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New insect assemblage from the early Oligocene in Ningming Basin, Guangxi, China

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Abstract

The Ningming Basin was characterized by a humid subtropical monsoon climate during the early Oligocene, which supported a rich assemblage of plant and fish fossils. However, the insect fauna from this period has remained poorly documented, with only a single damselfly species formally described. Recent investigations have yielded a distinct collection of insect fossils, comprising at least five orders and represented by 98 specimens, among which ants are the predominant group. In addition, we report four distinct types of herbivory traces and one pathogen-related damage type on contemporaneous leaves, providing direct evidence of biological interactions. These findings significantly expand the known early Oligocene entomofauna from southern China and enhance our understanding of terrestrial ecosystems under a humid subtropical monsoon regime during this epoch.

Key words: Insect fossils, entomofauna, Insect damage types, Ningming Formation

Introduction

The Ningming Basin is situated in Ningming County, Chongzuo City, in the Guangxi Zhuang Autonomous Region of southwestern China. It lies in close proximity to, and is nearly contiguous with, the Na Duong Basin in northern Vietnam (Chen, G. *et al*., 2018). The Palaeogene strata in the basin comprises the Eocene Dazha Formation and the overlying Oligocene Ningming Formation (Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region, 1985; Ning *et al*., 1994). The Ningming Formation consists predominantly of gray mudstones interbedded with yellow siltstones and fine sandstones, representing a suite of lacustrine deposits (Dong *et al*., 2015). From this formation, the Ningming biota has yielded a diverse fossil assemblage, including plants, insects, fishes, fungi, as well as spores and pollen (Wang *et al*., 2003; Shi *et al*., 2010; Ma *et al*., 2015; Chen, G. *et al*., 2018; Ling *et al*., 2021; Xu *et al*., 2021).

The absence of volcanic materials and mammal fossils has long contributed to uncertainties regarding the age of the Ningming Formation (Dong *et al*., 2015). Initially, studies of fish fossils suggested a Miocene age for the

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formation (Chen *et al*., 2004). However, subsequent palynostratigraphic analysis indicated an Oligocene age (Wang *et al*., 2003), a view corroborated by plant fossil evidence (*e.g*., Li *et al*., 2003; Chen *et al*., 2005; Shi *et al*., 2010, 2012) and subsequently widely adopted (Chen Y. *et al*., 2018; Chen *et al*., 2011, 2021; Dong *et al*., 2016, 2018). More recently, biostratigraphic studies within an Eastern Asian framework have constrained the fossil-bearing beds of the Ningming Formation to the early Oligocene (Rupelian) (Li *et al*., 2021). This refined chronology has been embraced in the latest research (*e.g*., Li *et al*., 2021; Huang *et al*., 2022).

The early Oligocene Ningming flora was dominated by angiosperms, with subordinate components of gymnosperms and ferns. Represented families include Juglandaceae, Fagaceae, Fabaceae, Lauraceae, Moraceae, Arecaceae, Anacardiaceae, Hamamelidaceae, Betulaceae, Simaroubaceae, Ulmaceae, Sapindaceae, Pinaceae, Cupressaceae, Cephalotaxaceae, Taxodiaceae, and Osmundaceae (Chen, Y. *et al*., 2018). Evidence of epiphyllous and endophytic fungi has also been documented on fossil leaves and within fruits (Shi *et al*., 2010; Ma *et al*., 2015; Xu *et al*., 2021). Climate reconstruction using the Climate Leaf Analysis Multivariate Program (CLAMP) indicates that the flora developed under a humid subtropical climate with weak monsoon influence at mid-altitudes (approximately 1.24–1.35 ± 0.52 km) (Ling *et al*., 2021). While some plant fossil evidence suggests cooler conditions than present (Shi *et al*., 2012; Chen 2015, 2017), CLAMP-based estimates imply broadly comparable temperatures (Ling *et al*., 2021). In contrast, carbon isotope analyses point to a warmer and more humid palaeoclimate than today (Wang *et al*., 2020). Additionally, early Oligocene atmospheric CO_2 concentrations in the Ningming Basin have been estimated between 255 and 972 ppmv (Sun *et al*., 2017).

In addition, the Ningming Formation contains abundant fish fossils, primarily represented by Cypriniformes, †Ellimmichthyiformes, Siluriformes, and Gobiiformes (Chen, G. *et al*., 2018). The presence of †Ellimmichthyiformes and Gobiiformes in the assemblage suggests that the area may have experienced marine incursions during this period (Chen, G. *et al*., 2018).

Numerous Oligocene or Oligocene-Miocene biotas worldwide have documented the insect diversity of these periods (*e.g*., CoBabe *et al*., 2002; Wedmann *et al*., 2010; Gaudant *et al*., 2018; LaPolla, 2023; Nel *et al*., 2023, 2024; Córdova-Tabares *et al*., 2024; Engel *et al*., 2024; Kaulfuss *et al*., 2024). In contrast, the fossil insect record from the Ningming Formation remains notably scarce. Although initial collections were reported by earlier researchers (Kuang *et al*., 2004), no illustrations or formal descriptions have been published to date, with the sole exception of the damselfly species *Guangxicalopteryx huashanensis* (Huang *et al*., 2022). In this study, we present a collection of insect fossils obtained in recent years from outcrops near Ningming County town. These specimens represent an assemblage comprising at least five orders: Odonata, Hemiptera, Coleoptera, Diptera, and Hymenoptera. Additionally, we report fossil leaves from the same strata that exhibit distinct damage traces, providing key clues for investigating biological interactions in the early Oligocene Ningming Basin.

Material and methods

Fossil material was collected from exposures adjacent to Luoyue Avenue in Chengzhong Town, Ningming County, Chongzuo City, Guangxi, southwestern China (Fig. 1). A total of 109 specimens, comprising both insect fossils and leaves with insect damage, were examined. The majority of fossils are preserved in thin layered mudstones, with a minority of insects occurring in fine sandstones (Fig. 2). Preservation is generally moderate to poor; most insect specimens are fragmentary, represented by isolated wings or incomplete bodies lacking detailed morphological structures. As a result, comprehensive taxonomic description remains pending for most material, and only one new odonatan species is formally established in this study.

Specimens were carefully prepared using fine needles and sharp knives. Photographs were taken with a digital camera mounted on a Zeiss Discovery V16 microscope, and image adjustments and plate compositions were performed using Adobe Photoshop 2020. All illustrated specimens are deposited in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS), Nanjing, China.

In the section of systematic palaeontology, wing venation terminology follows Riek and Kukalová-Peck (1984), as amended by Nel *et al*. (1993) and Bechly (1996). Insect damage types (DTs) on fossil leaves were identified using the established *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* within the functional feeding group (FFG)—DT framework (Labandeira *et al*., 2007). Recognition of insect-derived traces was based on the presence of plant reaction tissues responsive to herbivory, insect-specific structural patterns, and repeated occurrences of damage morphologies on host plants, allowing distinction from physical degradation, detritivory, or taphonomic artifacts (Maccracke *et al*., 2022).

FIGURE 1. Map of fossil locality, red triangle indicating fossil site.

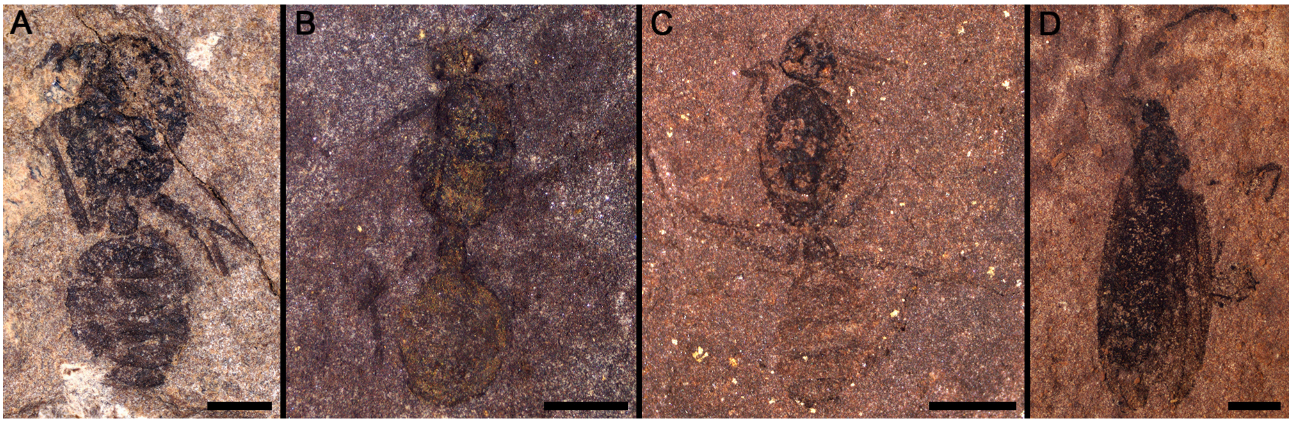

FIGURE 2. Formicids and a march fly from fine sandstones of Ningming Formation. **A**–**C**, Unidentified formicids, NIGP200719–200721. **D**, *Plecia* sp., female, NIGP200722. Scale bars: 1.25 mm in **A**; 2 mm in **B** and **D**; 2.5 mm in **C**.

Results

Hymenopterans constitute the most abundant group among the insect fossils, with ants (Formicidae) accounting for approximately 53% of all specimens (Figs 2A–C, 3C–N). Most ant individuals are preserved as complete, wingless bodies (Figs 2A–C, 3G–N). In addition to the ant specimen, two wasp wings were also preserved separately (Fig. 3A, B). While one specimen consists solely of a detached forewing, the other comprises a hindwing with an associated partial body fragment, which is tentatively attributed to the family Vespidae (Fig. 3B). Coleoptera represent the most taxonomically diverse component of the assemblage. All collected beetles belong to the suborder Polyphaga (Fig. 4), and several specimens can be assigned to the families Brentidae, Hydrophilidae, and Coccinellidae, respectively (Fig. 4A, B, D). In addition, one specimen is attributable to the superfamily Elateroidea (Fig. 4E), though its precise familial affinity remains uncertain.

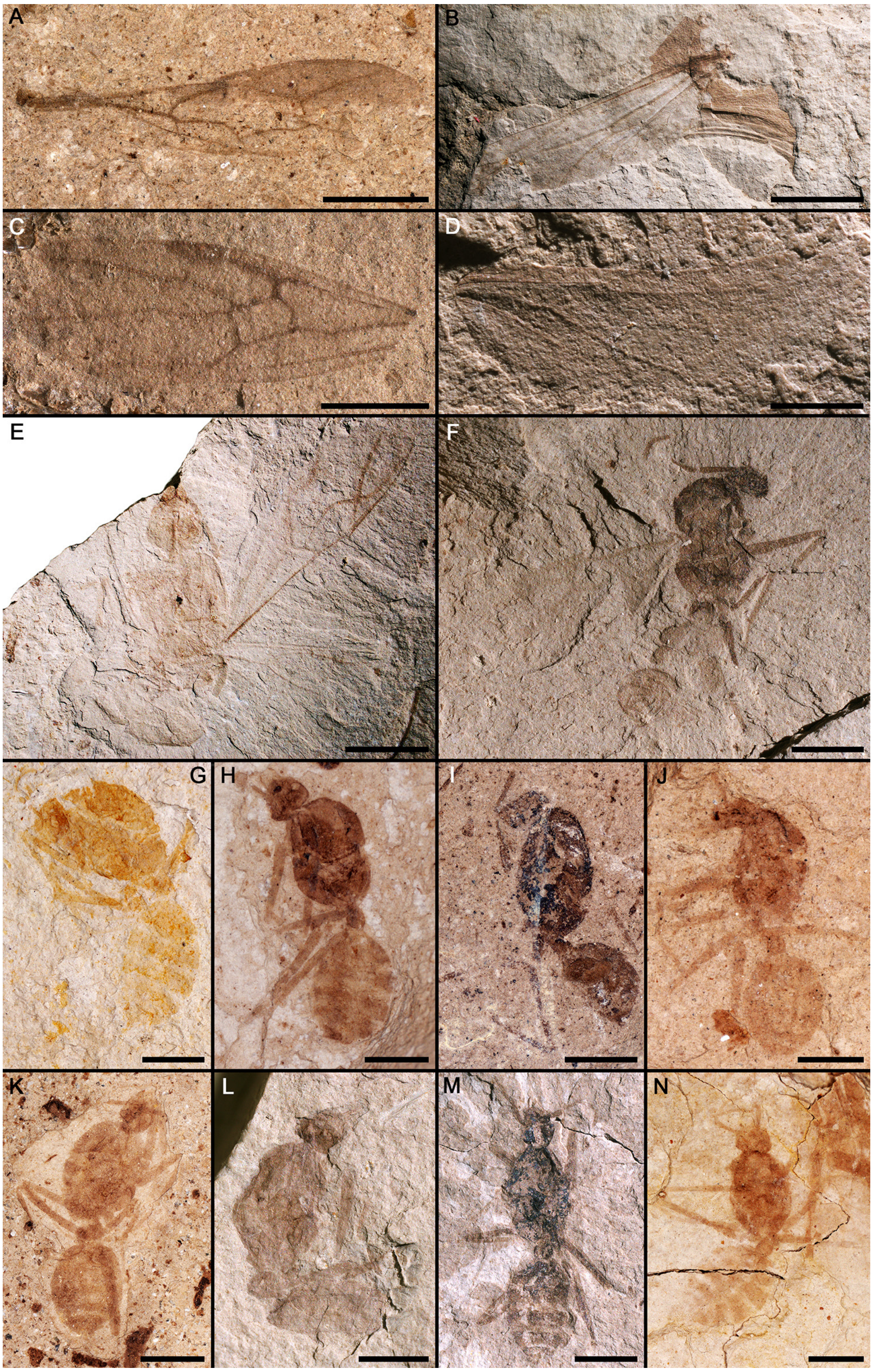

FIGURE 3. Hymenopterans from Ningming Formation. **A**, Unidentified wasp forewing, NIGP200706. **B**, Unidentified wasp hindwing, NIGP200695. **C**–**N**, Unidentified formicid specimens, NIGP200707–200718. Scale bars: 5 mm in **B**, **E**; 2 mm in others.

FIGURE 4. Beetles from the Ningming Formation. **A**, Unidentified brentid specimen, NIGP200696. **B**, Unidentified coccinellid specimen, NIGP200700. **C**, Unidentified polyphagan specimen, NIGP200697. **D**, Unidentified hydrophilid specimen, NIGP200698. **E**, Unidentified elateroid specimen, NIGP200699. Scale bars: 500 µm in **A**, **B**, **D**, **E** and **F**; 1 mm in **C**, **D**.

As commonly documented in other Palaeogene insect taphocoenoses globally (*e.g*., Wilson, 1978; McCobb *et al*., 1998; CoBabe *et al*., 2002; Wedmann *et al*., 2010; Gaudant *et al*., 2018), march flies (Bibionidae) are also relatively well represented in the Ningming Basin material (Figs 5A–D, 7D). Furthermore, one unidentified dipteran wing as well as one dipteran larva was recovered from the site (Fig. 5E, F). In contrast, hemipteran diversity is low, with only two specimens tentatively assigned to Pentatomidae (Fig. 6). Although the preservation of the odonatan fossil is suboptimal, diagnostic characteristics observed in the specimen have enabled the establishment of a new genus and species within the family Whetwhetaksidae (Fig. 7). Further details are provided in the systematic palaeontology section.

Leaf fossils recovered during recent fieldwork exhibit a range of insect-mediated herbivory traces. A betulaceous leaf displays skeletonization damage (Fig. 8A, B), characterized by interveinal tissue removal resulting in a reticulate pattern, with patches exhibiting roughly equivalent maximum and minimum diameters. This damage is consistent with either DT16 or DT24. However, the absence of a well-defined reaction rim and the lack of preferential distribution along the primary vein support its assignment to DT16.

FIGURE 5. Dipterans from Ningming Formation. **A**, **B**, A relatively completed Bibionidae, *Plecia* sp., male, NIGP200701a, b. **C**, **D**, Forewings of *Bibio* sp., NIGP200702–200703. **E**, Unidentified dipteran wings, NIGP200704. **F**, Dipteran larva, NIGP200705. Scale bars: 1 mm in **C**, **D** and **F**; 2 mm in **A**, **B** and **E**.

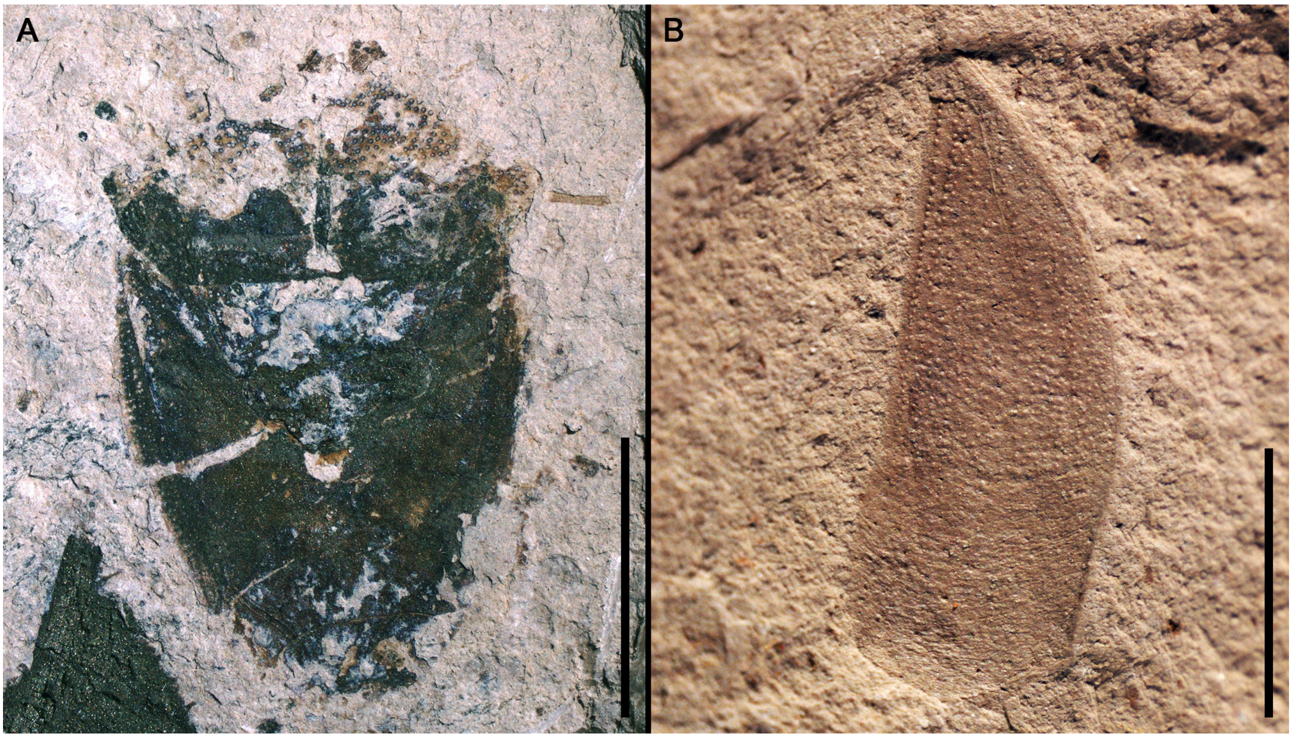

FIGURE 6. True bugs from Ningming Formation. **A**, Nearly complete specimen of Pentatomidae, NIGP200693. **B**, Possible tegmen of Pentatomidae, NIGP200694. Scale bars: 5 mm in **A**; 3 mm in **B**.

A lauraceous leaf shows a distinct form of skeletonization (Fig. 8C, D), manifesting as a slender, curved, and branched trace with variable band width, conforming to the diagnostic criteria of DT22. Another leaf from Lauraceae exhibits hole-feeding damage (Fig. 8E, F), comprising perforations 1–3 mm in diameter situated between veins, with complete removal of leaf tissue. This damage pattern is consistent with either feeding trace DT02 or DT03. However, while DT02 typically produces circular to isodiametric lesions, DT03 is distinguished by irregular, often lobate to elongated-elliptical morphologies. Based on the clearly observed elongated-elliptical shape of the lesions in our specimen, we assign this damage to DT03.

Additional damage was observed on fabaceous and fagaceous leaves (Fig. 8G, H), consisting of ovoid lesions with a diffuse, dark reaction front, potentially indicative of tissue necrosis caused by pathogenic microorganisms such as fungi or bacteria. This damage is tentatively classified as DT58. Additionally, it is noteworthy that within the FFG–DT system, the vast majority of damage types originate from insects; however, a small number are attributed to other terrestrial invertebrates such as mites and myriapods, or even pathogens, with DT58 serving as a representative example (Labandeira *et al*., 2007).

One further leaf fossil, of uncertain familial assignment due to poor preservation, also exhibits skeletonization damage (Fig. 8I, J). The trace forms a broad, sub-rectangular patch oriented at an angle to the leaf axis, with a length-to-width ratio exceeding 3, supporting its assignment to DT19.

Systematic palaeontology

Order Odonata Fabricius, 1793

Suborder Zygoptera Sélys, 1854

Family Whetwhetaksidae Archibald & Cannings, 2021

Type genus. ***Whetwhetaksa*** **Archibald & Cannings, 2021**

Other genera. *Danowhetaksa* Simonsen, Ware & Archibald, 2022, *Sinowhetaksa* Nel **gen. nov.**

Remarks. Archibald *et al*. (2021) tentatively included the Whetwhetaksidae in the suborder Cephalozygoptera Archibald, Cannings & Erickson, 2021, mainly based on head characters, which are unknown in this family. Later Nel & Zheng (2021) suggested that this order is poorly defined on the basis of deformations of the heads of the concerned fossils. Archibald & Cannings (2021) denied the values of Nel & Zheng (2021)' arguments, but Nel & Jouault (2022) proposed new arguments to confirm their opinion. More recently, Ware *et al*. (2025: figs 3–4) proposed a phylogenetic analysis of the Cephalozygoptera, without defined outgroup(s), and thus also without strong proof of the monophyly of this set of taxa. Thus, the definition and value of the Cephalozygoptera remain dubious and we prefer to consider the Whetwhetaksidae as a family of 'Zygoptera' *sensu lato* (sister group to the Epiproctophora). A new analysis of these enigmatic damselflies is under study by Jouault *et al*.

Sinowhetaksa **Nel gen. nov.**

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Type species. *Sinowhetaksa incompleta* Nel **sp. nov.**

Etymology. Named after 'Sinica', Latin name for China and the suffix 'whetaksa', employed for the genera of Whetwhetaksidae. Gender feminine.

Diagnosis. Wing venation characters only. Base of RP2 five cells distad subnodus; 19 postnodal crossveins; base of IR2 one cell basad nodus, one row of cells in area between C and RA just distad pterostigma.

Sinowhetaksa incompleta **Nel sp. nov.**

urn:lsid:zoobank.org:act:5500D7E4-A836-4A4D-821F-317199603CFC

Material. Holotype, a fragmented wing attached to thorax (Fig. 7), NIGP200692, stored at NIGPAS.

FIGURE 7. Wing fragments of *Sinowhetaksa incompleta* Nel, **gen. et sp. nov. A**, Holotype, general view, NIGP200692. **B**, Enlargement of pterostigma area. Scale bars: 2 mm in **B**; 5 mm in **A**.

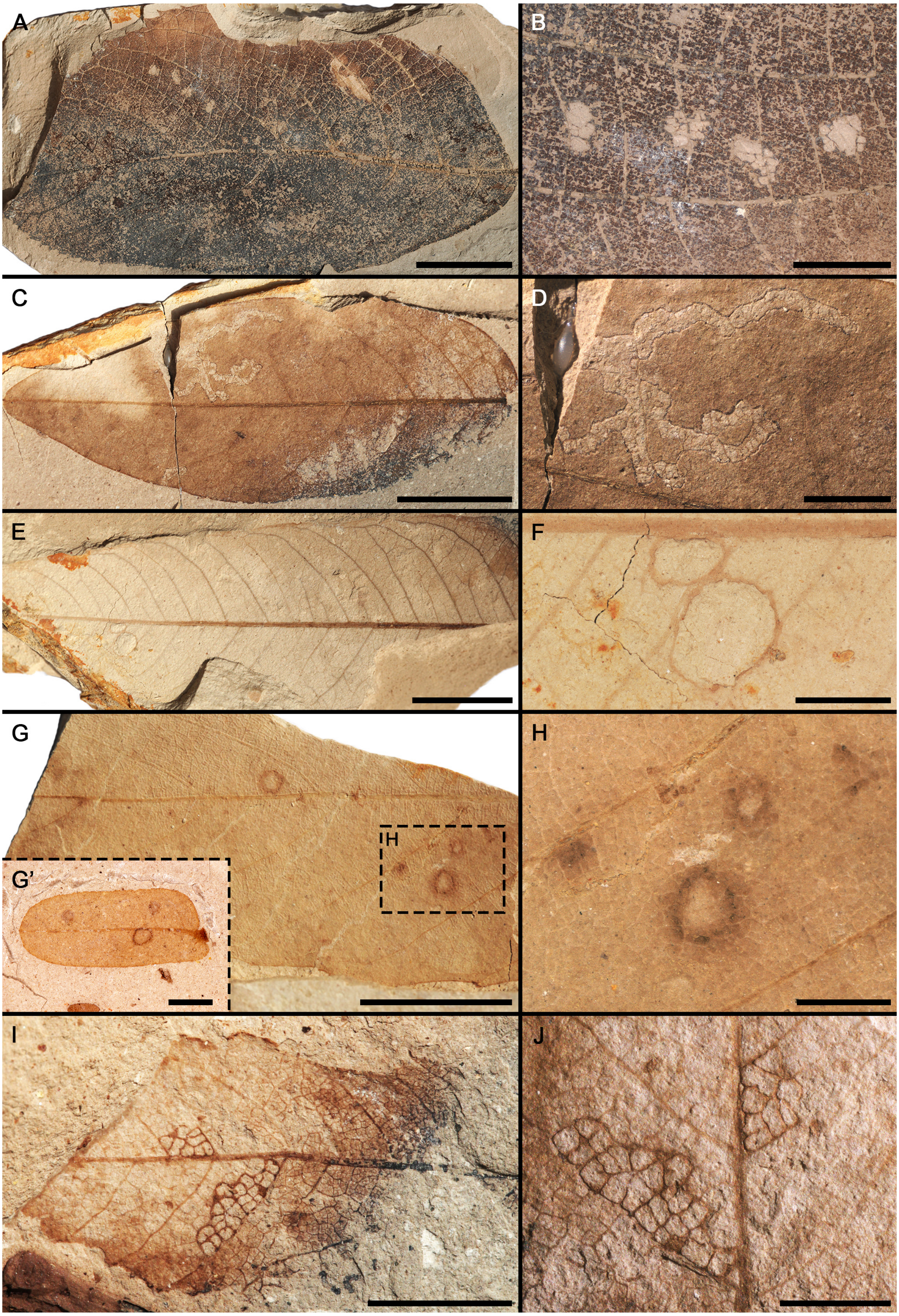

FIGURE 8. Leaves with diverse damages from Ningming Formation. **A**, **B**, A betulaceous leaf with DT 16, NIGP200723. **C**, **D**, A lauraceous leaf with DT 22, NIGP200724. **E**, **F**, A lauraceous leaf with DT 03, NIGP200725. **G**, **H**, A fagaceous leaf with probably DT 58, NIGP200726; **G'** indicates the same damage type on a fabaceous leaf, NIGP209584. **I**, **J**, An unidentified leaf with DT 19, NIGP200727. Scale bars: 2 mm in **F**, **G'**, **H**, **J**; 3mm in **D**; 5 mm in **B** and **I**; 10 mm in **C**, **E** and **G**; 20 mm in **A**.

Etymology. Named after the incomplete state of preservation of the holotype.

Diagnosis. As for the genus.

Locality and horizon. Ningming Formation; along the Luoyue Avenue, Chengzhong Town, Ningming County, Chongzuo City, Guangxi, China; early Oligocene (Rupelian).

Description. Wing hyaline with brown pterostigma; wing ca. 27.0 mm long, ca. 7.7 mm wide; petiole rather short, 2.9 mm long; CuP just basad base of AA; anal area narrow below subdiscoidal cell, with one row of cells; distance from base to nodus 6.6 mm; from nodus to pterostigma 14.2 mm; from pterostigma to wing apex ca. 1.9 mm; pterostigma elongate, 3.3 mm long, width between 0.6 mm and 0.8 mm (the vein RA along its posterior margin compressed and deformed so that the pterostigma seems to be wider than it should be); basal side of pterostigma very oblique; distal side even more oblique and very long, with a distinct 'prolongation' along costal margin, 0.3 mm long; one row of cells in area between C and RA just distad pterostigma but two rows distally; no oblique pterostigmal brace; 19 postnodal crossveins, basal-most ones being well aligned with postsubnodal crossveins and distal ones not aligned; nodal crossvein and subnodus well aligned and strongly oblique; base of RP2 five cells distad subnodus; base of IR1 ca. six cells distally; base of IR2 one cell basad nodus; CuA terminating at margin over half wing length, well distad nodus; MA close to, subparallel with RP3-4 to posterior margin; MA and MP diverging to posterior margin; MP and CuA subparallel to posterior margin.

Remarks. Although fragmentary, this wing is attributed to Zygoptera *sensu lato* because of the presence of a petiole, shape of subdiscoidal cell, and very long postnodal area. It does not fit in the epiproctophoran Isophlebioptera Bechly, 1996 that have also these characters, because of the narrower anal area and subdiscoidal cell. This last clade was still present during the Eocene through the family Pseudostenolestidae (Garrouste & Nel, 2015). There are rather few damselfly families with such broad wings, elongate pterostigma, long postnodal area compared to antenodal one, and so numerous postnodal crossveins, viz. the Dysagrionidae, Sieblosiidae, Whetwhetaksidae, Shundeagrionidae, Menatlestidae, Latibasaliidae, Thaumatoneuridae, and Heliocharidae. Affinities with the Heliocharidae are excluded because of the longer petiole, and base of IR2 close to nodus; affinities to Thaumatoneuridae are excluded because the base of RP2 is only five cells distad subnodus (Münz, 1919). Affinities with the Sieblosiidae are excluded because the subnodus is in straight line with the nodal crossvein and of strong 'normal' obliquity, and the base of IR2 is one cell basad the nodus. Affinities with the Shundeagrionidae, Menatlestidae, and Latibasaliidae are excluded because the base of IR2 is one cell basad nodus vs midway between nodus and arculus, and distal side of the pterostigma is strongly oblique vs much less in the latter groups (Petrulevičius & Nel, 2007; Nel & Jouault, 2022; Huang *et al*., 2025). Affinities with the Dysagrionidae are excluded because the subnodus is much more oblique than in this family (with a weak 'normal' obliquity to perpendicular to RP in the Dysagrionidae) (Archibald *et al*., 2021: figs 67-67; Simonsen *et al*., 2022: figs 1A, 2A). Also the distal side of the pterostigma of the new fossil has a very particular shape, very oblique with a short but distinct 'prolongation' along costal margin. This character is present in the Whetwhetaksidae, but not in the other families, even if some Dysagrionidae (*e.g*., *Okanagrion*, *Dysagrion*) also have an oblique distal side of the pterostigma, but less than in the new fossil and the Whetwhetaksidae, and no costal 'prolongation'. This character is not listed in the diagnoses proposed by Archibald *et al*. (2021: 110), Simonsen *et al*. (2022: 587), and Ware *et al*. (2025) for the Whetwhetaksidae, but it is a putative synapomorphy for this family, present in the type genus *Whetwhetaksa* and in *Danowhetaksa*.

The preserved characters of the new fossil fit well with those listed in the diagnoses of this family, viz. distinctively long pterostigma [Simonsen *et al*. indicated 'length at least seven times width', while it is five to eight times, depending if we count the width of the vein RA along its posterior margin in the new fossil, but this character can greatly vary in representatives of the same family, *e.g*., see the different situations in the Dysagrionidae]; nodus to base of pterostigma 55–60% of nodus to apex [75% in the new fossil, due to the slightly shorter pterostigma]; arculus just distal to Ax1, closer to it than to Ax2 [unknown in the new fossil]; oblique vein O absent [probably shared by the new fossil]; nodal, subnodal crossveins of 'normal' obliquity [shared by the new fossil]; base of RP2 close to nodus [shared by the new fossil]; CuA terminates at margin over half wing length [shared by the new fossil]; MA close to, subparallel with RP3-4 to margin [shared by the new fossil]; MA and MP diverge to margin [shared by the new fossil]; MP and CuA remain subparallel to margin [shared by the new fossil].

In conclusion, the new fossil can be attributed to the Whetwhetaksidae, especially because of the specialized shape of the distal margin of the pterostigma.

Its base of RP2 is five cells distad subnodus, vs. only two to four cells in *Whetwhetaksa*, and eight cells in *Danowhetaksa*. It also has only 19 postnodal crossveins, vs. ca. 20 in *Whetwhetaksa*, and ca. more than 25 in

Danowhetaksa. Its base of IR2 is one cell basad the nodus, vs. in a well basal position in *Whetwhetaksa* and two small cells basad in *Danowhetaksa*. Lastly, there is only one row of cells in area between C and RA just distad the pterostigma, vs. two rows in *Whetwhetaksa* and *Danowhetaksa*, but this last character is more of species level than the preceding.

It is not very surprising to find a representative of the Whetwhetaksidae in China as this family is present in the Paleogene of Eastern North America and Western Europe. This group is either quite ancient, Cretaceous or probably could 'migrate' between Eurasia and North America through the 'Beringian Bridge' as for some other Odonata (Garrouste & Nel, 2019).

Discussion

The Cenozoic era was marked by profound climatic shifts driven by transient climatic events, tectonic activity, and astronomical cycles, which collectively induced significant ecosystem transformations. A pronounced global cooling trend occurred by the latest Eocene to earliest Oligocene, associated with the Oi-1 glaciation event and accompanied by increased climatic seasonality (Ivany *et al*., 2000; Zachos *et al*., 2001, 2008). In response, hardy and drought-tolerant vegetation began to assume more critical roles in Oligocene ecosystems, as evidenced in tropical and subtropical regions of China (Wang *et al*., 2015).

In the Nanning Basin of Guangxi, located approximately 160 km northeast of the Ningming Basin outcrops, the Oligocene Yongning Formation has yielded a diverse fossil assemblage including bivalves, gastropods, ostracods, fish, reptiles, mammals, plants, and fungi (Tian *et al*., 2018). More recently, amber deposits have also been reported from the upper section of this formation (Liu *et al*., 2021). Palynological analyses from the lower Yongning Formation indicate a warm and humid climate, with an upward-decreasing trend in Pinaceae pollen interpreted to reflect gradual warming during the early–middle Oligocene following rapid cooling at the Eocene–Oligocene boundary (Wang *et al*., 2015). In contrast, other studies infer a cool temperate environment based on palynomorph assemblages dominated by Pinaceae, *Abies*, and/or *Tsuga*, interpreted as a cold signal following the Oi-1 glaciation (Tian *et al*., 2018). Despite taphonomic biases, both interpretations reveal an increase in conifer abundance compared to Eocene greenhouse floras, indicating a floristic response to climatic change.

Recent CLAMP results indicate that the early Oligocene Ningming flora comprised evergreen gymnosperms, palms, and broad-leaved deciduous or evergreen trees and shrubs, existing under a humid subtropical climate characterized by hot summers and warm winters (Ling *et al*., 2021). This climatic interpretation is further supported by fungal remains from the same paleoflora (Ma *et al*., 2015). While Oligocene insect deposits are rarely reported from China, they are well documented from Europe and North America, *e.g*., the Creede Formation (Colorado, USA), Canyon Ferry and Ruby River Basin (Montana, USA), Céreste, Bois d'Asson, and Aix-en-Provence (France), and the Rott and Enspel Lagerstätten (Germany) (Grimaldi & Engel, 2005). The Creede insect fauna is largely representative of high-altitude, conifer-dominated environments, whereas other sites such as Canyon Ferry, Ruby River Basin, Rott, Céreste, Aix-en-Provence, and Enspel are typically dominated by taxa such as water boatmen, weevils, or march flies—distinct from the composition of the Ningming entomofauna (CoBabe *et al*., 2002; Wedmann *et al*., 2010; Gaudant *et al*., 2018; Carpenter *et al*., 1938; Wilson *et al*., 1978). Notably, a substantial assemblage of ant fossils has recently been documented from the early Oligocene Canyon Ferry Reservoir deposit, establishing it as the only definitively Oligocene-aged fossil locality in North America known to contain ants (LaPolla, 2023). The Eocene–Oligocene transition has been proposed as a potential inflection point in the evolution of modern ant generic composition, as evidenced by the North American record (LaPolla, 2023). In this context, the discovery of ant fossils within the Ningming biota provides valuable new material for understanding the evolutionary trajectory of ant communities through time. Furthermore, a comparison with the late Eocene insect assemblage from the Insect Bed of the Bembridge Marls (Isle of Wight, England; ~36 Ma) reveals a striking similarity: both are strongly dominated by ants (McCobb *et al*., 1998). Cluster analysis associates the Bembridge Marls insect fauna with modern tropical and subtropical forests experiencing pronounced seasonal rainfall, suggesting that the Ningming entomofauna may reflect a comparable paleoclimatic regime. This interpretation aligns with early Oligocene climatic reconstructions for the Ningming Basin derived from CLAMP analyses, and further supports the hypothesis that this region served as a refugium, preserving Eocene-like ecosystem structures during the early Oligocene cooling period.

Conclusion

This study presents a new insect assemblage from the Ningming Formation, comprising Odonata, Hemiptera, Coleoptera, Diptera, and Hymenoptera, with ants (Formicidae) representing the most abundant component. In addition, we document multiple fossil leaves exhibiting diverse damage types, offering unique clues to biological interactions. Together, these findings provide the first comprehensive characterization of the early Oligocene entomofauna in the Ningming Basin, enhancing our understanding of Northern Hemisphere subtropical ecosystems and their ecological restructuring following the Eocene–Oligocene climate transition.

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References

Archibald, S.B. & Cannings, R.A. (2021) The head of Cephalozygoptera (Odonata). *Zootaxa*, 5047 (1), 97–100.
https://doi.org/10.11646/zootaxa.5047.1.10

Archibald, S.B., Cannings, R.A., Erickson, R.J., Bybee, S.M. & Mathewes, R.W. (2021) The Cephalozygoptera, a new, extinct suborder of Odonata with new taxa from the early Eocene Okanagan Highlands, western North America. *Zootaxa*, 4934, 1–133.
https://doi.org/10.11646/zootaxa.4934.1.1

Bechly, G. (1996) Morphologische Untersuchungen am Flügelgeäder der rezenten Libellen und deren Stammgruppenvertreter (Insecta; Pterygota; Odonata), unter besonderer Berücksichtigung der Phylogenetischen Systematik und des Grundplanes der Odonata. *Petalura*, 2, 1–402.

Bureau of Geology and Mineral Resources of Guangxi Zhuang Autonomous Region. (1985) *Regional Geology of Guangxi Zhuang Autonomous Region*. Geological Publishing House, Beijing, 853 pp.

Carpenter, F.M., Snyder, T.E., Alexander, C.P., James, M.T. & Hull, F.M. (1938) Fossil insects from the Creede Formation, Colorado. *Psyche*, 45 (2–3), 105–119.
https://doi.org/10.1155/1938/46082

Chen, G.J. & Chang, M. (2011) A new early cyprinin from Oligocene of South China. *Science China: Earth Sciences*, 54 (4), 481–492.
https://doi.org/10.1007/s11430-011-4182-5

Chen, G.J., Chang, M.M., Wu, F.X. & Liao, X.W. (2021) *Guiclupea superstes*, gen. et sp. nov., the youngest ellimmichthyiform (clupeomorph) fish to date from the Oligocene of South China. *PeerJ*, 9, e11418.
https://doi.org/10.7717/peerj.11418

Chen, G.J., Liu, J. & Chang, M.M. (2018) Evolutionary hotspot of Cenozoic fish: Paleogene ichthyofauna from the onshore basins around Beibu Gulf. *Chinese Science Bulletin*, 63 (27), 2863–2875.
https://doi.org/10.1360/N972018-00569

Chen, G.Q., Chen, Y.F., Kuang, G.D. & Zhu, Q.P. (2004) Biostratigraphy of Tertiary fossil fishes from Ningming Basin, Guangxi. *Vertebrata PalAsiatica*, 42 (1), 81–85.

Chen, Y.F. & Manchester, S.R. (2015) Winged fruits of *Deviacer* in the Oligocene from the Ningming Basin in Guangxi, South China. *PLoS ONE*, 10 (12), e0144009.
https://doi.org/10.1371/journal.pone.0144009

Chen, Y.F. & Zhang, D.X. (2005) *Bauhinia larsenii*, a fossil legume from Guangxi, China. *Botanical Journal of the Linnean Society*, 147 (4), 437–440.
https://doi.org/10.1111/j.1095-8339.2005.00373.x

Chen, Y.F., Wang, H.S., Liufu, Y.Q., Hu, Q., Fu, Q.Y. & Xie, Z.M. (2018) A new species of *Palaeocarya* (Juglandaceae) from the Ningming Basin in Guangxi, South China. *Phytotaxa*, 367 (1), 55–62.
https://doi.org/10.11646/phytotaxa.367.1.6

Chen, Y.F., Wong, W.O., Hu, Q., Liufu, Y.Q. & Xie, X.M. (2017) A new fossil-species of *Acer* (Sapindaceae) from the Ningming Basin in Guangxi, South China. *Phytotaxa*, 298 (2), 158–164.
https://doi.org/10.11646/phytotaxa.298.2.5

CoBabe, E.A., Chamberlain, K.R., Ivie, M.A. & Giersch, J.J. (2002) A new insect and plant Lagerstätte from a Tertiary lake deposit along the Canyon Ferry Reservoir, southwestern Montana. *Rocky Mountain Geology*, 37 (1), 13–30.

https://doi.org/10.2113/gsrocky.37.1.13

Córdova-Tabares, V.M., Riquelme, F., Varela-Hernández, F. & Estrada-Ruiz, E. (2024) Spider-ant predation in Oligo-Miocene Mexican amber. *Palaeoentomology*, 7 (3), 435–442.
https://doi.org/10.11646/palaeoentomology.7.3.13

Dong, J.L., Sun, B.N., Ma, F.J., Wang, Q.J., Jin, P.H., Wang, W.J., Deng, P., Yang, Y. & Li, X.J. (2015) *Paliurus* fruits from the Oligocene of South China and their phytogeographic implications. *PLoS ONE*, 10 (11), e0140653.
https://doi.org/10.1371/journal.pone.0140653

Dong, J.L., Sun, B.N., Mao, T., Liu, C.H., Wang, X.L., Sun, M.X., Ma, F.J. & Wang, Q.J. (2018) The occurrence of *Burretiodendron* from the Oligocene of South China and its geographic analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 512, 95–105.
https://doi.org/10.1016/j.palaeo.2017.07.004

Dong, J.L., Wang, W.J., Deng, P., Wang, J., Ma, F.J., Wang, Q.J., Yang, Y. & Sun, B.N. (2016) New material of *Palaeocarya* from the Oligocene of Ningming, Guangxi, South China. *PalZ*, 90 (2), 399–412.
https://doi.org/10.1007/s12542-016-0302-z

Engel, M.S., Nguyen, L.T. & Nel, A. (2024) A new genus of polistine wasps from the Oligocene of Aix-en-Provence, France (Hymenoptera: Vespidae). *Palaeoentomology*, 7 (2), 217–220.
https://doi.org/10.11646/palaeoentomology.7.2.4

Garrouste, R. & Nel, A. (2015) New Eocene damselflies and first Cenozoic damsel-dragonfly of the isophlebiopteran lineage (Insecta: Odonata). *Zootaxa*, 4028 (3), 354–366.
https://doi.org/10.11646/zootaxa.4028.3.2

Garrouste, R. & Nel, A. (2019) Alaskan Palaeogene insects: a challenge for a better knowledge of the Beringian ‘route’ (Odonata: Aeshnidae, Dysagrionidae). *Journal of Systematic Palaeontology*, 17 (22), 1939–1946.
https://doi.org/10.1080/14772019.2019.1572235

Gaudant, J., Nel, A., Nury, D., Véran, M. & Carnevale, G. (2018) The uppermost Oligocene of Aix-en-Provence (Bouches-du-Rhône, Southern France): A Cenozoic brackish subtropical Konservat-Lagerstätte, with fishes, insects and plants. *Comptes Rendus Palevol*, 17 (7), 460–478.
https://doi.org/10.1016/j.crpv.2017.08.002

Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, Cambridge, 755 pp.

Huang, D.Y., Liu, Q., Lian, X.N., Fu, Y.Z. & Nel, A. (2022) A new calopterygid damselfly (Odonata, Zygoptera) from the Oligocene Ningming Basin, Guangxi, South China. *Palaeoentomology*, 5 (2), 113–119.
https://doi.org/10.11646/palaeoentomology.5.2.3

Huang, D.Y., Lian, X.N. & Nel, A. (2025) A new damselfly family from the Paleocene of the Sanshui Basin, South China (Odonata, Zygoptera). *Journal of Paleontology*, 98 (6), 1041–1047.
https://doi.org/10.1017/jpa.2024.43

Ivany, L.C., Patterson, W.P. & Lohmann, K.C. (2000) Cooler winters as a possible cause of mass extinctions at the Eocene/Oligocene boundary. *Nature*, 407 (6806), 887–890.
https://doi.org/10.1038/35038044

Kaulfuss, U., Szawaryn, K., Lee, D. & Ruta, R. (2024) The first beetle species described from Oligocene New Zealand amber (Coleoptera: Scirtidae). *Palaeoentomology*, 7 (4), 529–538.
https://doi.org/10.11646/palaeoentomology.7.4.12

Kuang, G.D., Chen, G.Q. & Chen, Y.F. (2004) New information on the Tertiary biostratigraphy of the Ningming Basin, Guangxi. *Journal of Stratigraphy*, 28 (4), 362–366.

Labandeira, C.C., Wilf, P., Johnson, K.R. & Marsh, F. (2007) *Guide to insect (and other) damage types on compressed plant fossils*, version 3.0. Smithsonian Institution, Washington, D.C., 25 pp.

LaPolla, J.S. (2023) Fossil ants (Hymenoptera: Formicidae) of the early Oligocene Canyon Ferry Reservoir deposit. *Palaeoentomology*, 6 (4), 385–397.
https://doi.org/10.11646/palaeoentomology.6.4.10

Li, H.M., Chen, Y.F., Chen, G.J., Kuang, G.D. & Huang, Z.T. (2003) Tertiary fossil winged fruits of *Palaeocarya* from Ningming of Guangxi, South China. *Acta Palaeontologica Sinica*, 42 (4), 543–547.

Li, S.F., Valdes, P.J., Farnsworth, A., Davies-Barnard, T., Su, T., Lunt, D.J., Spicer, R.A., Liu, J., Deng, W.Y.D., Huang, J., Tang, H., Ridgwell, A., Chen, L.L. & Zhou, Z.K. (2021) Orographic evolution of northern Tibet shaped vegetation and plant diversity in eastern Asia. *Science Advances*, 7 (5), eabc7741.
https://doi.org/10.1126/sciadv.abc7741

Ling, C.C., Ma, F.J., Dong, J.L., Zhou, G.H., Wang, Q.J. & Sun, B.N. (2021) A mid-altitude area in southwestern China experienced a humid subtropical climate with subtle monsoon signatures during the early Oligocene: Evidence from the Ningming flora of Guangxi. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 579, 110601.
https://doi.org/10.1016/j.palaeo.2021.110601

Liu, Q., Zeng, G.C., Lian, X.N., Fu, Y.Z., Cai, C.Y. & Huang, D.Y. (2021) A new amber outcrop from the Oligocene Nanning Basin of Guangxi, southern China. *Palaeoentomology*, 4 (4), 326–330.
https://doi.org/10.11646/palaeoentomology.4.4.7

Ma, F.J., Sun, B.N., Wang, Q.J., Dong, J.L., Yang, G.L. & Yang, Y. (2015) A new species of *Meliolinites* associated with Buxus

leaves from the Oligocene of Guangxi, southern China. *Mycologia*, 107 (3), 505–511.
https://doi.org/10.3852/14-270

Maccracken, S.A., Miller, I.M., Johnson, K.R., Sertich, J.M. & Labandeira, C.C. (2022) Insect herbivory on *Catula gettyi* gen. et sp. nov. (Lauraceae) from the Kaiparowits Formation (Late Cretaceous, Utah, USA). *PLoS ONE*, 17, e0261397.
https://doi.org/10.1371/journal.pone.0261397

McCobb, L.M.E., Duncan, I.J., Jarzembowski, E.A., Stankiewicz, B.A., Wills, M.A. & Briggs, D.E.G. (1998) Taphonomy of the insects from the insect bed (Bembridge Marls), late Eocene, Isle of Wight, England. *Geological Magazine*, 135 (4), 553–563.
https://doi.org/10.1017/S0016756898001204

Münz, P.A. (1919) A venational study of the suborder Zygoptera (Odonata) with keys for the identification of genera. *Memoirs of the American Entomological Society*, 3, 1–78.
https://doi.org/10.5962/bhl.title.8499

Nel, A. & Jouault, C. (2022) The odonatan insects from the Paleocene of Menat, central France. *Acta Palaeontologica Polonica*, 67 (3), 631–648.
https://doi.org/10.4202/app.00960.2021

Nel, A. & Zheng, D.R. (2021) The recently proposed odonatan 'suborder' Cephalozygoptera: Fact or fiction. *Palaeoentomology*, 4 (2), 165–170.
https://doi.org/10.11646/palaeoentomology.4.2.5

Nel, A., Martínez-Delclòs, X., Paicheler, J.C. & Henrotay, M. (1993) Les 'Anisozygoptera' fossiles. Phylogénie et classification (Odonata). *Martinia, Numéro Hors Série*, 3, 1–311.

Nel, A., Nel, P. & Garrouste, R. (2024) A new *Plecia* Wiedemann from the Oligocene of Lubéron (France) (Diptera: Bibionidae). *Palaeoentomology*, 7 (4), 465–467.
https://doi.org/10.11646/palaeoentomology.7.4.4

Nel, A., Wei, M.C., Niu, G.Y., Garrouste, R. & Jouault, C. (2023) Description of a new fossil genus of conifer sawfly (Hymenoptera: Diprionidae) revealed by UV light. *Palaeoentomology*, 6 (3), 313–320.
https://doi.org/10.11646/palaeoentomology.6.3.14

Ning, Z.S., Zhou, T.M., Hu, Y.K. & Liang, Z.H. (1994) *Tertiary in Petroliferous Regions of China*. Petroleum Industry Press, Beijing, 374 pp.

Petrulevičius, J.F. & Nel, A. (2007) Enigmatic and little known Odonata (Insecta) from the Paleogene of Patagonia and northwest Argentina. *Annales de la Société Entomologique de France, (N.S.)*, 43 (3), 341–347.
https://doi.org/10.1080/00379271.2007.10697530

Riek, E.F. & Kukalová-Peck, J. (1984) A new interpretation of dragonfly wing venation based upon Early Carboniferous fossils from Argentina (Insecta: Odonatoidea) and basic character states in pterygote wings. *Canadian Journal of Zoology*, 62 (6), 1150–1166.
https://doi.org/10.1139/z84-166

Shi, G.L., Zhou, Z.Y. & Xie, Z.M. (2010) A new *Cephalotaxus* and associated epiphyllous fungi from the Oligocene of Guangxi, South China. *Review of Palaeobotany and Palynology*, 161 (3–4), 179–195.
https://doi.org/10.1016/j.revpalbo.2010.04.002

Shi, G.L., Zhou, Z.Y. & Xie, Z.M. (2012) A new Oligocene *Calocedrus* from South China and its implications for transpacific floristic exchanges. *American Journal of Botany*, 99 (1), 108–120.
https://doi.org/10.3732/ajb.1100331

Simonsen, T.J., Archibald, S.B., Rasmussen, J.A., Sylvestersen, R.L., Olsen, K. & Ware, J.L. (2022) *Danowhetaksa* gen. nov. with two species from the early Eocene Ølst Formation from Denmark, the first Palearctic Whetwhetaksidae (Odonata: Cephalozygoptera). *Zootaxa*, 5099 (5), 586–592.
https://doi.org/10.11646/zootaxa.5099.5.5

Sun, B.N., Wang, Q.J., Konrad, W., Ma, F.J., Dong, J.L. & Wang, Z.X. (2017) Reconstruction of atmospheric CO_2 during the Oligocene based on leaf fossils from the Ningming Formation in Guangxi, China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 467, 5–15.
https://doi.org/10.1088/1475-7516/2019/10/019

Tian, Y., Shaw, D. & Schneider, S. (2018) Oligocene fossil assemblages from Lake Nanning (Yongning Formation; Nanning Basin, Guangxi Province, SE China): Biodiversity and evolutionary implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 505, 100–119.
https://doi.org/10.1016/j.palaeo.2018.05.033

Varela-Hernández, F., Riquelme, F. & Estrada-Ruiz, E. (2024) *Elektroformica azquil* gen. et sp. nov., a new formicine ant from Oligo-Miocene Mexican amber. *Palaeoentomology*, 7 (5), 684–692.
https://doi.org/10.11646/palaeoentomology.7.5.11

Wang, Q.J., Zheng, J., Sun, B.N., Ma, F.J., Wang, Z. & Wang, W.M. (2020) Carbon isotope and paleoclimatic implications of three plants from the Oligocene Ningming Formation, Guangxi. *Acta Sedimentologica Sinica*, 38 (2), 358–366.
https://doi.org/10.1088/1475-7516/2019/10/019

Wang, W.M., Chen, G.J. & Liao, W. (2015) Oligocene palynoflora from Nanning Basin in Guangxi and its palaeoenvironmental significance. *Quaternary Sciences*, 35 (3), 650–659.

Wang, W.M., Chen, G.J., Chen, Y.F. & Kuang, G.D. (2003) Tertiary palynostratigraphy of the Ningming basin, Guangxi. *Journal of Stratigraphy*, 27 (4), 324–327.

Ware, J.L., Simonsen, T.J., Rasmussen, J.A. & Archibald, S.B. (2025) Systematics of the extinct suborder Cephalozygoptera (Odonata): a wing-based analysis comparing its genera with those of extant Zygoptera. *American Museum Novitates*, 4043, 1–19.
https://doi.org/10.1206/4043.1

Wedmann, S., Poschmann, M. & Hörnschemeyer, T. (2010) Fossil insects from the Late Oligocene Enspel Lagerstätte and their palaeobiogeographic and palaeoclimatic significance. *Palaeobiodiversity and Palaeoenvironments*, 90 (1), 49–58.
https://doi.org/10.1007/s12549-009-0013-5

Wilson, M.V.H. (1978) Paleogene insect faunas of western North America. *Quaestiones Entomologicae*, 14 (1), 13–34.

Xu, S.L., Kodrul, T.M., Wu, Y., Maslova, N.P. & Jin, J.H. (2021) Early Oligocene fruits and leaves of *Burretiodendron* (Malvaceae s.l.) from South China. *Journal of Systematics and Evolution*, 59 (5), 1100–1110.
https://doi.org/10.1111/jse.12577

Zachos, J.C., Dickens, G.R. & Zeebe, R.E. (2008) An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature*, 451 (7176), 279–283.
https://doi.org/10.1038/nature06588

Zachos, J.C., Shackleton, N.J., Revenaugh, J.S., Pälike, H. & Flower, B.P. (2001) Climatic response to orbital forcing across the Oligocene-Miocene boundary. *Science*, 292 (5515), 274–278.
https://doi.org/10.1126/science.1058288