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ABSTRACT

Leaf skeletonization represents a distinctive form of insect feeding behavior. It commonly occurs in angiosperm leaves after their initial appearance during the Early Cretaceous. This type of feeding behavior rarely has been documented in pre-Mesozoic fossils. We describe the earliest evidence of insect-skeletonized leaves of *Dictyophyllum nathorstii* Zeiller, affiliated with the extant fern family Dipteridaceae in the Late Triassic Yipinglang flora from southwestern China. The skeletonization generally is located adjacent to the pinna rachilla of the distal free portion of the leaf. In the skeletonized area, the interveinal tissue is completely removed, exposing the pinna rachilla, pinnule midveins, and lateral veins. Most nonvascular tissue has been removed between the vascular bundles, the latter forming polygonal meshes of varying size. Our report of insect-mediated skeletonization of fern leaves from southwestern China fills a spatiotemporal gap in the published data on the paleogeographical distribution and stratigraphic occurrence of plant–arthropod associations, and indicates an antagonistic relationship between a fern host and its insect herbivore.

INTRODUCTION

Plants and insects are the two most species-rich groups of higher organisms, and together they represent 71% of Earth's modern biodiversity (Wilson, 1992; Schoonhoven et al., 2005). The associations between plants and insects are recognized as a major force influencing the evolution of both groups and the development of complexity in terrestrial ecosystems (Krassilov et al., 2008). Based on the fossil record, the history of plant–insect associations can be dated back to the Early Devonian (Labandeira, 2006, 2007; Labandeira et al., 2013). Evidence of insect-mediated damage preserved in various fossil plants indicates that diverse feeding strategies evolved early in the history of land plants and developed continuously over a long period (Scott et al., 1992). Such records provide a primary source of information on the evolutionary dynamics of plants and insects and the patterns of tissue consumption through geological time (Labandeira, 2013; Labandeira and Currano, 2013). Although the range of external foliage feeding behavior of insects extends to very rare hole feeding and skeletonization, mostly on gigantopterid plant hosts during the Early Permian (Labandeira, 1998; Glasspool et al., 2003), skeletonization is scarcely documented on Triassic floras and is mostly represented by a relatively simple feeding style that requires better historical understanding of its early development.

Here we report definitive insect-mediated skeletonization on a distinctive type of fern leaf from the well-preserved Late Triassic Yipinglang flora of central Yunnan Province in southwestern China. This occurrence represents the oldest known fossil evidence of this insect feeding behavior on the extant fern family, Dipteridaceae.

MATERIALS AND METHODS

The fossil plant materials examined in our study were obtained from two coal mines of the Yipinglang Coal Field, Xingwujing (25°04′49″N, 101°55′51″E) and Yangqiaoqing (25°09′22″N, 101°55′29″E), in Lufeng County, central Yunnan Province, southwestern China (Fig. 1). Both sites yield fossil plants from the Ganhaizi and Shezi Formations (Bureau of Geology and Mineral Resources of Yunnan Province, 1990).

The fossil plants from Yipinglang Coal Field were briefly discussed and assigned a Late Triassic age by Hsü (1946, 1950). The Yipinglang flora was geographically constrained, floristically characterized, and defined as a biostratigraphic unit by Lee et al. (1976), who systematically described more than 60 plant species in 34 genera from the Yipinglang Coal Field, including members of the Filicales and Bennettitales that conspicuously dominated the flora. Although a few species remain unidentified, the composition of the flora indicates a Norian–Rhaetian age. The presence of intact, typically nonabraded leaves as much as 250 mm long indicates minimal transportation prior to burial. These parautochthonous plant fossils in the Yipinglang Coal Field are preserved as bulk addpressions, more frequently as impressions, in a matrix ranging from medium-grained siltstone to claystone.

The specimens described here were not prepared. In order to increase the contrast, specimens were immersed in ethanol (100%) during macrophotography and microphotography. Macrophotographs were taken using a Nikon D3X camera with an AF-S Micro NIKKOR 60 mm (or 105 mm) 1:2.8G ED lens, which was mounted on a Kaiser camera stand. Microphotographs were taken using a Leica M205C stereomicroscope equipped with a Leica DFC 500 digital camera system. The line drawings for accompanying figures and photographs were prepared using CorelDRAW® (version X4;) and Adobe Photoshop® CS5 Extended programs, respectively. Images were corrected only for contrast.

The specimens used in this study are housed in the paleobotanical collections of the Yunnan Key Laboratory for Palaeobiology, Yunnan University (catalogue numbers YKLP20011 and YKLP20012).

RESULTS

We collected 514 fossil plant specimens from the Xingwujing and Yangqiaoqing coal mines, including 89 specimens of *Dictyophyllum nathorstii* Zeiller; 18 specimens of *D. nathorstii* show skeletonization, but only two exceptionally well preserved specimens are illustrated in this study and form the basis of the following description. Skeletonization typically is present on the distal free portion of the *D. nathorstii* leaf. The damage generally occurs at the base of pinnules adjacent to the pinna rachilla (Figs. 2A and 2B; arrows), but in some cases it is also present in the middle portion of the pinnules. Skeletonization is a type of external feeding wherein the softer parenchymatous interveinal tissue is completely removed without removal of the lignified vascular or sclerenchymatous tissues (Fig. 2C). Polygonal removal of tissue is surrounded by indistinct reaction rims that enclose a continuous reticulum of secondary vena-

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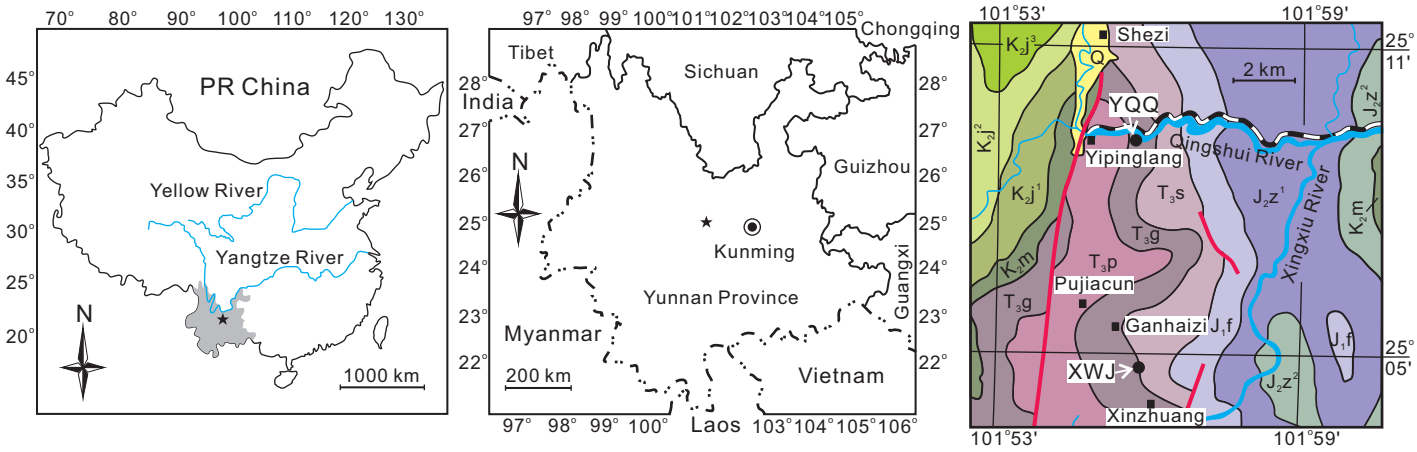

Figure 1. Geographical and geological maps of Yipinglang Coal Field (star; central Yunnan Province, southwestern China) that yielded insect skeletonization on *Dictyophyllum nathorstii* Zeiller. YQQ—Yangqiaoqing Coal Mine; XWJ—Xingwujing Coal Mine; T_3p—Late Triassic Pujiacun Formation; T_3g—Late Triassic Ganhaizi Formation; T_3s—Late Triassic Shezi Formation; J_1f—Early Jurassic Fengjiahe Formation; J_2z^1—lower member of Middle Jurassic Zhanghe Formation; J_2z^2—upper member of Zhanghe Formation; K_2m—Late Cretaceous Matoushan Formation; K_2j^1—lower member of Late Cretaceous Jiangdihe Formation; K_2j^2—middle member of Jiangdihe Formation; K_2j^3—upper member of Jiangdihe Formation; Q—Quaternary (modified from Bureau of Geology and Mineral Resources of Yunnan Province, 1990).

tion (Fig. 2D). Nonvascular tissue is generally absent between the vein meshwork. Locally, even minor portions of the secondary and subsidiary veins have been removed (Fig. 2E). In these cases, the strands of vascular tissue project into the excavated area to varying degrees (Fig. 2F, arrows), or the vascular tissue remnants are discontinuous (Fig. 2G, arrow).

DISCUSSION

Skeletonization on *D. nathorstii* Zeiller in the Yipinglang flora represents the first documented example of an insect herbivory from the Triassic of China. Skeletonization represents a distinctive kind of insect feeding behavior in which an insect feeds on interveinal tissues composed of softer cells, when compared to the more resistant and unherbivorized veins of vascular tissue. This distinctive type of plant–insect interaction is rare to uncommon on Cenozoic angiosperm leaves (Labandeira, 2006, 2007; Vasilenko, 2006). However, the reasons for the rarity of skeletonization on late Paleozoic and early Mesozoic plants remain poorly understood.

Late Paleozoic insect-mediated skeletonization of leaves is very rare (Labandeira and Allen, 2007). Unequivocal examples of skeletonization have not been recorded in pre-Permian floras; the oldest records are from two Permian deposits, the mid-Artinskian Waggoner Ranch Formation at the so-called Taint site in Baylor County (Beck and Labandeira, 1998), and the late Sakmarian Coprolite Bone Bed site (Labandeira and Allen, 2007), both in north-central Texas (USA). These Permian records show taxonomically disparate associations between herbivorous insect lineages and their vascular host plants. Thus, no obvious coevolutionary links can be extrapolated from these relationships.

Ash (1996) illustrated a few examples of slot hole feeding damage on *Zamites* sp. from the Late Triassic Chinle Formation of southwestern Utah (USA). The host plant is an extinct bennettitalean with parallel-veined leaflets. The nonmarginal feeding traces in *Zamites* sp. typically have rounded ends, are bracketed by adjacent veins, and reach more than 26 mm in length (Ash, 1996). However, this relatively simple feeding behavior on *Zamites* is considerably different from the complex and extensive skeletonization on the specimens reported herein.

Grauvogel-Stamm and Kelber (1996) summarized the diverse Middle Triassic plant–insect associations of western Europe that include evidence of external marginal feeding, galls, and ovipositional damage. However, no evidence of insect-mediated skeletonization was observed from the three European localities.

Arthropod interactions with Dipteridaceae were identified from the Southern Hemisphere by Webb (1982), who documented two patches of small rounded bodies on one specimen of *D. bremerense* Shirley from the Late Triassic Blackstone Formation near Denmark Hill, Queensland. These bodies differed from sporangia in shape and size, and were interpreted as possible arthropod galls or ovipositional scars (Webb, 1982). No similar structures were identified in our materials.

The Late Triassic (early Carnian) Molteno Formation in the Karoo Basin of South Africa yields diverse plant compressions and insects (Scott et al., 2004; Labandeira, 2006; Labandeira and Currano, 2013). It provides abundant evidence for external foliage feeding, piercing and sucking, leaf mining, galling, seed predation, and oviposition (Anderson and Anderson, 1989, 2003; Scott et al., 2004; Labandeira, 2006). However, very few examples of insect-mediated skeletonization recently have been recognized from this rich assemblage (C.C. Labandeira, 2013, personal commun.).

The skeletonized *D. nathorstii* Zeiller described here belongs to the fern family Dipteridaceae (Webb, 1982). It may have possessed chemical features similar to those of the living ferns, e.g., alkaloids and cyanogenic glycosides. Leaf nitrogen levels are also generally regarded as an important determinant of leaf quality for herbivorous insects (Sinclair and Hughes, 2010). The specialization of insects to feed on particular plant tissues that contain secondary plant compounds can either stimulate herbivory by phagostimulants or deter consumption through antiherbivore defenses, including digestibility reducers (Theis and Lerdau, 2003). Various insect species may target different portions of the leaf lamina according to the physical and chemical properties of the plant tissues (Schoonhoven et al., 2005). It is obvious from our specimens that the interveinal tissues of *D. nathorstii* were selectively targeted, and that the vascular bundles were conspicuously avoided, presumably because of their coarse texture and/or low nutritive status.

Nonmarginal leaf feeding is a more challenging mode of tissue consumption for insects, requiring specific anatomical modifications (Edwards and Wratten, 1980; Scott et al., 1992). Skeletonization tends to be generated by holometabolous insects that have distinct larval and adult stages, e.g., Coleoptera, Hymenoptera, Diptera, and Lepidoptera (Bernays and Janzen, 1988). The Yipinglang Coal Field is richly fossiliferous, and large numbers of plants were collected together with estheriid conchostracans and a few insect fragments. Only one insect species, *Lufengnecta corrugis* Lin of the Heteroptera, has been described from the fossil

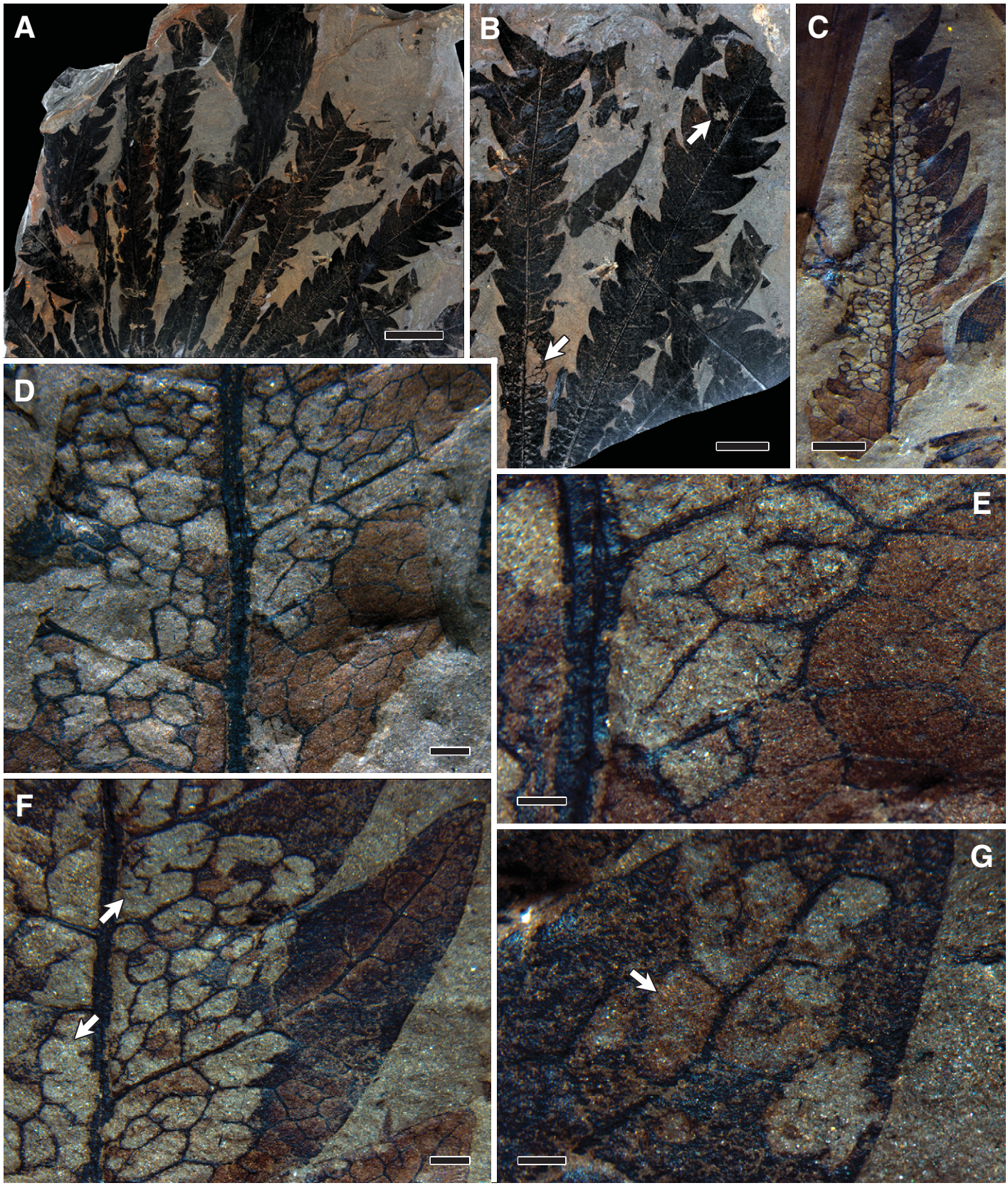

Figure 2. Skeletonization on *Dictyophyllum nathorstii* Zeiller from Late Triassic Yipinglang flora, central Yunnan Province, southwestern China. A: Specimen YKLP20011. Cluster of pinnae form distal portion of leaf; scale bar = 25 mm. B: Enlargement of A; arrows indicate insect-mediated skeletonization occurring close to pinna rachis; scale bar = 15 mm. C: Specimen YKLP20012. Heavily skeletonized pinna; scale bar = 10 mm. D: Enlargement of C, showing polygonal excavations of leaf parenchyma surrounded by indistinct reaction rims; note retention of vascular reticulum within excavated area. Scale bar = 1 mm. E: Enlargement of D. Note local absence of major and minor lateral veins. Scale bar = 500 μm. F: Enlargement of C; arrows indicate vascular strands projecting into skeletonized area to varying degrees. Scale bar = 1 mm. G: Enlargement of C, showing vascular bundles that do not join centrally (arrow); scale bar = 500 μm.

site (Lin, 1977). Because insect body fossils are rarely observed in this and other associated Late Triassic deposits of central Yunnan Province, it is not possible to identify with any certainty insect taxa candidates responsible for the foliar damage described here.

The Triassic remains one of the most poorly known periods in the evolutionary history of terrestrial arthropods (Fraser et al., 1996), and the end of the Triassic Period is pivotal in the evolution of modern ecosystems (Padian, 1986; Labandeira, 2006). Fossilized plant–animal associations, such as herbivory from external foliage feeding, may offer insights into the behavior of ancient animals, and provide information on the autecology of ancient plants and their relationship with herbivorous insects (Pott et al., 2012). Although we are unable to ascertain the insect culprit responsible for the foliar skeletonization described here, our study nonetheless provides the first evidence for a distinctive feeding behavior on a Late Triassic fern that closely resembles its living descendants.

CONCLUSIONS

The oldest known example of insect-mediated skeletonization on the extant fern family Dipteridaceae was documented from the Late Triassic Yipinglang flora of southwestern China. Skeletonization on the host plant is a major category of external feeding manifested by complete removal of interveinal tissue and retention of vascular tissue. Approximately 20% of *Dictyophyllum nathorstii* Zeiller leaves were skeletonized by insect herbivores. Our study sheds light on the early evolutionary history of interactions between extant ferns and their insect consumers.

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REFERENCES CITED

Anderson, J.M., and Anderson, H.M., 1989, Palaeoflora of southern Africa Molteno Formation (Triassic), Volume 2: Gymnosperms (excluding *Dicroidium*): Rotterdam, A.A. Balkema, 567 p.

Anderson, J.M., and Anderson, H.M., 2003, Heyday of the gymnosperms: Systematics and biodiversity of the Late Triassic Molteno fructifications: Strelitzia 15: Pretoria, South Africa, National Botanical Institute, 398 p.

Ash, S., 1996, Evidence of arthropod-plant interactions in the Upper Triassic of the southwestern United States: Lethaia, v. 29, p. 237–248, doi:10.1111/j.1502-3931.1996.tb01657.x.

Beck, A.L., and Labandeira, C.C., 1998, Early Permian insect folivory on a gigantopterid-dominated riparian flora from north-central Texas: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 142, p. 139–173, doi:10.1016/S0031-0182(98)00060-1.

Bernays, E.A., and Janzen, D.H., 1988, Saturniid and sphingid caterpillars: Two ways to eat leaves: Ecology, v. 69, p. 1153–1160, doi:10.2307/1941269.

Bureau of Geology and Mineral Resources of Yunnan Province, 1990, Regional geology of Yunnan Province: Beijing, Geological Publishing House, 728 p. (in Chinese).

Edwards, P.J., and Wratten, S.D., 1980, Ecology of insect-plant interactions: Institute of Biology Studies in Biology Volume 121: London, Edward Arnold Ltd., 60 p.

Fraser, N.C., Grimaldi, D.A., Olsen, P.E., and Axsmith, B., 1996, A Triassic Lagerstätte from eastern North America: Nature, v. 380, p. 615–619, doi:10.1038/380615a0.

Glasspool, I., Hilton, J., Collinson, M., and Wang, S.J., 2003, Foliar herbivory in late Palaeozoic Cathaysian gigantopterids: Review of Palaeobotany and Palynology, v. 127, p. 125–132, doi:10.1016/S0034-6667(03)00107-6.

Grauvogel-Stamm, L., and Kelber, K.-P., 1996, Plant-insect interactions and coevolution during the Triassic in western Europe: Paleontologia Lombarda, Nuova Serie, v. 5, p. 5–23.

Hsü, J., 1946, Mesozoic plants from central Yunnan: Geological Review, v. 11, p. 405–406 (in Chinese).

Hsü, J., 1950, Rhaetic plants from the I-Ping-Lang Coalfield, central Yunnan: Indian Botanical Society Journal, v. 29, p. 19–20.

Krassilov, V., Silantieva, N., and Lewy, Z., 2008, Part I. Traumas on fossil leaves from the Cretaceous of Israel, *in* Krassilov, V., and Rasnitsyn, A., eds., Plant-arthropod interactions in the early angiosperm history. Evidence from the Cretaceous of Israel: Sofia, Bulgaria, Pensoft Publishers, p. 1–187.

Labandeira, C.C., 1998, Early history of arthropod and vascular plant associations: Annual Review of Earth and Planetary Sciences, v. 26, p. 329–377, doi:10.1146/annurev.earth.26.1.329.

Labandeira, C.C., 2006, The four phases of plant-arthropod associations in deep time: Geologica Acta, v. 4, p. 409–438.

Labandeira, C.C., 2007, The origin of herbivory on land: The initial pattern of live tissue consumption by arthropods: Insect Science, v. 14, p. 259–275, doi:10.1111/j.1744-7917.2007.00152.x.

Labandeira, C.C., 2013, Deep-time patterns of tissue consumption by terrestrial arthropod herbivores: Naturwissenschaften, v. 100, p. 355–364, doi:10.1007/s00114-013-1035-4.

Labandeira, C.C., and Allen, E.M., 2007, Minimal insect herbivory for the Lower Permian Coprolite Bone Bed site of north-central Texas, USA, and comparison to other late Paleozoic floras: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 247, p. 197–219, doi:10.1016/j.palaeo.2006.10.015.

Labandeira, C.C., and Currano, E., 2013, The fossil record of plant-insect dynamics: Annual Review of Earth and Planetary Sciences, v. 41, p. 287–311, doi:10.1146/annurev-earth-050212-124139.

Labandeira, C.C., Tremblay, S.L., Bartowski, K.E., and VanAller Hernick, L., 2013, Middle Devonian liverwort herbivory and antiherbivore defence: New Phytologist, doi:10.1111/nph.12643.

Lee, P.C., Tsao, C., and Wu, S., 1976, Mesozoic plants of Yunnan, *in* Mesozoic fossils from Yunnan, Part I: Beijing, Science Press, p. 87–150 (in Chinese).

Lin, Q.B., 1977, Fossil insects of Yunnan, *in* Mesozoic fossils from Yunnan, Part II: Beijing, Science Press, p. 373–381 (in Chinese).

Padian, K., ed., 1986, The beginning of the age of dinosaurs: Faunal change across the Triassic-Jurassic boundary: Cambridge, Cambridge University Press, 378 p.

Pott, C., McLoughlin, S., Wu, S., and Friis, E.M., 2012, Trichomes on the leaves of *Anomozamites villosus* sp. nov. (Bennettitales) from the Daohugou beds (Middle Jurassic), Inner Mongolia, China: Mechanical defense against herbivorous arthropods: Review of Palaeobotany and Palynology, v. 169, p. 48–60, doi:10.1016/j.revpalbo.2011.10.005.

Schoonhoven, L.M., van Loon, J.J.A., and Dicke, M., 2005, Insect-plant biology (second edition): New York, Oxford University Press, 421 p.

Scott, A.C., Stephenson, J., and Chaloner, W.G., 1992, Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic: Royal Society of London Philosophical Transactions, ser. B, v. 335, p. 129–165, doi:10.1098/rstb.1992.0016.

Scott, A.C., Anderson, J.M., and Anderson, H.M., 2004, Evidence of plant-insect interactions in the Upper Triassic Molteno Formation of South Africa: Geological Society of London Journal, v. 161, p. 401–410, doi:10.1144/0016-764903-118.

Sinclair, R.J., and Hughes, L., 2010, Leaf miners: The hidden herbivores: Austral Ecology, v. 35, p. 300–313, doi:10.1111/j.1442-9993.2009.02039.x.

Theis, N., and Lerdau, M., 2003, The evolution of function in plant secondary metabolites: International Journal of Plant Sciences, v. 164, p. S93–S102, doi:10.1086/374190.

Vasilenko, D.V., 2006, Margin feeding damage on the leaves of conifers and ginkgoales from the Mesozoic of Transbaikalia: Paleontological Journal, v. 40, p. 286–289, doi:10.1134/S0031030106030087.

Webb, J.A., 1982, Triassic species of *Dictyophyllum* from eastern Australia: Alcheringa, v. 6, p. 79–91, doi:10.1080/03115518208566988.

Wilson, E.O., 1992, The diversity of life: Cambridge, Massachusetts, Harvard University Press, 440 p.

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