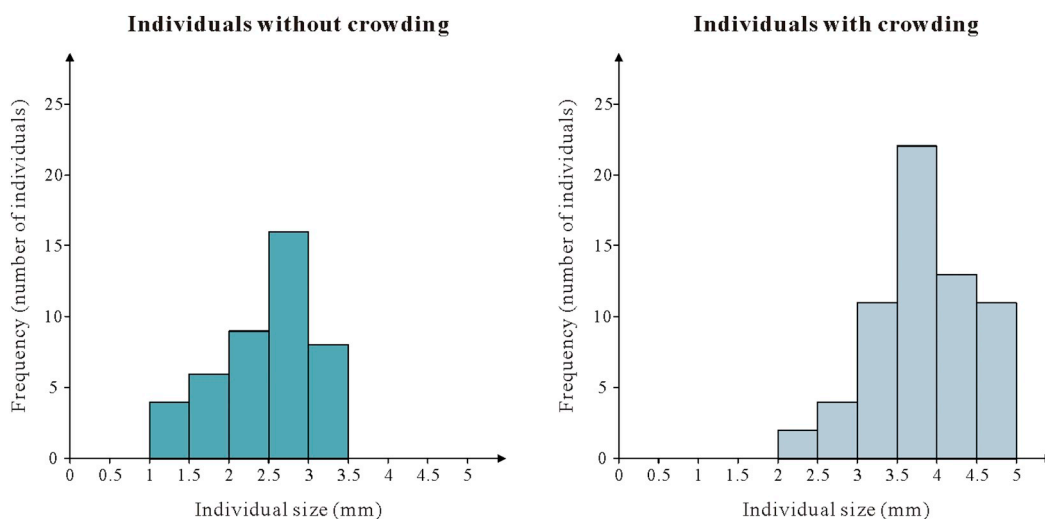


Fig. 13. Relationship between size and crowded growth bands, showing 43 individuals without crowding (left histogram) and 63 individuals with crowding (right histogram). To reduce ecophenotypic size variability, the histograms represent randomly selected clam shrimp sizes of only four bedding planes: C1, C2 in the north site and C, K in the south site.

5. Discussion

5.1. Autecology

Excavated aquatic organisms include clam shrimp, mayfly nymphs and water boatmen. Extant clam shrimp live in transient bodies of freshwater (Timms and Richter, 2002), and they adopt a general life style as benthic filter-feeders that occasionally swim (Vannier et al., 2003), but habits vary among groups (Schwentner et al., 2015). They hatch from eggs capable of surviving drying, freezing and other hostile conditions (Frank, 1988). However, even though hatching is commonly associated with the filling of a pool, eggs may hatch as readily without having been dried beforehand (Bishop, 1967; Belk, 1972), in line with recent claims that clam shrimp thrived in perennial lakes during pre-Cenozoic times (Hethke et al., 2019).

Population densities of living clam shrimp can reach 318 individuals/m² in small, temporary pools and 4488 individuals/m² in modern fish culture ponds (Emberton and Kenneth, 1980; Luzier and Summerfelt, 1996), which is similar to Daohugou densities (Figs. 4, 5). Rearing experiments indicate a strong effect of population density on carapace size with lower densities triggering fast carapace growth (Hethke et al., 2019), which has also been observed in *T. haifangouensis*: A bivariate fit of size by population density indicates a strong density dependency (Supplementary 1).

In addition, clam shrimp growth is strongly dependent on temperature during the first few days after hatching (Huang and Chou, 2017; MH pers. obs.). Hence, the observed size difference between the south site and the north site should indicate variable physico-chemical conditions through time. Hypotheses on possible causes for growth-band crowding include the timing of reproductive maturity and a high level of unfavourable fluctuations in environmental conditions. However, the cause for growth-band crowding has not been fully resolved yet. In *T. haifangouensis*, specimens as small as 2.48 mm yield crowded growth bands, which might be regarded as a possible minimum 'maturation length'.

Modern mayfly nymphs live primarily in streams and rivers under rocks or in sediments, but they can occur in all sorts of water bodies, including shallow areas of deep permanent lakes and ponds (Lyman, 1943; Menetrey et al., 2007; Brittain and Sartori, 2009). All known mayfly nymphs from the Jurassic and Early Cretaceous of China, including *Fuyous gregarius* and *Shantous lacustris*, lived in lacustrine rather than lotic environments (Zhang and Kluge, 2007). Modern water boatmen generally occur in shallower waters, and they can be the early colonizers of temporary water bodies by dispersal, but many species frequently appear in the bottom waters of permanent ponds and lakes as well as streams (Oscarson, 1987; Batzer and Wissinger, 1996; Jansson and Reavell, 1999; Brown, 2009).

All excavated terrestrial insects can be allocated to silvan, edaphic or alpine communities (Liu et al., 2010). Extant edaphic insects live in damp environments such as grasslands adjacent to water bodies that provide moisture for breeding and larvae. They are represented by members of Hemiptera (mainly Cicadomorpha) and Mecoptera in the palaeoecological community of the Daohugou site. Cicadomorpha live underground as nymphs for most of their lives and will be arboreal after moulting (e.g. Resh and Cardé, 2009). Mecoptera inhabit moist forests, the oviposition and pupation occur in soil, any factor reducing moisture could adversely affect Mecoptera populations (Byers and Thornhill, 1983). Silvan insects, represented by Blattaria and Coleoptera in Daohugou, prefer warm temperatures and densely vegetated areas such as forests (e.g. Ren et al., 1996; Liu et al., 2010). Modern species of Blattaria are commonly predatory cockroaches and live in moist niches such as rotting wood and leaf litter. Taxa of Blattaria in the Daohugou sites are here interpreted to indicate a similar environment near the lake (e.g. Liang et al., 2009; Liang et al., 2012). Phasmatodea and Xyelidae (Hymenoptera) from the Lower Cretaceous Yixian Formation preferred warm-temperate to subtropical climates at some distance

from the lake shore (Ren, 1997; Zhang and Zhang, 2000). Alpine insects, represented by Taeniopterygidae (Plecoptera), are adapted to cooler temperatures (e.g. Harper et al., 1991; Liu et al., 2008). Occasional cooler climates on high mountains are also indicated by the discovery of the long-haired tettiartid *Hirtaprosbole erromera* (Fig. 8C; Liu et al., 2016).

The flora of the lake surroundings was comparatively rich in plant species of different groups. Even if some floral components of our excavation reflect forests of drier hinterland environments, there is convincing evidence for a biased composition of the floral assemblage (Pott and Jiang, 2017). Many of the plants identified thrived in water- or moisture-related environments that may have surrounded the lake (wet or boggy soil, humid conditions, osmotic/acidic soils). Especially for bennettites, it has often been suggested that these plants grew in more or less monotypic stands in deltaic or lacustrine environments (e.g. Pott and McLoughlin, 2014; Pott et al., 2015). Similar interpretations have been made for some larger-leaved and phylloclade conifers (e.g. Farjon, 2010), many modern relatives of which (e.g. *Phyllocladus*, *Podocarpus*) live in altitudes up to 700–800 m above sea level on acidic soils or in evergreen rainforests. Some Triassic–Jurassic ginkgophytes probably grew in forests of similar conditions (e.g. Pott et al., 2007). Additional evidence of plant fossils and palynological studies corroborate the reconstruction of a moist forest landscape with moderate to relatively high air and soil humidity (e.g., Zhang and Zheng, 1987; Na et al., 2015; Pott et al., 2015; Huang et al., 2016; Dong et al., 2017).

5.2. Taphonomic model

The two excavated sections revealed a mixed fauna of both aquatic and terrestrial organisms. All of the terrestrial insects identified must have been transported into the lake. Without external force, terrestrial insects can hardly sink completely in static water. As experiments show, freshly killed, lightly sclerotized animals display considerable resistance to skeletal damage during transport. This resistance diminishes as decay advances. In addition, a high degree of decay-induced disarticulation may occur with minimal transport (Duncan et al., 2003). For example, coleopterans are fully disarticulated after an average time of 37.19 days (Smith et al., 2006); extant cicadas will largely disarticulate and lose their head and wings within 25 days of decay (Wang et al., 2013); freshly killed cockroaches reach their final decay stage after 30 weeks in still water but after only 70 h in moving water (Duncan et al., 2003). Insects with higher SM indices (wing surface / (body mass)^{0.67}; Wagner et al., 1996) require longer floating times, which negatively affect preservation (Archibald and Makarkin, 2006). For example, Lepidoptera can remain on the water surface and experience severe decomposition within 14 days (Martínez-Delclós and Martinell, 1993). The overall high preservation quality of the uncovered terrestrial insects reflects that at least half of them were quickly buried after their death, probably within 2–3 weeks. This is consistent with lithological evidence that indicates rapid settling of hosting sediments, caused by a combination of subaqueous density flows, volcanic ash falls and water turbulence (Yang et al., 2019).

Aquatic organisms may have been transported over short distances, indicated by clam shrimp clusters (Fig. 3D), the loss of details such as tergalia and cerci in mayfly nymphs, and the separation of several cephalothoraces from abdomina. Depositional conditions remained generally calm, but preferred orientations of aquatic insects detected on four of nine bedding planes (Fig. 12, Table 3) indicate the repeated presence of currents, corroborated by the frequent alternation of subaqueous density current deposits with the fossiliferous levels. The high clam shrimp density of 93 individuals/m² (bedding plane π5, north site) to 14,487 individuals/m² (bedding plane F, south site) indicates a combination of high initial population densities and time averaging.

The co-occurrence of abundant aquatic and terrestrial fossils in several thin levels (e.g. levels C and E, north site), sometimes even on the same bedding plane, indicates that these communities may have

been killed simultaneously or during a relatively short period, implying mass mortality events. This inference is supported by the presence of abundant clam shrimp with variable individual sizes on the same bedding plane. Generally, polymodal distributions (e.g. bedding planes B1 and I3, north site) indicate a combination of natural death after reproductive senescence (larger individuals) and abrupt death of a cohort of juveniles or young adults. In addition to seasonal environmental fluctuations, there is strong evidence for a volcanic trigger for mass mortalities: Alternations of thin lacustrine deposits and thick volcanoclastic apron deposits (Yang et al., 2019). Similar volcanically-induced mass mortalities have been reported from the Early Cretaceous (Fürsich et al., 2007; Hethke et al., 2019) and from more recent events (Dale et al., 2005; Christenson et al., 2015).

5.3. Palaeoenvironmental implications

The two studied lacustrine successions in the Daohugou area have been interpreted as deposits of the marginal regions of a single lake or of many short-lived lakes, based on frequently alternating lacustrine and volcanoclastic apron facies (Yang et al., 2019). This is consistent with the aquatic community. All three aquatic taxa could survive and flourish in transient water bodies or shallow areas of deeper permanent lakes. The high terrestrial-aquatic interchange indicated by the common co-existence of terrestrial and aquatic organisms on many bedding planes, and the absence of aquatic predators such as fishes favour the scenario of short-lived lakes or ponds (Søndergaard et al., 2005). The lack of larger predators or scavengers in our excavation, and a high proportion of well-preserved insect fossils indicate that macroscopic scavengers were rare or even absent between the time of death and burial, implying either that burial was extremely rapid or that the environment was not suitable for such scavengers (Chen, 2000).

Clam shrimp were successful in maintaining their presence in high abundance, indicated by the high density of *Triglypta haifanggouensis* fossils on bedding planes of both excavation sites, which might relate to their exceptional tolerance to extreme environmental conditions, highlighted by low oxygen requirements in some extant species (e.g. Horne, 1971; Eriksen and Brown, 1980). The lake probably contained well-maintained egg reserves that would hatch on large scale following suitable hatching conditions. In contrast, aquatic insects require more oxic conditions. Mayfly nymphs are highly sensitive to oxygen depletion, and are therefore commonly used as bioindicators (e.g. Hubbard and Peters, 1978). The absence of aquatic insects on some bedding planes (e.g. bedding planes M, N, P, Q, south site) corresponds to couplets of clay-poor and clay-rich laminae, which reflect dysoxic to anoxic depositional conditions caused by seasonal stratification of the lake (Sturm and Matter, 1978), under which aquatic insects could not survive.

Terrestrial insects and plants were much more diverse but less abundant than the benthic community. Modern edaphic insects play an important role in habitats near water bodies, as they require high moisture conditions. Of all terrestrial insects of the Daohugou sites, specimens of edaphic insects are most abundant and best preserved. By comparison, specimens of alpine insects occur sporadically, preserved in varying stages of decomposition, suggesting longer distances of post mortem transportation. This is consistent with the scenario inferred from the flora of the same site, which reflects a well-vegetated forest landscape (Na et al., 2015; Pott and Jiang, 2017). The high diversity of conifers, bennettites and ginkgophytes, as well as the presence of silvan insects in the lake deposits suggest that forests existed adjacent to the lake.

6. Conclusions

The fauna of the Daohugou area was characterized by a low-diversity, high to medium-density aquatic community (four species) and a high-diversity, low-density terrestrial community (over 60 species of

insect species and 23 plant species). Biotic and sedimentary evidence are generally pointing to a shallow, small lake environment. The clam shrimp *Triglypta haifanggouensis* dominated almost all excavated fossil communities (with only one exception), generally accounting for 90–100% of all individuals. The absence of aquatic insects on bedding planes indicates recurrent intervals of unfavourable conditions, such as dysoxic conditions caused by seasonal stratification. Bimodal to polymodal size distributions of *T. haifanggouensis* indicate mass mortalities caused by volcanic activity or lake-intrinsic factors such as temperature fluctuations. Also, the difference in carapace size between the two excavation sites represents variability in the physico-chemical conditions of the water bodies in the Daohugou area through time. The preferred orientation of aquatic insects detected on four out of nine bedding planes indicates the repeated presence of weak currents, which contributed to the concentration of aquatic animals. The terrestrial community is highly diverse, dense vegetation and abundant terrestrial insects indicate an overall humid climate. Animals from various ecological niches were simultaneously killed and quickly buried. As a result of rapid burial, 49.8% of terrestrial insects are excellently preserved and articulated. Mass mortality events triggered by volcano eruptions may have frequently occurred in the studied area, corroborated by alternations of lacustrine deposits and volcanoclastic apron deposits.

Data availability

The raw data of this work is hosted in the Mendeley repository.

Acknowledgments

We would like to thank Qi Zhang, He Wang and Miao Ge for their help in the field. The staff at the Daohugou National Geopark provided their maximum support. Christian Pott kindly assisted us with the identification and classification of the plant fossils. We are grateful to three anonymous reviewers for their careful manuscript reviews. This work was supported by the National Natural Science Foundation of China, China (41672010; 41688103; 41572010) and the Strategic Priority Research Program (B) of the Chinese Academy of Sciences, China (XDB26000000).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2019.05.028>.

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