

Arthropod interactions with the Permian *Glossopteris* flora

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ABSTRACT

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An extensive survey of literature on the Permian floras of Gondwana reveals over 500 discrete arthropod–herbivory–damage/plant–taxon/stratigraphic–unit associations spanning all regions of the supercontinent from the earliest Asselian to the latest Changhsingian. Margin– and apex–feeding damage is the most common style of herbivory but hole– and surface–feeding, galling, and oviposition damage are locally well represented. Evidence for skeletonization and mucivory is sparse and that for leaf mining is equivocal. Wood and root boring is recognized widely but only where depositional conditions were conducive to the permineralization of plant axes. Wood boring and detritivory may have been especially favoured arthropod feeding strategies in Permian high latitudes where living foliage was scarce during the polar winters. Herbivory damage is most strongly apparent on glossopterid remains; other groups of broad–leafed gymnosperms and sphenopsids host moderate levels of damage. Damage features are under–represented on lycophytes, ferns and spine– and scale–leafed conifers. A survey of insect body fossils from the Gondwanan Permian reveals that most records are from a small number of rich assemblages that are dominated by Blattodea, Hemiptera, Grylloblattida, Mecoptera and Protelytroptera, accompanied by significant representations of Coleoptera, Glosselytrodea, Miomoptera, Neuroptera, Odonata, Protorthoptera, Palaeodictyopteroidea, Paoliida, Paraplecoptera, Plecoptera, Psocoptera, Thysanoptera and Trichoptera, which collectively adopted a broad range of feeding styles. Oribatid mites and collembolans appear to have been important components of the wood–boring and detritivorous communities. Although temporal trends in herbivory styles and diversity are difficult to resolve from mostly incidental observations and illustrations of plant damage across Gondwana, the results of this study provide a baseline of qualitative data for future studies that should adopt a quantitative approach to the analysis of herbivory, spanning the shift from icehouse to hothouse conditions through the Permian of the Southern Hemisphere.

Key–words—Gymnosperms, Insects, Gondwana, Functional feeding groups, Herbivory, Pathogens.

INTRODUCTION

PLANTS have been engaged in an ancient arms race with terrestrial arthropod herbivores. The earliest signs of herbivory on terrestrial plants date back to the late Silurian (Hagström & Mehlqvist, 2012), and feeding on multiple plant groups occurred by the Early Devonian (Kevan *et al.* 1975; Labandeira, 2007; Labandeira *et al.*, 2014). In response, plants have developed an arsenal of morphological and chemical defences and physiological strategies to combat herbivores (Fernandes, 1994; Walling, 2000). Nevertheless, for the plants,

there is a constant trade–off between the allocation of energy and resources for defence versus investment in growth and reproduction (Herms & Mattson, 1992). During this > 400 Myr interval of co–evolution, some plants also developed sophisticated associations with arthropods, including entomophily (insect pollination), zoochory (seed dispersal by animals) and provision of nutritive rewards or domatia (e.g., in myrmecophytes) for mutual benefit (Speight *et al.*, 2008; Larsen & Burns, 2012; Faegri & Van der Pijl, 2013). In a few cases, arthropods have become the prey, as certain

plants evolved insectivorous strategies to supplement their nutrient supply (Ellison & Gotelli, 2009).

Through the history of life on land, herbivory and detritivory have been dominated by arthropods. For example, in the modern African savanna, termites alone consume an equal or greater plant biomass than all mammalian herbivores (Okullo & Moe, 2011). Moreover, herbivorous arthropods (especially insects and mites) are vastly more diverse and employ a far greater range of feeding strategies than other major herbivorous clades, such as vertebrates.

Following the evolution of seeds, secondary growth, and sophisticated root systems in the Late Devonian, plants established complex tiered ecosystems ranging from humid coastal peat swamps to dry or frigid open shrublands and herblands in tropical to polar latitudes through the Carboniferous and Permian (Gastaldo *et al.* 2020a, b). During this interval, all the major categories of herbivory became established—the sole exception being leaf mining, for which the first confident examples are reported from the Early Triassic (Krassilov & Karasev, 2008).

Detailed studies of fossil plant–arthropod interactions began in the late 1800s (e.g., Scudder, 1886), but some features that probably represent insect–mediated damage (oviposition or small hole–feeding scars) were recorded on fossil leaves as early as the 1860s (Bunbury, 1861). Episodic contributions to the study of plant–arthropod interactions continued through the 20th Century, comprising primarily isolated reports of leaf or wood damage. A more rigorous approach to the quantitative analysis of plant utilization in the fossil record was instituted by Wilf & Labandeira (1999). These authors also introduced a scheme for the recognition of broad categories of feeding guilds (functional feeding groups: FFGs) and more specific damage types (DTs) that has been widely employed by subsequent authors. This scheme was refined and expanded by Labandeira *et al.* (2007) and provides a basis for the description and classification of damage features represented on fossil plants (Fig. 1). As with most ichnofossils, it is important to note that different arthropods can produce similar damage types on plants and, conversely, a single organism can generate various herbivory features. Moreover, other more–or–less distantly related biological groups, including nematodes, pulmonate molluscs, fungi, oomycetes, bacteria and even viruses can produce damage that may be remarkably similar to arthropod herbivory scars (Labandeira & Prevec, 2014). Insect damage also provides an avenue for infection by pathogens, such as bacteria and fungi. In some cases, the insects themselves can act as disease vectors, including complex cases of multitrophic interactions in which adult insects transport fungal spores between plants, after which the larvae feed on the xylophilic fungi (Kirkendall *et al.*, 2015).

Abiotic factors acting on living plant tissue, for example, water stress, physiological responses to micronutrient deficiencies, wind, hail and frost can also cause damage

that may be difficult to distinguish from biogenic traces (Labandeira & Prevec, 2014). Hail damage can produce lesions similar in appearance to oviposition scars and galls on woody stems (Schubert, 1991), and extreme cold can result in root damage, leading to scorch symptoms in the leaves, caused by water stress (DT114 of Labandeira *et al.*, 2007).

Physical damage from wind–induced torsion or particulate matter generally results in simple tears between leaf veins, necrotic leaf edges or tip damage (Michels *et al.*, 1995). Such damage is widely expressed in Gondwanan glossopterid leaves (see, e.g., Pant & Gupta, 1968, 1971; Chandra & Surange, 1979; Edirisooriya *et al.* 2018).

Evidence of post–senescence damage to leaves is abundant in the fossil record, caused by mechanical damage during transport, or even cracking of the leaf by desiccation and rupturing or staining by sulphate crystallization after extraction of the fossil from moist sediments (Pant & Gupta, 1971, pl. 19, fig. 23; McLoughlin, 1992b, pl. 4, fig. 12). Additionally, many leaves may have been damaged by detritivores after accumulation on the sediment surface. For example, several of the coprolite types illustrated from the Guadalupian of Antarctica by Slater *et al.* (2012) contain a mix of plant tissues that are suggestive of production by generalist detritivores.

This review deals specifically with damage to living plant tissues. In general, such damage can be recognized in the fossil record by the development of a distinctive callus or reaction tissue around the damage feature, which may manifest in the fossil as a discrete ridge and/or narrow region of differential staining (Johnson & Lyon, 1991; Sohn *et al.*, 2017). Reasonably definitive fossil evidence of arthropod feeding in particular can include (1), the targeting of a certain organ or host–plant taxon that is relatable to a specific herbivore (e.g., Stone & Cook, 1998; Stone *et al.*, 2008), and (2), features indicative of feeding behaviours seen in modern herbivore analogues, including selective feeding and systematic repetition of damage features, in terms of shape, size, and position on the host plant (e.g., Sarzetti *et al.*, 2008; Kambli *et al.*, 2017).

To date, the recognition of herbivory on Gondwanan Permian plants has been patchy, most studies of the floras being focused on plant taxonomy. Much of the work on palaeoherbivory has targeted Northern Hemisphere fossil assemblages, particularly those of Cretaceous and Cenozoic age (Curran *et al.*, in press). Nevertheless, the vast array of literature on the Gondwanan floras now provides a solid understanding of the floristic composition of the austral Permian vegetation and its temporal and geographic variation. Many of the fossils illustrated in these studies also host examples of distinctive to probable arthropod damage, which are collated in this study.

The Permian vegetation of southern Gondwana (> 30°S palaeolatitude) was overwhelmingly dominated by one group of arborescent gymnosperms—commonly identified

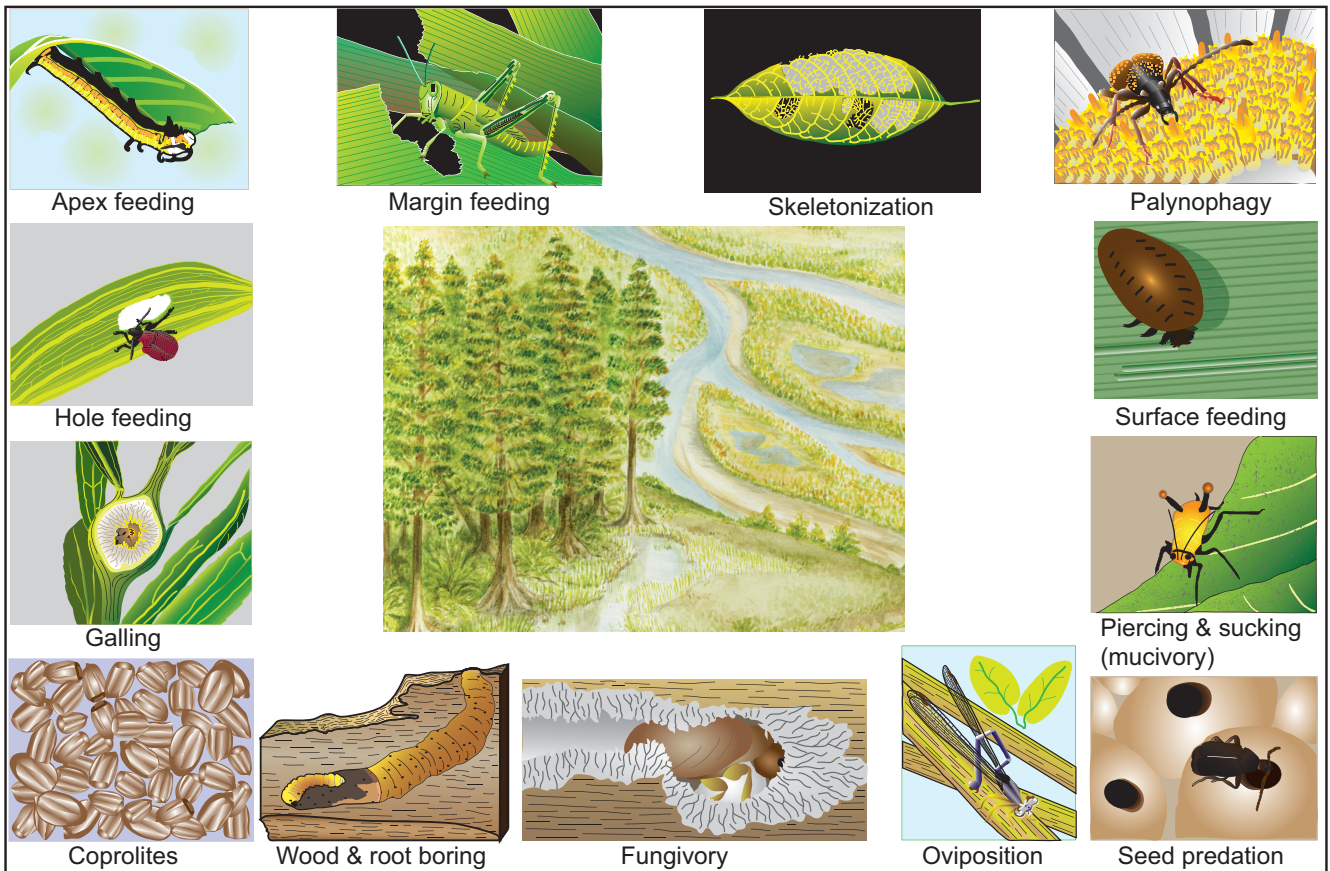


Fig. 1—Schematic diagram of the dominant herbivore feeding strategies in the Gondwanan Permian. Peripheral panels provide a pictorial representation of key forms of evidence for herbivory and surround a central panel portaying a reconstruction of the *Glossopteris* flora (after Slater *et al.*, 2015).

as Glossopteridales (although various other names including Arberiales, Ottokariales and Dictyopteridiales have been used for this group: McLoughlin, 2021). Glossopterids were particularly specialized for growth in the humid lowlands of middle to high southern latitudes (McLoughlin, 2001, 2011b). Their distinctively chambered root systems were well adapted to growth in waterlogged substrates. Their spatulate mesh-veined leaves are ubiquitous as fossils in floodplain facies and they were the prime contributors of organic matter to the extensive Permian coals of Gondwana (Holdgate *et al.*, 2005; Prevec, 2012; McLoughlin *et al.*, 2019). The glossopterid forests also hosted a range of other vascular plants including lycopsids, sphenopsids, ferns, cycads, ginkgoaleans, cordaitaleans, conifers, and several seed plants of uncertain affinity (Surange, 1966; Pant, 1982; Anderson & Anderson, 1985; Cúneo, 1990; Slater *et al.*, 2015). Glossopterids were predominantly large, broad-leaved, deciduous trees with pycnoxylic trunks (McLoughlin 2011b, 2021). Their reproductive biology, recently reviewed by McLoughlin & Prevec (in press), involved mostly wind dispersal of pollen and seeds, but some representatives may have employed entomophily or asexual reproductive strategies. Glossopterids originated around the Carboniferous–Permian transition

(298.9 Ma) and the group was one of the major casualties of the end–Permian mass extinction (251.9 Ma).

Previous studies of plant–arthropod interactions in the Gondwanan Permian *Glossopteris* flora have consisted chiefly of isolated accounts of foliar damage, commonly as incidental reports among systematic descriptions of plant assemblages (e.g., Plumstead, 1963; McLoughlin, 1994a, b; Weaver *et al.*, 1997). Only in the past two decades have extensive assemblages of plant fossils with arthropod damage been documented (Adami–Rodríguez *et al.* 2004a, b; Prevec *et al.*, 2009; Cariglino & Gutiérrez, 2011; McLoughlin, 2011a; Srivastava & Agnihotri, 2011; Pinheiro *et al.*, 2012a, b; Gallego *et al.*, 2014; Cariglino, 2018; Dos Santos *et al.* 2020). Many of these studies have provided more secure identification of the style of damage and the potential trace maker(s), but the results were primarily descriptive. Only the work of Prevec *et al.* (2009) has so far provided a more quantitative approach to the analysis of herbivory guild representation in a fossil assemblage. On the other hand, certain styles of plant preservation (e.g., permineralized peats) have offered opportunities for identifying specific categories of plant–arthropod interactions, such as coprolites and borings (Slater *et al.*, 2012, 2015).

The body fossil record of insects in Permian strata of Gondwana is locally rich. However, the vast majority of these insect fossils (particularly those that are well preserved) derive from a handful of lagerstätten. Although these assemblages offer unparalleled snapshots of insect life in Permian Gondwana, their rarity and sporadic spatiotemporal distribution mean they are of limited value in tracking broader macroevolutionary trends. In the absence of a more consistent insect body fossil record, herbivory damage on fossilized plant parts provides the best evidence for reconstructing the feeding guilds represented in the Permian southern high-latitude glossopterid forest biome.

Here we aim to tabulate all previous records of insect-mediated damage on Gondwanan Permian plants documented over the past 200 years and to summarize the patterns of damage on plant groups. We assess the relative importance of herbivory strategies through the course of the Permian and evaluate the regional patterns in the representation of damage types and of target plants. We also compile a complementary list of all published non-aquatic arthropods recovered from Gondwanan Permian continental strata. Finally, we assess whether Gondwanan Permian plants developed novel strategies to mitigate herbivore attack. Our aim is to compile all existing data on arthropod damage as a baseline for future studies of herbivory in Gondwanan Permian floras.

MATERIALS AND METHODS

We conducted a literature-based search for all published records of arthropod interactions with plants preserved in Permian strata of southern Gondwana. These are supplemented with our own observations of field and museum collections. For our purposes, the region of study corresponds to the geographic extent of confident records of glossopterid gymnosperms (see fig. 1 of McLoughlin 2011b; and Fig. 2). We exclude records from other phytogeographic regions where rare reports of putative *Glossopteris* are not supported by co-occurrences of typical glossopterid reproductive structures or roots (e.g., Asama, 1966; Zimina 1967; Bercovici *et al.*, 2012; Naugolnykh & Uranbileg, 2018). This area also excludes northern portions of the Gondwanan supercontinent that lay outside the geographic range of *Glossopteris* (e.g., northern Africa and northern South America: Iannuzzi *et al.*, 2015). For each record, we document the author(s), illustrations, age, stratigraphic unit, geographic location, type of damage, and host plant. Where possible we apply the damage type (DT) categories of Labandeira *et al.* (2007) but we note that, in many cases, variance in form has meant that many damage features are difficult to assign categorically to any one DT and, in such cases, a simple description is provided. To complement the record of herbivory, we collated all published records of non-aquatic continental arthropod body fossils (primarily insects and mites) from the same region and stratigraphic

interval to assess some of the potential candidates responsible for the examples of herbivory.

We can not guarantee that our lists of occurrences of either herbivory traces or arthropod body fossils are complete, since the nature of some damage features on plants illustrated in various reports, and the recognition of some insect remains, are equivocal. In cases where there is a small to moderate degree of doubt as to an arthropod causative agent, we have indicated 'probable' or 'possible' damage. We have excluded records where we consider the damage features to be more likely attributable to physical processes before or after burial or attrition during preparation. We are also aware that our survey of the literature may not be comprehensive, since some taxonomic studies published in conference proceedings and in provincial journals remain difficult to access. A further caveat is the undoubtedly strong bias in the fossil plant taxonomic literature towards illustration of specimens that are well preserved and complete, hence showing more and better morphological details (Guerra-Sommer, 1995) rather than specimens that have been degraded by arthropod, fungal or bacterial damage. We are also cognizant of uncertainties in the dating of many non-marine rock units where biostratigraphic data is limited and correlation to the international chronostratigraphic scheme is poor. Even where radiogenic isotopic dates are available, these have not always provided consistent age constraints on fossiliferous rock units. For example, dating of tuffs from the Rio Bonito Formation of Brazil has yielded ages ranging from Asselian to Roadian (Matos *et al.*, 2001; Cagliari *et al.*, 2014; Griffis *et al.*, 2018; Rocha-Campos *et al.*, 2019), although following Bicca *et al.* (2020), and on palaeobotanical grounds, we would argue that the unit is predominantly of late Sakmarian to Artinskian age. For these reasons, quantitative evaluation of the herbivory records on a Gondwana-wide scale is greatly constrained. Nevertheless, we consider our survey of the literature provides a foundation for assessing the general representation of arthropod herbivory in the *Glossopteris* flora and provides a solid basis for future studies employing more quantitative approaches.

To supplement these data, we illustrate a selection of representative examples of arthropod damage from various institutional collections to highlight the general range of herbivory styles. Macro photographs were taken with a Canon Eos 40D or Sony Cybershot digital cameras, generally with low-angle lighting from the upper left. Light micrography of thin sections was undertaken using an Olympus BX51 microscope equipped with a Lumenera Infinity-2 digital camera, an Olympus SZX10 stereomicroscope with an Industrial Digital Camera, or a Zeiss Stemi SV6 dissecting microscope equipped with a Sony Soundvision digital camera. Some permineralized peat samples were digested in acid according to the bulk-maceration methods outlined by Slater *et al.* (2012), whereafter mesofossils were picked from residues using a camel-hair brush then mounted on

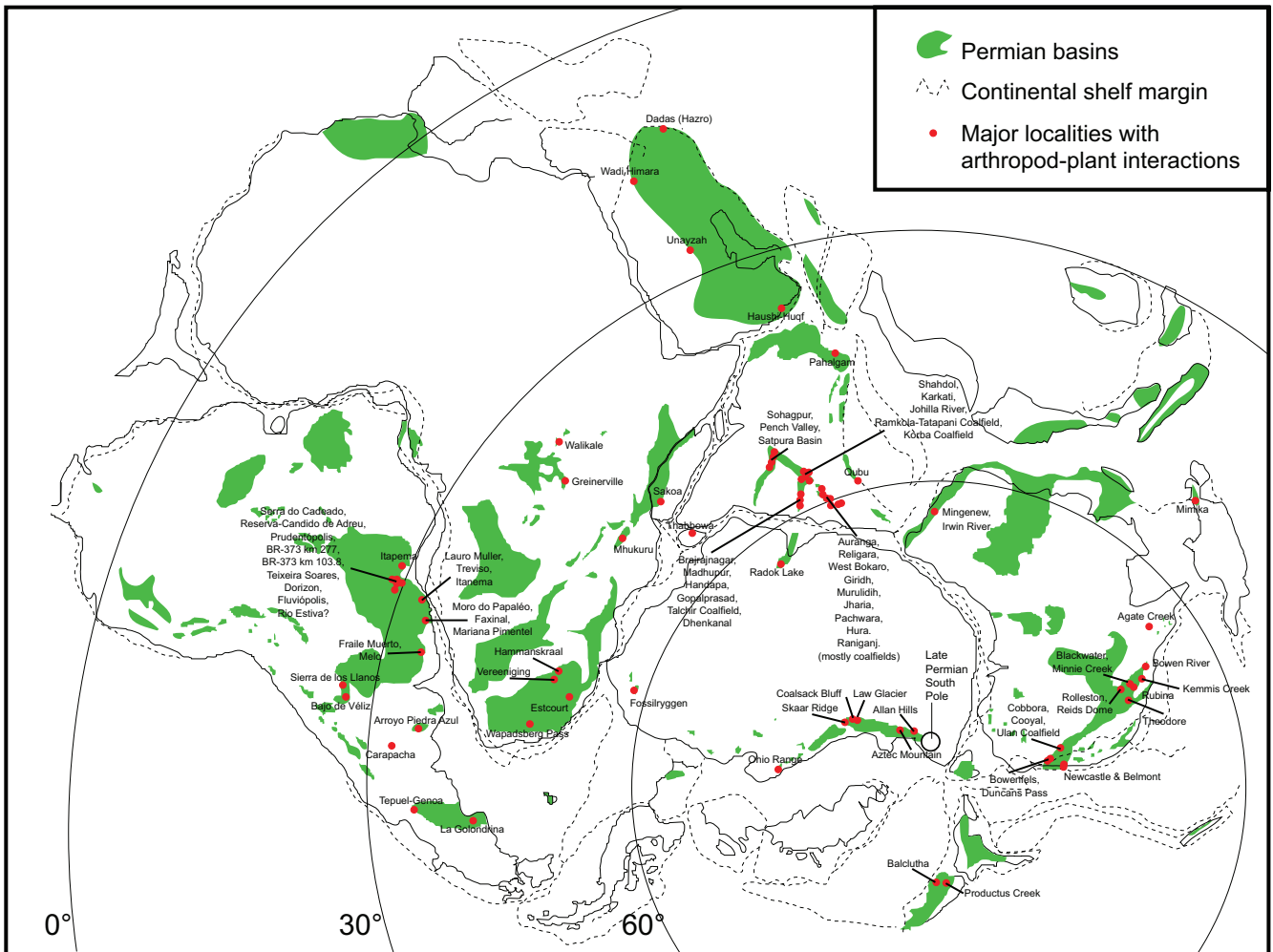


Fig. 2—Permian reconstruction of Gondwana showing the distribution of sedimentary basins (shaded) and the major localities hosting examples of plant–arthropod interactions.

aluminium stubs, coated with gold and imaged with the use of a Hitachi S–4300 field emission scanning electron microscope at the Swedish Museum of Natural History. Graphical reconstructions of plant organs and herbivory styles were produced by the authors using Adobe Creative Cloud software. Illustrated specimens are held in the collections of various institutions according to the following prefixes: BP—Evolutionary Studies Institute (formerly the Bernard Price Institute) of the University of the Witwatersrand, Johannesburg; VM—Vaal Teknorama Museum (formerly the Vereeniging Museum), Vereeniging; AM—Albany Museum, Makhanda (Grahamstown); UQ—University of Queensland and GSQ—Geological Survey of Queensland now integrated with the Queensland Museum, Brisbane; AM—Australian Museum, Sydney; MM—Geological Survey of New South Wales, Londonderry, New South Wales; GA—Geoscience Australia, Canberra; MV—Museum Victoria, Melbourne; GSI—Geological Survey of India, Calcutta; UCB—Botany Department of the University of Calcutta, Calcutta; BSIP—

Birbal Sahni Institute of Palaeosciences, Lucknow; and NRM—Swedish Museum of Natural History, Stockholm.

RESULTS AND DISCUSSION

Our survey of over 2000 papers, unpublished theses and technical reports on aspects of the *Glossopteris* flora yielded over 500 combinations of DT–plant associations from the full Permian stratigraphic spectrum spanning all major provinces of Gondwana (Tables 1, 2). We have not attempted to revise the taxonomy of the host plants, except for a few instances where we correct the identifications (stated in parentheses) based on current generic demarcations. We advise caution in applying the species-level identifications of the host plants to analyses of interspecific variation in foliar herbivory, since widely used names of morphotaxa, such as *Glossopteris angustifolia*, do not necessarily represent the same biological species across the disparate parts of Gondwana. Here we summarize the distribution of the major functional feeding

groups and subgroups and the representation of host plants through the Permian across Gondwana.

External foliage feeding

External foliage feeding involves the consumption of live leaf tissue by an external herbivore, and in fossils it is generally marked by the presence of a raised or differentially stained rim surrounding the damaged area, representing the thickened, callus tissue produced by the living plant in response to the damage (Labandeira 1998b). This functional feeding group is subdivided into various subgroups, such as margin feeding, hole feeding, surface feeding and skeletonization (Fig. 1). We treat each of these subgroups separately and summarize their representation in Permian plant assemblages across Gondwana.

Margin and apex feeding

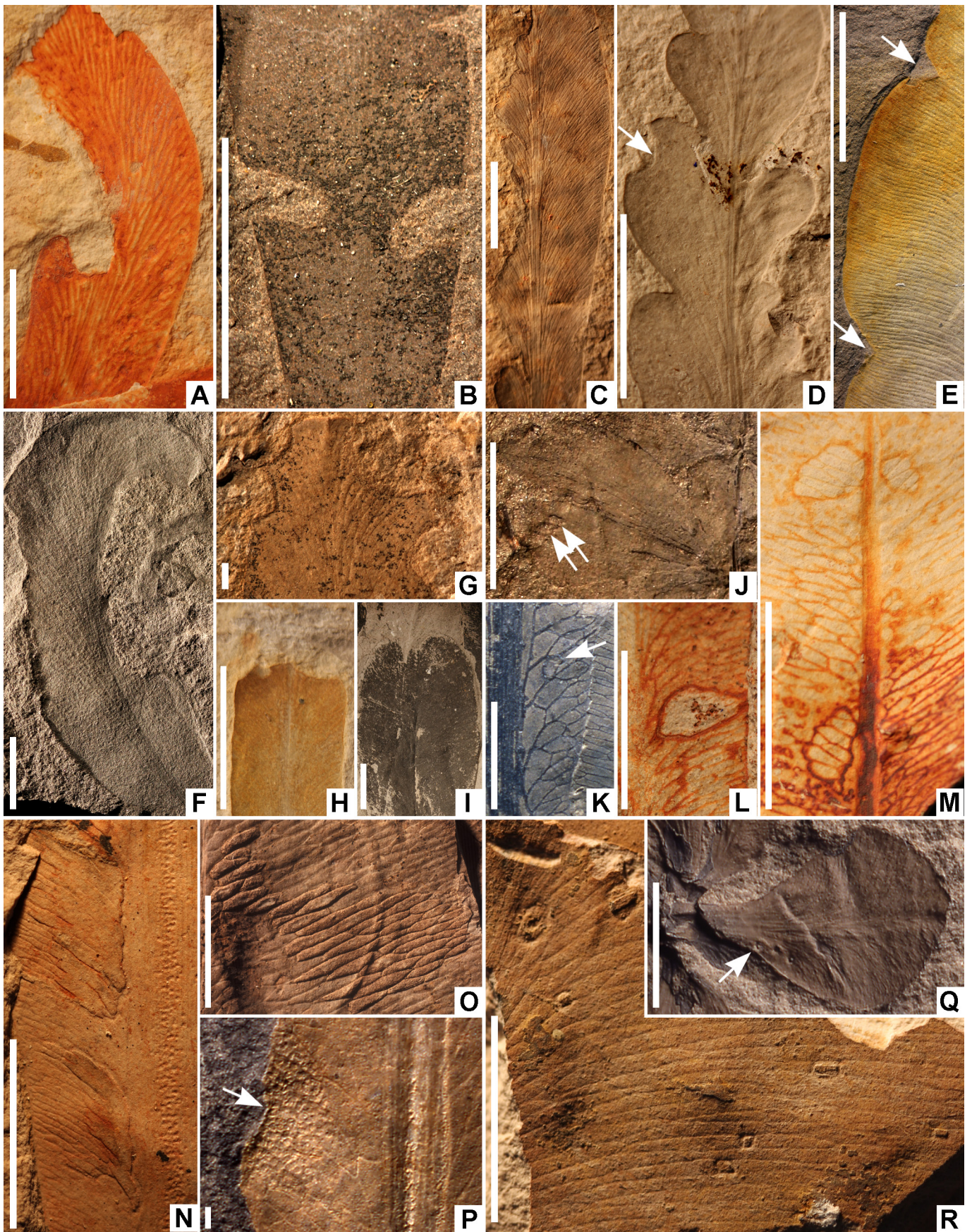
Margin feeding (Fig. 1) is the most common and obvious form of damage to leaves in the *Glossopteris* flora. We identified over 140 examples (damage/host–plant/stratigraphic–unit associations) of margin feeding across Gondwana (Tables 1, 2). Most such herbivory traces are simple C-shaped, excisions of the outer lamina with thin reaction tissue (Figs 3D, G; 4D; 5H) referable to DT12 of Labandeira *et al.* (2007). A few excisions extend to the midrib (DT14: Fig. 3A, F) and some are more notably U-shaped (Fig. 3B) or with a keyhole morphology (DT15: Fig. 5F), narrowly rectangular, V-shaped (Fig. 3D, E; 5B) or trench-like (Fig. 5D; e.g., Saksena, 1962, pl. 1, figs 4, 7, 8; Appert, 1977, pl. 6, figs 4, 5; Cariglino, 2018, fig. 3F; Fernández & Chiesa, 2019, fig. 2A–C). Several other variants of margin feeding, including polylobate and continuous irregular cusped traces

(Figs 3C; 5E), have been illustrated (e.g., Appert, 1977, pl. 4, fig. 4; Anderson & Anderson 1985, pl. 80, fig. 1a, b; Srivastava, 1988c, pl. 1, figs 4, 5; Adami–Rodríguez *et al.* 2004b, fig. 5A, B; Cariglino, 2018, fig. 3G). Since richness in damage types broadly correlates with herbivore diversity in modern angiosperm–dominated floras, our data suggests that a diverse array of herbivores was involved in producing the varied margin–feeding traces on plants of the *Glossopteris* flora. However, the correlation is not always straightforward, since many herbivores can each produce multiple types of feeding traces (see Carvalho *et al.* 2014).

A subset of margin feeding is represented by herbivory targeted on the leaf apex (Fig. 1: apex feeding). This is typically represented in the *Glossopteris* flora by either roughly transverse excisions of the leaf apex (Fig. 3H; e.g., McLoughlin, 1994b, pl. 4, fig. 2; Adami–Rodríguez *et al.*, 2004b, fig. 5A) or by various U–to V–shaped notches commonly associated with callus formation or distortion of the apical veins (Figs 3I; 5G; Leguizamon, 1979, fig. 5; Anderson & Anderson, 1985, pl. 70, fig. 5a; Melchor & Césari, 1997, fig. 8.1; Labandeira & Prevec, 2014, fig. 8B; Fernández & Chiesa, 2019, fig. 2G).

The vast majority of both typical margin–feeding and more targeted apex–feeding damage is expressed on glossopterid leaves. However, various authors have also noted similar damage on leaves of *Noeggerathiopsis*, *Cheirophyllum*, *Rhipidopsis*, *Botrychiopsis* and, in rare cases, on pinnules of various ferns (Tables 1, 2). Very rare examples are represented on the leaflets of *Trizygia* and *Sphenophyllum* species (Feistmantel, 1880; Archangelsky, 1958b, fig. 7; Appert, 1977, pl. 6, figs 4, 5; Adami–Rodríguez *et al.*, 2017), and possibly on *Schizoneura* (Feistmantel, 1880) and *Annularia* (Cúneo, 2000, fig. 1A). Margin feeding (DT12–15) was recorded as the dominant herbivory style (23.4% of

Fig. 3—Representative examples of arthropod–plant interactions from the Permian of Gondwana. **A**, Deeply incised margin feeding (DT15) on *Glossopteris browniana*; AMF57491. **B**, Pair of U-shaped margin–feeding excisions on *Glossopteris* sp.; AMF128464. **C**, Separate broad and deep V-shaped margin feeding on *Glossopteris xiphophylla*; AMF46508. **D**, Deep V-shaped and shallow C-shaped (DT12 arrowed) margin feeding; AMF26680b. **E**, Broad, shallow V-shaped margin feeding (arrowed) on *Glossopteris ampla*; NRMS0893949b–0. **F**, Broad margin–feeding excision (DT14) to midrib causing curvature of *Glossopteris* leaf; GNS B1013/1. **G**, Series of C-shaped margin excisions (DT12) around *Glossopteris* leaf apex; AMF39860b. **H**, Truncate apex feeding on *Glossopteris xiphophylla*; AMF39918. **I**, V-shaped apex–feeding on *Glossopteris browniana*; AMF81278b. **J**, Small hole feeding (DT01 arrowed) on distal portion of *Trizygia speciosa* leaflet; GSI5612. **K**, Small interveinal hole feeding scar (DT01 arrowed) on *Belemnopteris elongata*; GSQF12341. **L**, Elliptical hole feeding (DT02) on *Glossopteris* sp. **M**, Small areas of either interveinal surface feeding (DT31) or skeletonization retaining secondary vein stringers adjacent to midrib (DT24) on *Glossopteris* sp. **N**, Polylobate area of surface feeding damage (DT30) predominantly following secondary veins on *Glossopteris* sp.; BSIP2637c. **O**, Broad polylobate area of interveinal surface feeding with weak reaction rim (DT29?) on *Glossopteris chevronata*; UQF19246. **P**, Polylobate area of roughened surface feeding damage (arrowed) spanning multiple areolae on leaf linked to *Austroglossa walkomii*; AMF51835. **Q**, Series of punctures (mucivory damage) along basal secondary veins (DT138 arrowed) of *Glossopteris walkomii*; AMF43178. **R**, Isolated punctures (mucivory damage) at secondary vein junctions in a *Glossopteris* sp.; BSIP34026c. Sources: **A**, Dunedoo Formation (Lopingian), Dunedoo, Gunnedah Basin, eastern Australia; **B–D**, **G**, **H**, Newcastle Coal Measures (Lopingian), Belmont, Sydney Basin, eastern Australia; **E**, Illawarra Coal Measures (Lopingian), Cobbora, Sydney Basin, eastern Australia; **F**, undetermined unit (Permian), Transantarctic Mountains; **I**, Whittingham Coal Measures (Guadalupian–Lopingian), Saxonvale Mine, Sydney Basin, eastern Australia; **J**, Raniganj Formation (Lopingian), Raniganj Coalfield, India; **K**, Moranbah Coal Measures (Wuchiapingian), Rosella Creek, Bowen Basin, eastern Australia; **L**, **M**, Koogah Formation (Artinskian), Mount Wingen, Gunnedah Basin, eastern Australia; **N**, **R**, Kamthi Formation (Lopingian) Hinjrida Ghati, Odisha, India; **O**, Black Alley Shale (Changhsingian), Inglis Dome, Bowen Basin, eastern Australia; **P**, Illawarra Coal Measures (Changhsingian), Cooyal, Sydney Basin, eastern Australia; **Q**, Illawarra Coal Measures (Changhsingian), Duncans Pass, Sydney Basin, eastern Australia. Scale bars = 10 mm except for **G** and **P** (=1 mm).



occurrences) on leaves (predominantly glossopterids) from the Lopingian Clouston Farm assemblage in the Karoo Basin (Prevec *et al.*, 2009). Possible candidate producers of such marginal foliage feeding damage include various proto-coleopterans and orthopteroids (Guerra–Sommer, 1995; Labandeira, 1998a). Targeted feeding at the foliar apex has been tentatively attributed to the activities of orthopteroid insects (Adami–Rodrigues *et al.*, 2004b).

Hole feeding

Hole feeding consists of excision of tissues through the entire depth of the leaf (Fig. 1), the lamina developing callus tissue completely surrounding the damaged area (Figs 3J–L; 5A, C, L). Hole feeding appears to be the second most common style of damage to leaves in the *Glossopteris* flora. We noted over 60 records of hole feeding (with varying degrees of confidence) on the leaves of assorted plant groups (Tables 1, 2). Prevec *et al.* (2009) recorded hole feeding in low to moderate abundance on at least 10 morphotypes of glossopterid leaves and bracts, and also on an unidentified axis in a quantitative study of the Lopingian Clouston Farm flora in the Karoo Basin. As per margin feeding, hole feeding is most heavily represented on the dominant glossopterid leaves throughout Gondwana. However, putative examples are also evident on various other gymnosperms including ginkgoaleans, cordaitaleans and *Botrychiopsis* (Kurtz, 1921; White, 1962; Pant & Verma, 1964; Cúneo, 1987; Jasper *et al.*, 2003, Pinheiro *et al.*, 2012b, 2015; Gallego *et al.*, 2014), and on glossopterid protective or reproductive bracts (Cridland, 1963; Van Dijk *et al.*, 1979; Adami–Rodrigues *et al.*, 2004b). Rare examples have also been reported or illustrated on *Sphenophyllum* (Adami–Rodrigues *et al.*, 2017) and *Neomariopteris* (Singh & Chandra, 1999, pl. 3, fig. 2) leaves. In the geographic transition zone between the typical Gondwanan and Cathaysian floras, examples of gigantopterid leaves also appear to bear hole–feeding damage (Wagner, 1962, pl. 24, figs 2, 2a). The possible small circular

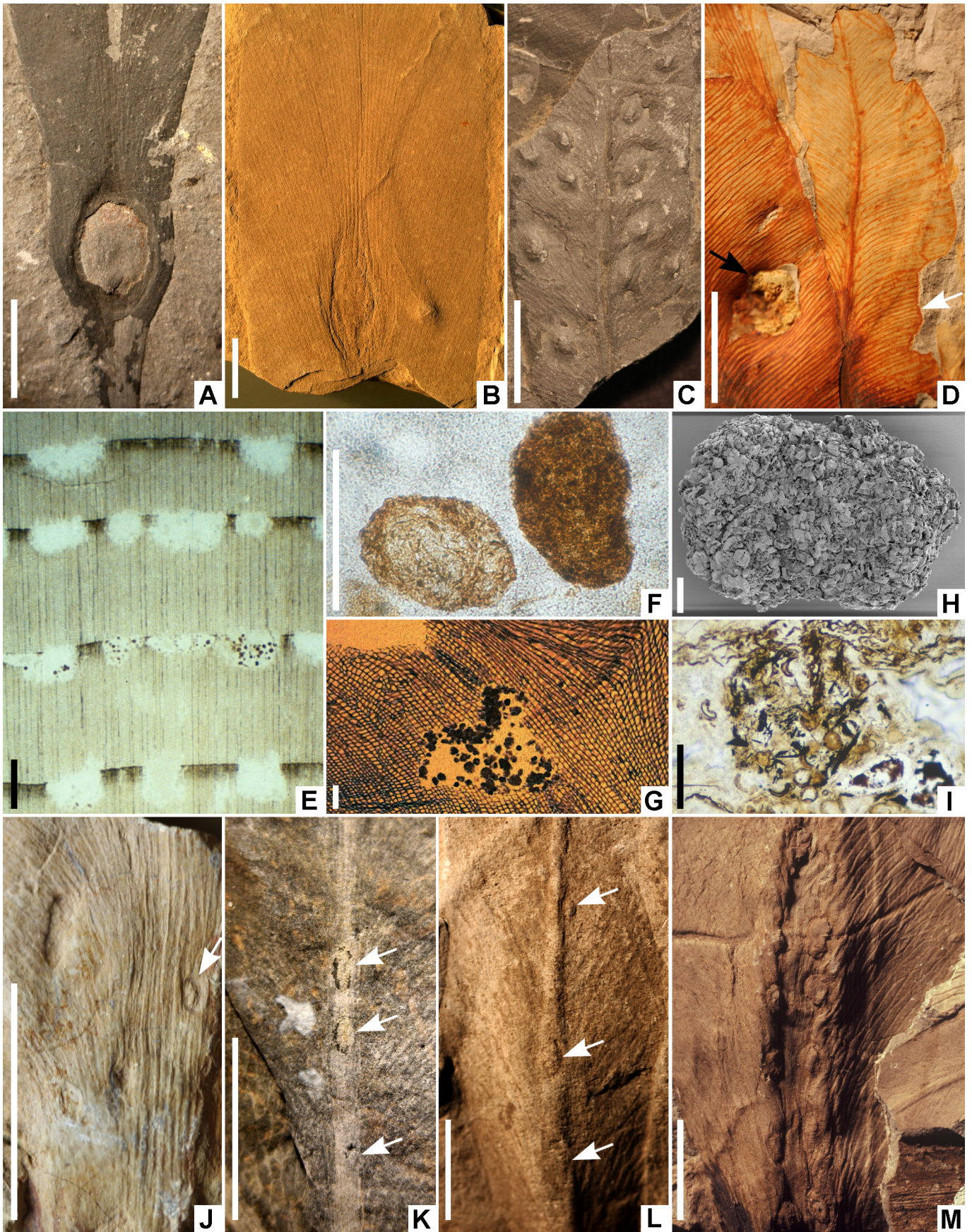
hole feeding traces on *Dicroidium* leaves from the Um Irna Formation, Jordan (Abu Hamad *et al.* 2008), are of uncertain age, being attributed to either the latest Permian or earliest Triassic.

Various insect groups can produce hole feeding damage, among which protorthopterans and early coleopterans are potential candidates. Pulmonate gastropods represent another group that produce this category of damage but have not been generally considered among potential Permian herbivores. Terrestrial gastropods have a fossil record that stretches back to the Carboniferous (Pek *et al.*, 1996; Stworzewicz *et al.*, 2009), and were especially abundant in some Early Permian palaeoequatorial terrestrial communities (Rößler *et al.*, 2012; Rößler, 2021). Modern snails produce scalloped margin–feeding damage and hole–feeding scars (of a large range of sizes and shapes), with large polylobate holes between veins grading into skeletonization. Such damage tends to avoid the larger veins, leading to the production of elongate trench feeding in leaves with parallel to sub–parallel venation. Terrestrial gastropods tend to be generalist feeders today, consuming both living and dead plant tissues (Speiser, 2001) and, although the body fossil record of gastropods in Gondwanan Permian continental ecosystems is minimal, they should not be dismissed as potential herbivores.

Surface feeding (or surface abrasion)

This feeding strategy involves the removal of one or more layers of leaf tissue (commonly in interveinal segments: Fig. 1) leaving at least one surface of the lamina intact (Figs 3N; K, M, O) and, in some cases leaving a roughened texture (Fig. 3P). Adami–Rodrigues *et al.* (2004a, b) illustrated possible examples of this feeding strategy as interveinal strips with callused rims on glossopterid and cordaitalean leaves from Brazil. Various other possible examples of this feeding strategy have been illustrated including interveinal damage (a broad area of raised areolae) flanking the midrib of *Glossopteris mosesi* leaves (Archangelsky, 1957, pl. 10, fig.

Fig. 4—Representative examples of arthropod interactions with plants from the Permian of Gondwana. **A**, Large circular gall (cf. DT117) on the proximal midrib of *Glossopteris acutifolia*; AMF119492. **B**, Large ovate gall (cf. DT84) on the proximal midrib of *Palaeovittaria kurtzii*; BP/2/13595. **C**, Elliptical galls (cf. DT80) or oviposition scars on the mid–lamina of *Glossopteris* sp.; UCB Mc 250. **D**, Shallow scalloped margin feeding (DT12: white arrow) and pseudoherbivory (root–penetration) damage (black arrow); un–numbered AMF specimen. **E**, Regular borings in late wood of growth rings in *Australoxylon mondii*; NMVP200040D. **F**, Enlargement of coprolites containing tracheid wall fragments from borings in *Australoxylon mondii* wood; NMVP200040D. **G**, Probable oribatid mite coprolites in a boring within permineralized *Vertebraria australis*; NRMS090127. **H**, Coprolite containing primarily bisaccate pollen (evidence of palynophagy); NRMS087857–07; **I**, Coprolite with mixed contents (evidence of detritivory); NRMS090126. **J**, Solitary elliptical oviposition scar (DT76 arrowed) on midline of *Gangamopteris cyclopteroides* var *major* leaf; NRMS047785. **K**, Series of elliptical oviposition scars (DT76 arrowed) on midrib of *Glossopteris* sp. cf. *G. browniana* leaf; GAF22174B. **L**, Series of elliptical oviposition scars (DT76? arrowed) on and adjacent to midrib of *Glossopteris intermedia* lectotype; GSI5257. **M**, Series of regular circular to elliptical oviposition scars (cf. DT76) flanking midrib of *Glossopteris bucklandensis*; UQF76185a. Sources: **A**, Illawarra Coal Measures (Lopingian), Ulan Coal Mine, Sydney Basin, eastern Australia; **B**, Vryheid Formation (Artinskian), Vereeniging, Karoo Basin, South Africa; **C**, Murulidih Colliery, Mohuda Basin, India; **D**, Koogah Formation (Artinskian), Gunnedah Basin, eastern Australia; **E–I**, uppermost Toploje Member (Wordian), Bainmedart Coal Measures, Radok Lake, Lambert Graben, East Antarctica; **J**, Egg Harbour Member (Lopingian), Bay of Harbours Formation, Dos Lomas, East Falkland Islands; **K**, **L**, Raniganj Formation (Lopingian), Raniganj Coalfield, India; **M**, Black Alley Shale (Changhsingian), Inglis Dome, Bowen Basin, eastern Australia. Scale bars = 10 mm except **F–I** (= 100 µm).



3; text–fig. 3.2). Similar features, either confined between a set of secondary veins or spanning several veins (attributed to DTs 28, 31, 103; Fig. 3O) were illustrated by Read (1941), Césari & Hünicken (1992), McLoughlin (1994a), Tybusch (2005), Srivastava & Agnihotri (2011), Pillai (2012), Pinheiro *et al.* (2012b), Gallego *et al.* (2014), Cariglino (2018) and Fernández & Chiesa (2019) on various glossopterid, ginkgoalean and cordaitalean leaves. Cariglino (2018) also illustrated polylobate surface (window) feeding on both sides of midrib (DT82) in an unidentified *Glossopteris* leaf. In their detailed study of the Lopingian Clouston Farm (Normandien Formation) assemblage from the Karoo Basin, Prevec *et al.* (2009) identified six surface feeding damage types (DTs 29, 30, 31, 75, 103, 106) spread across 11 primarily glossopterid leaf and bract morphotypes. Based on comparisons with the feeding behaviours of certain families of extant Coleoptera (Chysomelidae, Curculionidae), it has been suggested that this style of damage is potentially attributable to proto-coleopterans (Adami–Rodrigues *et al.*, 2004b).

Skeletonization

Leaf skeletonization is a somewhat specialized category of external foliage feeding involving the consumption of a non–marginal portion of the lamina while retaining a latticework of veins or veinlets (Labandeira, 2002; Fig. 1). Evidence for skeletonization is patchy and equivocal in illustrated plant remains from the Permian of Gondwana, and some examples may alternatively represent surface feeding (Fig. 3M). Adami–Rodrigues *et al.* (2004a, b) illustrated segments of roughened lamina tracking the secondary veins on Brazilian *Glossopteris* leaf impressions that might represent skeletonization. Cariglino (2018,

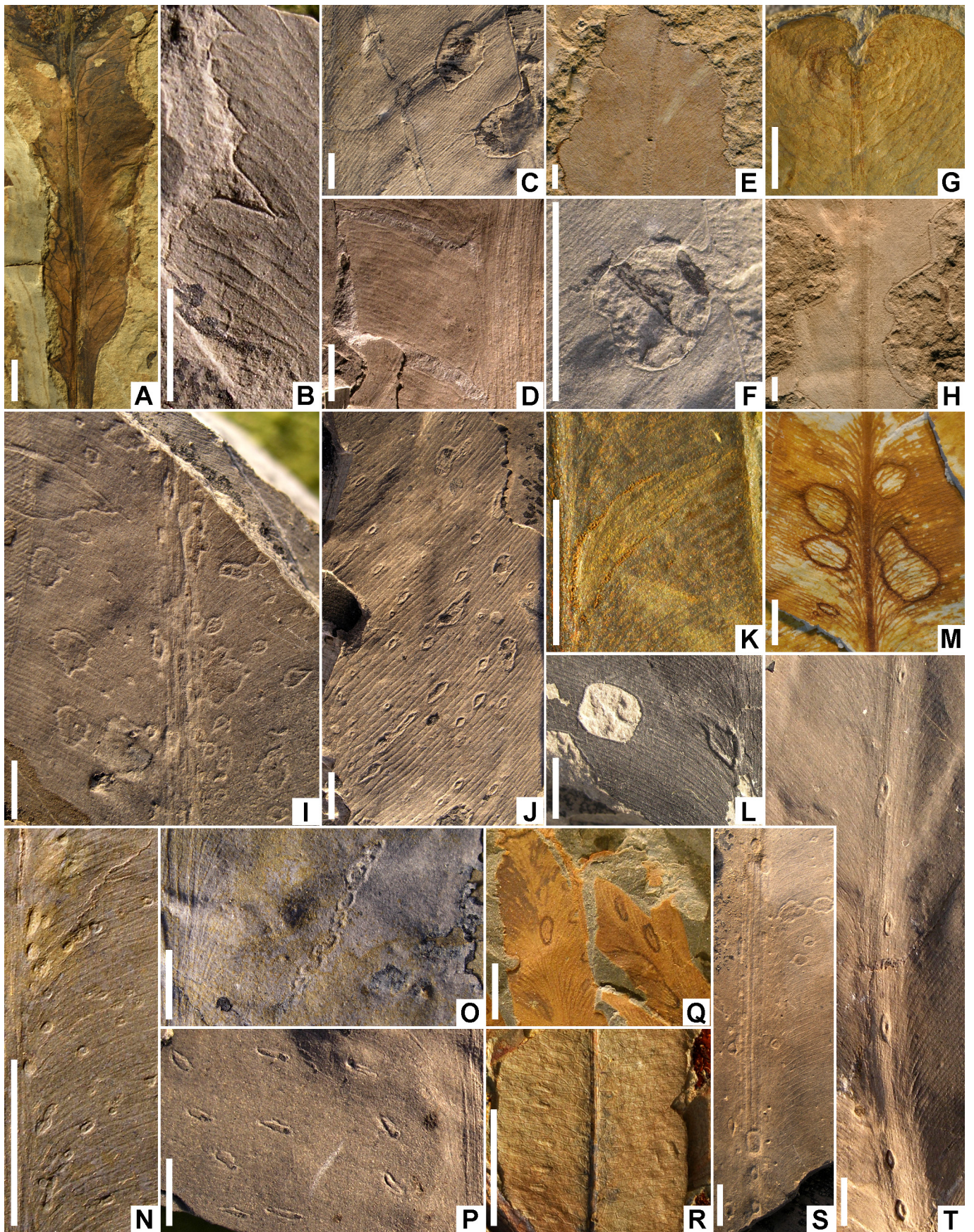
fig. 3S) illustrated similar possible skeletonization over much of the lamina of an unidentified *Glossopteris* leaf from Argentina. A further similar example of putative skeletonization was documented by Edirisooriya *et al.* (2018, fig. 4e) on *Glossopteris raniganjensis* from Sri Lanka. The detailed study of the Lopingian Clouston Farm (Normandien Formation) assemblage from the Karoo Basin similarly found skeletonization to be rare, with just single examples of DT16 and DT17 recorded on one *Glossopteris* morphotype. Larval hemipteroids and coleopteroids were potential producers of this style of damage in the Permian. Some orthopteroids may also have produced this style of skeletonization (Kazakova, 1985). Further, similar skeletonization can be produced by detritivory, so groups such as blattoids might have produced equivalent damage patterns.

Leaf mining

Leaf mining involves the consumption of tissues in the leaf interior without removing the cuticle apart from the production of small entry and exit holes. Several putative examples of leaf mining have been reported from Permian glossopterid leaves (Table 1). Archangelsky & Wagner (1983, figs 9, 10) illustrated a linear trace, < 1 mm wide, aligned parallel to and c. 2 mm from the margin of a *Glossopteris stricta* leaf. Adami–Rodrigues *et al.* (2004a, b) identified a single bifurcating curvilinear structure found on the basal and middle parts of a *Glossopteris* sp. cf. *G. indica* leaf. Pinheiro *et al.* (2012b) noted a possible leaf mine near the margin of a *Glossopteris communis* leaf. Cariglino (2018) identified semicircular traces with central circular marks near the margins of a *Glossopteris* leaf that are suggestive of a simple unspecialized mining strategy. All of these putative examples



Fig. 5—Representative examples of arthropod interactions with *Glossopteris* leaves from Permian strata of the Karoo Basin, South Africa. **A**, Continuous margin feeding (DT12 on lower left), polylobate hole feeding (DT03 on upper right), and oviposition scars on midrib (DT76) of leaf with attached *Estcourtia* polysperm; NM/1276a. **B**, Leaf with V-shaped to lobate margin feeding (DT12); BP7104. **C**, U-shaped margin feeding (DT12) and large, slightly polylobate hole feeding (DT05); BP7399. **D**, Trenched margin feeding to midrib following the course of secondary veins (DT14); BP7106. **E**, Lobate to scalloped continuous margin feeding (DT12); BP14341. **F**, Keyhole margin feeding (DT15); BP7399. **G**, Notched feeding on apex (DT13) causing distortion of venation; AM KY260a. **H**, Continuous broadly scalloped margin feeding with distinctive reaction zone (DT12); BP14113. **I**, Oviposition scars with irregular reaction rims, range of sizes and shapes from circular to elliptical, egg insertion point visible in centre of many of the scars (DT101), small elliptical oviposition scars on midrib (DT76), possible piercing and sucking (DT46); BP7135. **J**, Scattered, elliptical oviposition scars (some coalescing) on lamina (DT101); BP7135. **K**, Surface feeding damage tracking secondary veins (DT97) or possible fungal damage (DT58); AM KY712b. **L**, Circular hole feeding (DT04) in outer lamina and spindle-shaped oviposition scar (DT101) adjacent to midrib; BP7399. **M**, Oviposition scars (DT101, upper left and lower left) and polylobate surface feeding (DT31); BP25025. **N**, Small, scattered, elliptical to spindle-shaped oviposition scars (DT101), some aligned end-to-end or in clusters (DT100); possibly piercing-and-sucking damage (DT 48, DT138); BP7402. **O**, Oblique chain of contiguous elliptical oviposition scars across mid-lamina and aligned with vein course (new DT); BP7399. **P**, Spindle-shaped oviposition scars with linear to arcuate arrangement across lamina (DT100); BP7135. **Q**, Elliptical oviposition scars with prominent reaction rims (DT102; DT76), and with associated necrotic regions, possibly due to secondary fungal infection (DT136) on morphotype W1 of Prevec *et al.* (2010); AM WN 108a. **R**, Series of longitudinally arrayed, transversely aligned, spindle-shaped oviposition scars on mid-lamina (cf. DT54); AM KY346. **S**, Oviposition scars variably arrayed on midrib (DT76), flanking midrib, and on mid-lamina (DT101) and possible piercing and sucking scars alongside midrib (DT138); BP7135. **T**, Spindle-shaped oviposition scars regularly aligned along midrib (DT76); BP7135. **A**, Normandien Formation, (Lopingian), Mooi River; **B–D, F, I, J, L, N–P, S, T**, Hammanskraal Formation (Vryheid Formation equivalent: Artinskian), Hammanskraal; **E, H**, Vryheid Formation (Artinskian), Vereeniging; **G, K, R**, Emakwezini Formation (Wuchiapingian), Kwa Yaya; **M**, Geological outlier possibly in part equivalent to the Volksrust Formation (?Guadalupian), Lawley; **Q**, Elandsberg Member, Balfour Formation (Changhsingian), New Wapadsberg Pass. Scale bars = 10 mm.



of leaf mining remain equivocal and might alternatively represent other damage types or even indentations in the lamina caused by differential compaction over underlying curvilinear features, such as fine roots or burrows in the sediment. For example, Maheshwari and Bajpai, (1990, fig. 5) illustrated putative mines in a *Saportaea* leaf that probably constitute indentations caused by burrows in the underlying sediment. Such linear features are widely reported in the literature and some cross-cutting and looped examples have been responsible for misinterpretations of leaf features as fructifications (Rigby, 1983; McLoughlin, 2012).

Alternative evidence for leaf mining is in the form of sub-rounded to angular coprolites containing densely packed cell wall fragments preserved in interveinal cavities within mesophyll evidenced in transverse sections of permineralized *Glossopteris* leaves from Antarctica (Slater *et al.*, 2012). However, there is no reaction tissue around these cavities and they may represent detritivore traces. Importantly, the extensive investigation of plant damage from a Lopingian assemblage of plants from South Africa by Prevec *et al.* (2009) did not identify any undoubted cases of leaf mining. The earliest convincing examples of leaf mining in the fossil record come from the earliest Triassic of Russia (Krassilov & Karasev, 2008). This endophytic feeding strategy became more diverse by the late Middle to early Late Triassic with representative examples recorded across Gondwana and elsewhere (Rozeffelds & Sobbe, 1987; Zherikhin, 2002; Labandeira & Anderson, 2005; Labandeira *et al.*, 2017).

Piercing and sucking (mucivory)

In the absence of scars left by the carapaces of specialist fluid-feeding arthropods, such as scale insects (Harris *et al.*, 2007; Wappler & Ben-Dov, 2008; Tosolini & Pole, 2010), mucivory damage (Fig. 1) is commonly represented by very small, relatively featureless scar tissue especially clustered or aligned over primary and/or secondary veins (Figs 3Q, R; 5S). There are numerous potential examples of such damage illustrated on fossil leaves from the Gondwanan Permian but few have morphological or distributional characters that allow unequivocal assignment to piercing-and-sucking. Various glossopterid leaves have small scar-like pustules arranged along secondary veins (see e.g., Adami-Rodríguez *et al.*, 2004b, fig. 6J; Edirisooriya *et al.*, 2018, fig. 4g, h; Cariglino, 2018, fig. 4G, H, L) that probably represent piercing-and-sucking damage. An intensive investigation of one Lopingian assemblage from the Karoo Basin found mucivory to be rare and registered on just two *Glossopteris* leaf morphotypes (Prevec *et al.* 2009) but more recent unpublished work in this basin suggests that this damage type is more common than reported previously.

Mucivory damage (especially DT46 and 47) is primarily represented on the dominant glossopterid species, but there are also possible occurrences on *Noeggerathiopsis* (cordaitalean)

leaves (White, 1908, pl. 9, fig. 7) and lycopsid microphylls (Cariglino, 2018). Hemipteroid and palaeodictyopteroid insects were the likely prime mucivorous herbivores of Permian Gondwanan plants (Prevec *et al.*, 2009).

Galling

Galls are complex structures induced by various small herbivores, parasites and pathogens on almost any part of the host plant to provide both shelter and a food source (Fig. 1). Although representing one of the more sophisticated styles of herbivory, galls are relatively common on plants, especially glossopterid leaves, from the Permian of Gondwana (Fig. 4A–C). Various examples of galls have been reported on glossopterid leaves from most continents (e.g., Archangelsky *et al.*, 1981; Banerjee & Bera, 1998; Adami-Rodríguez *et al.*, 2004a, b; Prevec *et al.*, 2009; McLoughlin, 2011a; Cariglino, 2013, 2018; Fernández & Chiesa, 2019). Many of these structures are positioned on or adjacent to the leaf midrib but, in a few cases, they occur scattered across the lamina (Holmes, 1995, figs 55, 56; Cariglino, 2018, fig. 4S). Only a few examples of galls have been documented on non-glossopterid plants from this region. Of these, a possible isolated gall on a fern pinnule (Pant & Misra, 1977, pl. 3, fig. 1), and a solitary gall on the base of a *Sphenophyllum* leaflet (Cariglino, 2018, fig. 4U) are notable. Prevec *et al.* (2009) found galling to be rare, occurring on just two *Glossopteris* morphotypes, in the well-studied Coulston Farm (Lopingian) assemblage from South Africa.

The identification of galls is particularly convincing where distinctive radial markings and/or a central ostiole are preserved (Cariglino, 2018), or where the damage features are too large to represent oviposition scars (McLoughlin, 2011a). On this basis, the large circular to elliptical features on glossopterid midribs that lack ovules or seed scars (attributed to, e.g., *Bokarospermum maheshwari* of Singh, 2002, pl. 2, figs 1–4 and the ovuliferous organ of *Palaeovittaria kurzii*, see Anderson & Anderson, 1985, pl. 54, figs 1–5) may well represent prominent galls on the proximal to medial parts of the midrib. In the absence of organic remains or distinctive ornament, many small, simple, circular to elliptical, damage features on leaf impressions are difficult to discriminate with confidence between either galls or oviposition scars (e.g., Archangelsky, 1958b, fig. 3.4; Maithy, 1965, pl. 1, fig. 5, pl. 2, fig. 8; Maithy, 1977, pl. 1, fig. 2; Appert, 1977, pl. 3, figs 3, 4; Cúneo *et al.*, 1993, pl. 1, fig. 4). Generally, galls are more heavily stained than oviposition scars, and have a denser appearance with a rougher texture and greater relief relative to the healthy plant surface. No anatomically preserved galls have yet been documented from the Permian of Gondwana. However, the enigmatic spherical chambered fossil, *Breytenia plumsteadiae* (Melville, 1983a), from the Cisuralian of South Africa potentially represents a three-dimensionally preserved gall, although other interpretations are also possible.

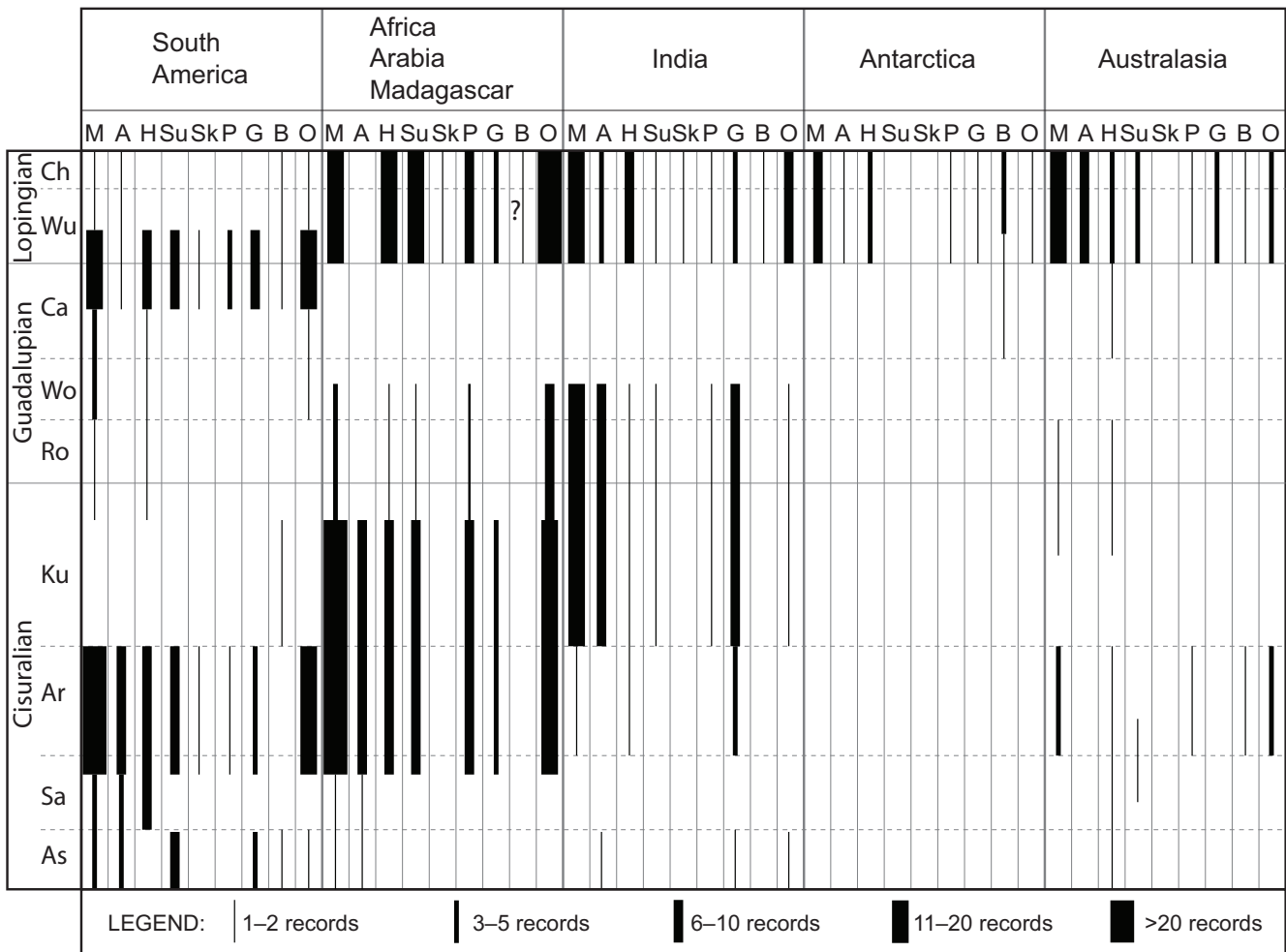


Fig. 6—Summary chart of the distribution of major functional feeding groups and subgroups recognized in the *Glossopteris* flora through the Permian of Gondwana. M = Margin feeding, A = Apical feeding, H = Hole feeding, Su = Surface feeding, Sk = Skeletonization, P = Piercing-and-sucking (mucivory) damage, G = Gallings, B = Boring in wood, O = Oviposition scarring. The thickness of vertical black lines relates to the number of discrete damage type/plant taxon/stratigraphic unit combinations. For the distribution of records of seed herbivory, coprolites, detritivory, fungivory, palynophagy and equivocal indications of leaf mining, see Table 1. As = Asselian, Sa = Sakmarian, Ar = Artinskian, Ku = Kungurian, Ro = Roadian, Wo = Wordian, Ca = Capitanian, Wu = Wuchiapingian, Ch = Changhsingian.

The producers of galls in these plants are uncertain. A broad range of arthropods can induce plant galls (Oldfield, 2005; Raman *et al.*, 2005; Ronquist & Liljebblad, 2001). Mites and sternorrhynchan hemipteroids were potential arthropod gall inducers in Gondwanan Permian ecosystems (Prevec *et al.*, 2009). However, gall formation (cecidogeny) can also be induced by a wide range of other organisms, including nematodes, fungi, bacteria and viruses (Mani, 1992; Shorthouse *et al.*, 2005).

Seed herbivory

Seed herbivory (also described as seed predation or seed boring; Fig. 1) is a form of attack by arthropods that involves penetration of the tough outer seed coat to target the nutritious internal material intended to aid the initial growth of the new plant. Seeds are rich in oils and carbohydrates and

so are naturally favoured targets for arthropod herbivores. The fossil record of damage to seeds extends back to the Early Pennsylvanian, some 50 million years after seeds are known to have evolved (Labandeira, 2006). The record of seed herbivory from the Permian of Gondwana is scanty (Tables 1, 2). Only the single study by Dos Santos *et al.* (2020) has recorded strongly convincing examples of this feeding strategy. They attributed various isolated to clustered seed herbivory scars on *Cordaicarpus* sp. seeds to DT74, DT399, DT400 and DT401 of the damage scheme established by Labandeira *et al.* (2007). They considered the likely producers of such damage features to be representatives of Permothemistida (Diathemidae) or Hemiptera (Sternorrhyncha). Chandra and Singh (1996, pl. 6, figs F, G) also illustrated *Cordaicarpus* seeds with circular markings on the integument that might represent seed predation. Further, Prevec and Labandeira (unpubl. data) have identified numerous examples of herbivory (DT73) on

Elatra leslii seeds from the Hammanskraal flora (Artinskian) of South Africa, also figured by Anderson & Anderson (1985, pl. 86, fig. 13).

Wood boring

The record of arthropod borings in plant axes (Fig. 1) extends back to the Early Devonian but excavations into true woody tissues (xylophagy) occur soon after the evolution of secondary wood production in the Late Devonian (Labandeira, 2006, 2013). Excavated cavities within gymnospermous secondary wood (Fig. 4E) are relatively common in Permian strata across Gondwana (Walkom, 1928; Maheshwari, 1967; Zavada & Mentis, 1992; Weaver *et al.*, 1997; Bolzon *et al.*, 2004; Kellogg & Taylor, 2004; Césari *et al.*, 2012; Slater *et al.*, 2012; Harper, 2015; Harper *et al.*, 2016). Some blind-ended, spindle-shaped, cavities undoubtedly represent pocket-rot generated by basidiomycote fungi (Stubblefield & Taylor, 1986; Harper *et al.*, 2016, 2017). However, other cases, especially where the cavities are positioned regularly in the latewood of growth rings, where the cells lining the cavities have abruptly truncated walls, and where the chambers are infilled by coprolites (Fig. 4E, F), certainly involved xylophagy (Weaver *et al.*, 1997; Kellogg & Taylor, 2004). In some cases, such cavity formation might have involved multitrophic associations of wood-consuming fungi and fungi-feeding arthropods. To date, more complex gallery forms, such as those attributed to beetles in coeval Chinese woods by Feng *et al.* (2017) have not been forthcoming from Gondwanan Permian assemblages.

Damage occurred in various wood taxa including *Agathoxylon*, *Australoxylon*, *Cuyoxylon*, *Megaporoxylon* and *Zallesskioxylon* (Table 1). Such woods are commonly attributed to glossopterids, but affinities with other gymnosperms are also possible. Boring damage is evident both in presumed subaerial axes and in the root systems (e.g., *Vertebraria*: Fig. 4G) of Gondwanan Permian gymnosperms (Slater *et al.*, 2012, 2015; Harper, 2015; Harper *et al.* 2016).

Oribatid mites are the primary candidates for producing boring damage in the Permian woods (Kellogg & Taylor, 2004; Césari *et al.*, 2012), although some of the larger cavities, especially where associated with fungi and where cross-galleries are evident, might have been produced by proto-coleopterans (Weaver *et al.*, 1997; Bolzon *et al.*, 2004).

Coprolites

Thus far, no gut contents are available from Gondwanan Permian insect fossils. A few studies have documented dispersed coprolites of arthropods identified in thin sections of silicified plant organs or from residues recovered from bulk acid-dissolution of permineralized peats (Table 1). Various coprolites identified within borings through the secondary tissues (or more rarely, the primary tissues) of

several gymnospermous wood taxa contain mostly tracheid wall fragments (Fig. 4E–G; Walkom, 1928; Weaver *et al.*, 1997; Kellogg & Taylor, 2004; Césari *et al.*, 2012; Decombeix *et al.*, 2012; Slater *et al.*, 2012, 2015; Harper, 2015; Harper *et al.*, 2016) and were probably produced by oribatid mites. The largest study of Permian Gondwanan microcoprolites by Slater *et al.* (2012) identified a series of additional dung pellets that indicate feeding strategies including specialist fungivory, palynophagy and possible leaf mining, to more generalist folivory and detritivory (Fig. 4H, I). Chauhan *et al.* (1985) also reported putative coprolites on the surface of *Belemnopteris* leaves but the internal details of these structures are not resolvable. Bulk maceration, thin sections and X-ray tomography of permineralized peats offer considerable potential for further investigations of coprolite form and content, and for resolving the architecture of borings with wood.

Oviposition

Although not strictly feeding traces, owing to their widespread and abundant occurrence, oviposition scars (Fig. 1) are treated functionally as a category of herbivory since the insertion of eggs by the insect ovipositor on or into the plant tissues typically generates traces that are analogous to the penetrative damage left by mucivory (Labandeira, 2002). Simple circular, ovate or elliptical scars have been illustrated on a wide range of Permian leaves and axes across Gondwana (Tables 1, 2). Some are difficult to differentiate from galls or even small examples of hole feeding or mucivory (Fig. 5I, J, N). However, where the damage features are arranged in linear files on one or both sides of the leaf midrib (Fig. 4M; Chandra & Singh, 1992; Melchor & Césari, 1997; Prevec *et al.*, 2009; McLoughlin, 2011a; Srivastava & Srivastava, 2016), on the midrib itself (Figs 4J–L; 5L, S, T; DT76: Harrington, 1934; Adami-Rodríguez *et al.*, 2004a, b; Cariglino, 2018), or in an arcuate configuration (Fig. 5O), attribution to oviposition scars is more convincing. Other examples of oviposition damage are arrayed in regular fashion near the leaf margins (Fig. 5Q; DT 102 of Prevec *et al.*, 2009, pl. 12, figs 1–5; Gallego *et al.*, 2014, fig. 5.1, 5.2). In a few cases, the distinctive shape and arrangement as elliptical features transverse to venation (Fig. 5R) demarcates distinctive styles (DT54, DT137) of oviposition (Gallego *et al.*, 2014, fig. 4.3). More irregularly scattered scars on mid-lamina regions of glossopterid leaves are common (Fig. 5I, J, N, P, Q) and have been accepted as oviposition features by Cariglino (2018, fig. 5D, G, J, K–M) and Prevec *et al.* (2009: DT101; pl. 11, figs 1, 2, 6, 7, 8; pl. 12, figs 6, 8, 9, 10), but others are difficult to discriminate with confidence even where they are arranged in a semi-regular fashion along secondary veins (e.g., Archangelsky, 1957, pl. 8, figs 3, 4).

Most examples of oviposition damage occur on glossopterid leaves (Tables 1, 2). However, some notable

examples have been recorded clustered on the internodes of sphenophyte axes (Beattie, 2007; Prevec *et al.*, 2009). Features suggestive of oviposition scars have also been illustrated on various non-glossopterid gymnosperms including Ginkgoales (Cúneo, 1987; Gallego *et al.*, 2014), *Noeggerathiopsis* (El-Khayal *et al.*, 1980; Anderson & Anderson, 1985), *Eremopteris* (Archangelsky, 1958a), and *Chiropteris* (Archangelsky, 1958b). Only rare cases of putative oviposition scars have been illustrated on fern leaves (Cazzulo-Klepzig & dos Reis Correia, 1981, pl. 2, fig. 2; Cariglino, 2018, fig. 5).

The enigmatic fan-shaped fossil *Satsangia campanulata*, documented from the Nidpur beds (uppermost Permian or lowermost Triassic) of India (Srivastava & Maheshwari, 1973, text-fig. 1, pl. 1, figs 1–4, 6) has been considered to represent a reproductive organ bearing scattered circular seed scars or pollen sacs. However, an alternative possibility is that this fossil represents a ginkgoalean leaf with numerous small (0.5-mm-diameter) oviposition or mucivory scars scattered across its surface.

Potential candidates for the production of oviposition damage are palaeodictyopteroid and odonatopteroid insects (Prevec *et al.*, 2009). Odonatopteroids are especially likely candidates for oviposition damage to semi-aquatic sphenophyte axes (Beattie, 2007), since these insects were obligate insect predators (Bechley, 1996) of lake- and stream-margin habitats. From Gondwana, protodonatan dragonfly body fossils have been recorded from the Permian of Brazil, the Falkland Islands and Australia (Table 3).

Other interactions

In addition to the examples given above, arthropods may have interacted with elements of the *Glossopteris* flora in other ways, including strategies that were mutually beneficial. For example, based on features in the apical region of the ovule, Archangelsky & Cúneo (1987) suggested that the conifer *Ferugliocladus patagonicus* might have been pollinated by insects. McLoughlin & Prevec (in press) have also presented evidence in terms of polysperm wing architecture and clustering of the ovules to suggest that some glossopterids may have been pollinated by insects. The general trends towards elaboration and enrolment of the marginal wings of glossopterid polysperms late in the Permian might have been responses to both attraction of specific pollinators and intensified herbivory on seeds.

Few Permian insects would have been large enough to transport the relatively robust intact seeds of Permian gymnosperms. However, it is notable that the small Permian seeds attributed to *Maheshwariella spinicornuta* (considered to be the seed of the conifer *Buriadia heterophylla*: Pant & Nautiyal, 1967) have 0.75-mm-long micropylar horns bearing recurved epidermal barbs (Maheshwari & Tewari, 1986, text-fig. 1, pl. 1, figs 1–4) that suggest a potential role in zoochory. Moreover, similar micropylar spines, some with barbs, are

present in various other Gondwanan Permian seeds (e.g., *Cornucarpus furcata* of Bernardes de Oliveira & Yoshida, 1981; *Birsinghia florinii* Pant *et al.*, 1995; Tiwari, 2008; seeds attributed to *Podozamites hlobanensis* Anderson & Anderson, 1985, pl. 162, figs 24–28) that might indicate an equivalent function. The seed *Stephanostoma crystallinum* (see Pant & Nautiyal, 1960; Tiwari, 2008) has a funnel-like extension around the micropyle that might have operated to hold a large pollen drop to encourage entomophily. Furthermore, the blunt lateral spine-like appendages on the integument of this seed possibly offered defence against seed herbivory.

Although evidence of insect-plant mimesis (a form of mimicry) extends back to at least the Permian (Garrouste *et al.*, 2016) and possibly the Carboniferous (Scott & Taylor, 1983), we did not detect any definitive examples from the Gondwanan Permian. However, the relatively even-sized polygonal areolae of *Stenoperlidium permianum* wings from eastern Australia (Tillyard, 1935c) are similar to the coarsely reticulate venation pattern of some *Glossopteris* leaves from the same region, such as *G. burngrovensis* (McLoughlin, 1994a). Other insects, e.g., *Phyllelytron folium* Kukalová, 1966 have ovate, acutely tipped wings that, in gross form and venation, are similar to the bud scales and reproductive bracts (scale leaves) of various glossopterids (see Jell, 2004).

Terrestrial arthropod body fossils of the glossopterid biome

Although all regions of Gondwana have yielded around 300 records of Permian insect (and other terrestrial arthropod) body fossils (Table 3), the spatiotemporal coverage of these occurrences is patchy and heavily influenced by a ‘lagerstätten effect’, whereby a few key lacustrine deposits and formations (e.g., the Lopingian Croudace Bay Formation of Australia) account for most of the reported specimens. At present, therefore, it is perhaps premature to attempt to read any apparent temporal trends as a genuine reflection of insect macroevolution within the Permian high southern latitudes. At a first approximation, the fossil record of Permian Gondwanan insects is also overwhelmingly a record of isolated wing impressions. Consequently, direct information on mouthparts is lacking in the majority of cases. Even in rare cases where insect body fossils are preserved more-or-less complete (e.g., *Anthracoblattina mendesi* from the Lontras Shale of Brazil; Ricetti *et al.*, 2016), the morphology of the mouthparts is frequently obscured or difficult to discern. Considering the dearth of well-preserved feeding-diagnostic mouthparts, an alternative means of assessing which groups of phytophagous insects were important in *Glossopteris*-dominated forests is to identify the dominant orders preserved as fossils, and draw analogies with the feeding modes of their extant counterparts.

The ‘Belmont insect beds’ of the Croudace Bay Formation, Newcastle Coal Measures, Australia, have produced a spectacular diversity of Lopingian insect

Table 1—Compendium of published records of plant–arthropod interactions from the Permian of Gondwana sorted by region and author(s). Abbreviations: (C) = compression/impression fossil; (AP) = anatomically preserved (permineralized) fossil.

Authors	Age	Stratigraphic unit	Locality, Basin	Damage features	Host plant/organ
South America					
Adami-Rodrigues & Iannuzzi, 2001; Adami-Rodrigues <i>et al.</i> , 2004a, fig. 2A, B, fig. 3A-C; Adami-Rodrigues <i>et al.</i> , 2004b, fig. 5A, B, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Faxinal Mine, Paraná Basin, Rio Grande do Sul, Brazil	Multi-lobed, shallow to deeply incised margin feeding and apex feeding	<i>Glossopteris</i> sp. (also said to occur on <i>Glossopteris</i> sp. cf. <i>G. communis</i> , <i>G. brasiliensis</i> , <i>G. angustifolia</i> , <i>G. browniana</i>)
Adami-Rodrigues & Iannuzzi, 2001; Adami-Rodrigues <i>et al.</i> 2004a, fig. 2A; Adami-Rodrigues <i>et al.</i> 2004b, fig. 5A, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Faxinal Mine, Paraná Basin, Rio Grande do Sul, Brazil	Elliptical hole feeding	glossopterid scale leaf
Adami-Rodrigues & Iannuzzi, 2001; Adami-Rodrigues <i>et al.</i> , 2004a, fig. 2D, E; Adami-Rodrigues <i>et al.</i> , 2004b, fig. 5D, E; Iannuzzi <i>et al.</i> , 2009, fig. 7E, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	(1) Lorate, elliptical and ovate hole feedings; (2) shallow irregular margin feeding	<i>Noeggerathiopsis hislopitii</i>
Adami-Rodrigues & Iannuzzi, 2001; Adami-Rodrigues <i>et al.</i> , 2004a, fig. 2F, G; Adami-Rodrigues <i>et al.</i> , 2004b, fig. 5F, G, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	Intervenal hole feeding or surface feeding	<i>Glossopteris</i> sp. cf. <i>G. communis</i> (also said to occur on <i>Gangamopteris obovata</i> and <i>Noeggerathiopsis hislopitii</i>)
Adami-Rodrigues & Iannuzzi, 2001; Adami-Rodrigues <i>et al.</i> 2004a, fig. 2F, G; Adami-Rodrigues <i>et al.</i> 2004b, figs 6B, 7A, B, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	Putative bifurcating leaf mine	<i>Glossopteris</i> sp. cf. <i>G. indica</i>
Adami-Rodrigues <i>et al.</i> , 2004b, figs 1B, 6C, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	(1) Linear slot feeding; (2) ellipsoidal to spherical gall-like structures	" <i>Gangamopteris</i> " <i>obovata</i>
Adami-Rodrigues <i>et al.</i> , 2004b, fig. 6E, F, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	Possible skeletonization	<i>Glossopteris communis</i> (also said to occur on <i>G. occidentalis</i>)
Adami-Rodrigues <i>et al.</i> , 2004b, fig. 6H, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	Lenticular oviposition scars on midrib	" <i>Gangamopteris</i> " <i>obovata</i>
Adami-Rodrigues <i>et al.</i> 2004b, fig. 6I, (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	Possible piercing and sucking marks scattered over secondary veins mid-lamina	<i>Glossopteris communis</i> (also said to occur on <i>Noeggerathiopsis hislopitii</i>)
Adami-Rodrigues <i>et al.</i> , 2017 (no figures) (C)	Wordian	Serrinha Member, Rio do Rasto Formation	BR-373, km 277, between Prudentópolis and Relógio, Paraná Basin, Paraná, Brazil	Putative continuous and discontinuous margin feeding, circular to elliptical hole feeding and complete detachment of leaflets basally	<i>Sphenophyllum parandense</i>
Archangelsky, 1957, pl. 1, fig. 2, (C)	Wordian–Wuchiapingian	La Golondrina Formation	Bajo de la Leona, La Golondrina Basin, Santa Cruz, Argentina	Possible V-shaped notched margin feeding	<i>Glossopteris ampla</i>
Archangelsky, 1957, pl. 2, fig. 3, (C)	Wordian–Wuchiapingian	La Golondrina Formation	Bajo de la Leona, La Golondrina Basin, Santa Cruz, Argentina	Irregularly lobed margin feeding	<i>Glossopteris argentina</i>
Archangelsky, 1957, pl. 7, fig. 2; Archangelsky, 1990, fig. 9.18, (C)	Wordian–Wuchiapingian	La Golondrina Formation	Bajo de la Leona, La Golondrina Basin, Santa Cruz, Argentina	Possible mid-lamina oviposition or piercing-and-sucking scar	<i>Glossopteris indica</i>

Archangelsky 1957, pl. 8, figs 3, 4. (C)	Wordian–Wuchiapingian	La Golondrina Formation	Bajo de la Leona, La Golondrina Basin, Santa Cruz, Argentina	Possible mid-lamina, vein-parallel, elliptical oviposition scars	<i>Gangamopteris angustifolia</i>
Archangelsky, 1957, pl. 10, fig. 3; text-fig. 3.2. (C)	Wordian–Wuchiapingian	La Golondrina Formation	Bajo de la Leona, La Golondrina Basin, Santa Cruz, Argentina	Possible interveinal surface feeding flanking midrib (broad area of raised areolae)	<i>Glossopteris moresi</i>
Archangelsky, 1958a, pl. 3. (C)	Wordian–Wuchiapingian	La Golondrina Formation	Bajo de la Leona, La Golondrina Basin, Santa Cruz, Argentina	(1) possible apex feeding (truncate pinnules); (2) possible paired mid-lamina circular oviposition scars	<i>Eremopteris golondrinensis</i>
Archangelsky, 1958b, fig. 7. (C)	Wordian–Wuchiapingian	La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz, Argentina	Simple scalloped margin feeding	<i>Sphenophyllum thonii</i>
Archangelsky 1958b, fig. 28.	Wordian–Wuchiapingian	La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz, Argentina	Possible simple broadly scalloped margin feeding	<i>Noeggerathiopsis hislopit</i>
Archangelsky, 1958b, fig. 42. (C)	Wordian–Wuchiapingian	La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz, Argentina	Possible simple broadly scalloped margin feeding	<i>Glossopteris decipiens</i>
Archangelsky, 1960, fig. 4. (C)	Wordian–Wuchiapingian	La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz, Argentina	Possible mid-lamina elliptical oviposition scar or gall	" <i>Chiropteris harrisi</i> "
Archangelsky & Arrondo, 1971, pl. 5, fig. 1. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Possible C-shaped margin feeding on pinnule	<i>Botrychiopsis plantiana</i>
Archangelsky & Arrondo, 1973, pl. 4, fig. 2. (C)	Asselian–Sakmarian	Arroyo Totoral Formation	Sierra de los Llanos, La Rioja Province, Argentina	Simple scalloped margin feeding	<i>Gangamopteris obovata</i>
Archangelsky & Cúneo, 1982, pl. 1, fig. 1; pl. 2, figs 1, 2. (C)	Sakmarian–Artinskian?	Nueva Lubecka Formation (upper fossiliferous level G)	Estancia la Casilda, north of Piedra Shotel, Chubut Province, Argentina	Simple scalloped margin feeding; acroscopic margin of pinnules	<i>Botrychiopsis valida</i>
Archangelsky & Cúneo, 1987 (C)	Cisuralian	Arroyo Totoral Formation	La Rioja Province, Argentina	Potential insect-mediated pollination mechanism	<i>Ferriogliadus</i>
Archangelsky <i>et al.</i> , 1981, pl. 2, fig. 8. (C)	Sakmarian–Artinskian?	Piedra Shotel Formation	Piedra Shotel area, Chubut Province, Argentina	Simple scalloped margin feeding	<i>Glossopteris wilsonii</i>
Archangelsky <i>et al.</i> , 1981, pl. 2, fig. 9. (C)	Sakmarian–Artinskian?	Piedra Shotel Formation	Piedra Shotel area, Chubut Province, Argentina	Simple scalloped margin or apex feeding	<i>Gangamopteris obovata</i>
Archangelsky <i>et al.</i> 1981, pl. 3, fig. 12. (C)	Sakmarian–Artinskian?	Piedra Shotel Formation	Piedra Shotel area, Chubut Province, Argentina	Possible gall on midrib	<i>Gangamopteris obovata</i>
Archangelsky <i>et al.</i> , 2004, pl. 3, fig. 4. (C)	Sakmarian–Artinskian?	Rio Genoa Group	Tepuel-Genoa Basin, Chubut Province, Argentina	Possible margin feeding (irregular rimmed indentations)	<i>Dichotomopteris pantii</i>
Bernardes de Oliveira & da Silva Pontes, 1977, pl. 2, fig. 3. (C)	Sakmarian–Artinskian	Rio Bonito Formation	São Marcos, Camada Irapuá, Santa Catarina, Brazil	Possible shallow to deeply scalloped margin feeding	<i>Noeggerathiopsis hislopit</i>
Bernardes de Oliveira <i>et al.</i> , 2000, pl. 2, figs 6, 7. (C)	late Artinskian	Assistência Formation (or Member), Irati Group (or Formation)	Formação Angatuba, Paraná Basin, São Paulo, Brazil	Probable spindle-shaped oviposition scar on midrib near base of leaf	<i>Glossopteris mussae</i>
Bolzon <i>et al.</i> 2004, fig. 1.1–1.6. (AP)	Kungurian	Serra Alta Formation	São Gabriel – Batovi road (km 18), Paraná Basin, Rio Grande do Sul, Brazil	Spindle shaped borings in secondary wood with some diagonal cross-connections forming galleries	Unidentified wood; damage probably from orbibatid mites

Cariglino, 2013, fig. 5D–H. (C)	Wordian–Wuchiapingian	La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Possible galls	On small ?axis associated with <i>Glossopteris conspicua</i>
Cariglino, 2018, fig. 3A. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Semicircular margin feeding (DT12)	Fern pinna (<i>Dichotomopteris?</i>)
Cariglino, 2018, fig. 3B. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Deeply incised U-shaped margin feeding (DT12)	<i>Sphenophyllum</i> sp.
Cariglino, 2018, fig. 3C, D. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Multiple shallow semicircular margin-feeding excavations (DT12)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3E. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Broad semicircular excision reaching midrib (DT14)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3F. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Deep V-shaped marginal incision (DT15)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3G. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Bilobate margin feeding (DT26)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3H. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Cuspedate margin feeding with a perpendicularly striate, thick rim (DT142)	<i>Glossopteris</i> sp.
Cariglino, 2018, figs 3I, 4G. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Small circular hole feeding (DT01)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3J, K. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Slender rectilinear slot feeding between veins (DT08)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3F, L. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Roughly circular hole feeding (DT02)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3M, N. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Possible irregular removal of tissue between secondary veins: margin to midrib (cf. DT78)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3O. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Circular hole feeding with thickened rim (DT113)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3P, Q. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Small circular hole-feeding or oviposition scars aligned just inside lamina margin (DT64)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 3R. (C)	Wordian–Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Hole-feeding damage or oviposition scars arranged as linear series on either side of midrib (DT50)	<i>Glossopteris</i> sp.

Cariglino, 2018, fig. 3S. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Possible skeletonization over much of lamina (DT17?)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4A. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Surface feeding: Abrasion between parallel veins (DT28)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4B. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Surface feeding: Circular abrasion of surface tissue (DT31)	<i>Sphenophyllum</i> sp.
Cariglino, 2018, fig. 4C. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Polylobate surface (window) feeding at both sides of midrib (DT82)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4D, E. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Surface feeding: (1) U-shaped abrasion surface (DT97); (2) removal of broad area of surface tissues with a weak reaction rim (DT29).	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4F. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Linear surface feeding between veins near midrib (DT103)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4G. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Piercing and sucking: Randomly distributed mid-lamina circular punctures (DT46)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4H, L. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Piercing and sucking: scattered circular punctures with a central dome (DT47)	<i>Glossopteris</i> sp., possibly in lycopsid microphylls
Cariglino, 2018, fig. 4I. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Piercing and sucking: elliptical punctures scattered across lamina (DT48)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4J. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Circular punctures on secondary veins (DT133)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4J, K. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Circular to elliptical punctures on midrib (DT138?)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4M, N. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Circular to slightly polylobate galls with thick reaction rim on or close to midrib (DT120)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4O. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Isolated circular gall surrounded by radiating partitions (DT52)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4P–R. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Circular to laciform galls with roughened surface and thin reaction tissue with central ostiole (DT107)	<i>Glossopteris</i> sp.

Cariglino, 2018, fig. 4S. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Numerous circular galls with pustulose surfaces scattered on leaf (DT260)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4T. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Elongate, diamond-shaped gall (DT85)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 4U. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Elliptical gall at base of leaflet	<i>Sphenophyllum</i> sp.
Cariglino, 2018, fig. 5. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Elliptical oviposition scar on rachis (DT72)	<i>Kladistamuus</i> sp. (fern)
Cariglino, 2018, fig. 5C, E. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Two linear series of spindle-shaped oviposition scars along the midrib (DT76)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 5D, G, J. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Various elliptical oviposition scars on mid-lamina (DT101)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 5F. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Possible interveinal surface feeding or clustered oviposition scars (DT100)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 5H. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Paired small elliptical oviposition scars in mid-lamina (DT136)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 5I. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Large elliptical oviposition scars inside margin (DT102)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 5K–M. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Longitudinal row of transverse orientated spindle-shaped oviposition scars on the midrib (DT137)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 5N. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Linear array of small circular oviposition scars along midrib	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 6A, B. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Possible row of bulbous oviposition scars flanking either side of midrib.	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 6C–E, H, I. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Semicircular traces on leaf margins with central circular marks (possible leaf mining)	<i>Glossopteris</i> sp.
Cariglino, 2018, fig. 6F, G. (C)	Wordian– Wuchiapingian	Laguna Polina Member, La Golondrina Formation	Laguna Polina, La Golondrina Basin, Santa Cruz Province, Argentina	Possible paired narrow lorate oviposition scars along each side of midrib	<i>Glossopteris</i> sp.
Cariglino & Gutiérrez, 2011, fig. 2.1–2.3. (C)	Wordian– Wuchiapingian	Lower part of Laguna Polina Member, La Golondrina Formation	Laguna Polina, Estancia La Golondrina, La Golondrina Basin, Santa Cruz, Argentina	Margin feeding: isolated, deep C-shaped excision	<i>Glossopteris brownitana</i>

Cariglino & Gutiérrez, 2011, fig. 3.1–3.4. (C)	Wordian–Wuchiapingian	Lower part of Laguna Polina Member, La Golondrina Formation	Laguna Polina, Estancia La Golondrina, La Golondrina Basin, Santa Cruz, Argentina	Margin feeding: Irregular deep excisions rimmed by thin reaction tissue	<i>Glossopteris damudica</i>
Cariglino & Gutiérrez, 2011, fig. 4.1–4.3. (C)	Wordian–Wuchiapingian	Upper part of Laguna Polina Member, La Golondrina Formation	Laguna Castellanos, La Golondrina Basin, Santa Cruz, Argentina	(1) Margin feeding: semi-regularly spaced, small, circular to semicircular excisions with thin reaction rim; (2) Hole feeding: semi-regular longitudinal files of small, circular, mid-lamina excisions with thin reaction rim	<i>Glossopteris</i> sp. cf. <i>G. ampla</i>
Cariglino & Gutiérrez, 2011, fig. 5.1–5.4. (C)	Wordian–Wuchiapingian	Upper part of Laguna Polina Member, La Golondrina Formation	Laguna Castellanos, La Golondrina Basin, Santa Cruz, Argentina	Small circular to elliptical oviposition scars irregularly arrayed along midrib and possibly on adjacent lamina	<i>Glossopteris</i> sp. cf. <i>G. ampla</i>
Cazzulo-Klepzig & Correia, 1981, pl. 2, fig. 2. (C)	Wordian	Serrhina Member, Rio do Rasto Formation	Serra do Cadeado, Paraná, Brazil	Possible ovate oviposition scars on rachis	<i>Dizeugotheca</i> sp.
Césari & Cúneo, 1989, pl. 1H. (C)	Gzhelian–Asselian	Bajo de Veliz Formation	Bajo de Veliz, San Luis Province, Argentina	Possible scalloped apical feeding	<i>Cheirophyllum specularare</i>
Césari & Hünieken, 1992, pl. 1, fig. 3. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Surface feeding between secondary veins: margin to midline	<i>Velizia inconstans</i>
Césari <i>et al.</i> , 2012, fig. 4B, J–L. (AP)	Asselian?	Upper San Ignacio Formation	Ñipas and Las Ánimas creeks, Sierra de Castaño, Andean Cordillera, San Juan Province, Argentina	20 µm – 1 mm diameter borings filled with ellipsoidal coprolites (10–100 µm diameter) in primary and secondary wood	<i>Cryoxyton</i> sp. (stem and root wood): oribatid mite damage
Crisafulli, 2003, fig. 6A. (AP)	Lopingian?	Yaguari Formation	Near Fraile Muerto, Cerro Largo, Uruguay	Possible borings: 1 mm diameter cavities in secondary wood	<i>Zalesskioxyton jamudhiense</i>
Cúneo, 1983, pl. 1, fig. 1. (C)	Sakmarian–Artinskian?	Piedra Shotel or Nueva Lubecka formations (Rio Genoa Group)	Estancia la Casilda, north of Piedra Shotel, Tepuel-Genoa Basin, Chubut Province, Argentina	Possible scalloped margin feeding	<i>Glossopteris wilsonii</i>
Cúneo, 1986 (C)	Permian	Not defined	Argentina	Suggested possible crypsis: similarity of insect wings to form and venation of glossopterid leaves	<i>Glossopteris</i> spp.
Cúneo, 1987, fig. 4. (C)	Sakmarian–Artinskian?	Rio Genoa Group	Betancourt, Tepuel-Genoa Basin, Chubut, Argentina	Oviposition or hole feeding	<i>Ginkgoites eximia</i>
Cúneo, 2000, fig. 1A, C. (C)	Sakmarian–Artinskian?	Rio Genoa Group	Betancourt, Tepuel-Genoa Basin, Chubut, Argentina	Possible scalloped margin feeding	<i>Annularia mucronata</i>
Dolianiti, 1953a, pl. 3, fig. 1, pl. 6, figs 1, 2. (C)	Sakmarian–Artinskian	Rio Bonito Formation	Bainha, Paraná Basin, Santa Catarina, Brazil	Possible apical and hole feeding	<i>Glossopteris</i> sp.
Dolianiti, 1953b, pl. 1. (C)	Sakmarian–Artinskian	Rio Bonito Formation	Bainha, Paraná Basin, Santa Catarina, Brazil	Possible deeply embayed margin feeding	<i>Glossopteris</i> or <i>Rhabdotaenia</i> sp. (= <i>Taeniopteris feddeni</i>)
Do Santos <i>et al.</i> , 2020, fig. 3A, B, I. (C)	Sakmarian–Artinskian	Uppermost Siderópolis Member, upper Rio Bonito Formation	Itanema II locality, Urussanga Municipality, Paraná Basin, Santa Catarina, Brazil	Seed herbivory: Isolated or clustered, circular, broadly elliptical to ovate cratered pits, <0.5 mm long, proximally on seed central body, rarely on wings (DT74)	<i>Cordaitcarpus</i> spp. 1 and 2: damage inferred to be from Permothemistida (Diathemididae) or Hemiptera (Sternorrhyncha)

Do Santos <i>et al.</i> , 2020, fig. 3G, H; 4I-L. (C)	Sakmarian–Artinskian	Uppermost Siderópolis Member, upper Rio Bonito Formation	Itanema II locality, Urussanga Municipality, Paraná Basin, Santa Catarina, Brazil	Seed herbivory: Solitary or locally clustered, near-circular, 0.09-mm-diameter crater with central tubercle or hole, on margin of seed central body (DT399)	<i>Cordiacarpus</i> sp. 2 and cupule-attached seed 1: damage inferred to be from Permothemistida (Diathemidae) or Hemiptera (Sternorrhyncha)
Do Santos <i>et al.</i> , 2020, fig. 3C-F; 4D-H. (C)	Sakmarian–Artinskian	Uppermost Siderópolis Member, upper Rio Bonito Formation	Itanema II locality, Urussanga Municipality, Paraná Basin, Santa Catarina, Brazil	Seed herbivory: Isolated, rarely clustered, on seed central body, c. 0.5 mm diameter, circular to elliptical craters with transverse ridges and furrows, weakly defined central pit or tubercle (DT400)	<i>Cordiacarpus</i> sp. 1, <i>Samaropsis</i> sp. 5, and Cupulate attached Seed 1: damage inferred to be from Permothemistida (Diathemidae) or Hemiptera (Sternorrhyncha)
Do Santos <i>et al.</i> , 2020, fig. 3C-F; 4A–C. (C)	Sakmarian–Artinskian	Uppermost Siderópolis Member, upper Rio Bonito Formation	Itanema II locality, Urussanga Municipality, Paraná Basin, Santa Catarina, Brazil	Seed herbivory: Isolated on central seed body, broadly elliptical, c. 1 × 2 mm, depressed scars, wispy extensions, central depression and robust rim (DT401)	Cupule-attached Seed 1: damage inferred to be from Permothemistida (Diathemidae) or Hemiptera (Sternorrhyncha)
Fernández & Chiesa, 2020, fig. 2A–C. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Deep marginal U-shaped to rectangular excisions (DT12)	<i>Glossopteris wilsonii</i>
Fernández & Chiesa, 2020, fig. 2G. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Deep apical U-shaped excision (DT13)	<i>Euryphyllum whittianum</i>
Fernández & Chiesa, 2020, fig. 2H. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Broad C-shaped marginal excision on lateral pinnule (DT12)	<i>Botrychopsis plantiana</i>
Fernández & Chiesa, 2020, fig. 2A, B, D. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Lorate-linear, inner to mid-lamina, interveinal surface feeding with prominent reaction rim (DT28, DT103)	<i>Glossopteris wilsonii</i>
Fernández & Chiesa, 2020, fig. 2F. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Linear, inner to mid-lamina, interveinal surface feeding with prominent reaction rim (DT97, DT103)	<i>Euryphyllum whittianum</i>
Fernández & Chiesa, 2020, fig. 2I, J. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Lorate-linear, inner to mid-lamina, interveinal surface feeding with prominent reaction rim (DT103)	<i>Gangamopteris obovata</i>
Fernández & Chiesa, 2020, fig. 2E, G. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Spindle-shaped scars parallel to venation in distal and marginal portions of lamina (DT102)	<i>Euryphyllum whittianum</i>
Fernández & Chiesa, 2020, fig. 2I. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Elliptical scars parallel to venation marginal/proximal portions of lamina (DT102)	<i>Gangamopteris obovata</i>

Fernández & Chiesa, 2020, fig. 3A, B. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	(1) Large, thick-rimmed elliptical oviposition? scars in mid-lamina; (2) Circular, 2–5 mm diameter, thick-rimmed gall on mid-line of lamina (DT32). (3) Thinner, but larger, 5–6 × 2–3 mm darkly contoured traces, parallel and perpendicular to venation also present (DT115)	<i>Euryphyllum whittianum</i>
Fernández & Chiesa, 2020, fig. 3C. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Elliptical raised galls? near leaf midline	<i>Gangamopteris obovata</i>
Fernández & Chiesa, 2020, fig. 3E. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Small circular to <1 mm galls inside terminal margin of distal pinnule (DT32)	<i>Botrychiopsis plantiana</i>
Fernández & Chiesa, 2020, fig. 3F. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Roughly semicircular excisions 1–3 mm diameter inside terminal margin of distal pinnule	<i>Botrychiopsis plantiana</i>
Fernández & Chiesa, 2020, fig. 3D. (C)	Gzhelian–Asselian	Pallero Member, Bajo de Veliz Formation	Bajo de Veliz, Paganzo Basin, San Luis Province, Argentina	Oviposition scars or galling: 3–4 elliptical, low-relief scars 1–3 mm diameter, parallel to venation in centre of leaf (cf. DT53)	<i>Gangamopteris obovata</i>
Freguelli, 1953, pl. 1, figs 1, 2. (C)	Sakmarian–Artinskian?	Río Genoa Group	Estancia Ferrarotti, Tepuel-Genoa Basin, Chubut, Argentina	Possible pinnule apex truncation	<i>Asterotheca feruglioi</i>
Gallego <i>et al.</i> , 2003, 2004, unfigured (C)	late Sakmarian–Artinskian	Melo Formation	Near Melo, Department of Cerro Largo, Uruguay.	U-shaped margin feeding	<i>Glossopteris wilsonii</i> , <i>Glossopteris</i> sp.: damage possibly from "protortopterans" (Protothoptera), "paratrioptera" (Paratrioptera or Mecoptera) and some "hyoperlids" (Hypoerperlida or Plecoptera)
Gallego <i>et al.</i> , 2014, fig. 2.1. (C)	Sakmarian–Artinskian	Río Genoa Group	Aguada Loca, Betancourt (SP XVI), Ferrarotti IIB and Pique Carbón localities, Tepuel-Genoa Basin, Chubut Province, Argentina	C-shaped margin feeding (DT81)	<i>Glossopteris</i> sp.
Gallego <i>et al.</i> , 2014, fig. 2.2, 2.5, 2.6. (C)	Sakmarian–Artinskian	Río Genoa Group	Aguada Loca, Betancourt (SP XVI), Ferrarotti IIB and Pique Carbón localities, Tepuel-Genoa Basin, Chubut Province, Argentina	Shallow scalloped to deeply U-shaped margin feeding (DT12)	<i>Glossopteris wilsonii</i>
Gallego <i>et al.</i> , 2014, fig. 2.3. (C)	Sakmarian–Artinskian	Río Genoa Group	Aguada Loca, Betancourt (SP XVI), Ferrarotti IIB and Pique Carbón localities, Tepuel-Genoa Basin, Chubut Province, Argentina	(1) Large, deeply excised C-shaped margin feeding (DT12); (2) Elliptical mid-lamina hole feeding (DT78)	<i>Ginkgoites eximia</i>

Gallego <i>et al.</i> , 2014, fig. 2.4. (C)	Sakmarian–Artinskian	Río Genoa Group	Aguada Loca, Betancourt (SP XVI), Ferrarotti IIB and Pique Carbón localities, Tepuel-Genoa Basin, Chubut Province, Argentina	(1) Large C-shaped margin feeding (DT 81)	<i>Glossopteris wilsonii</i>
Gallego <i>et al.</i> , 2014, fig. 2.5. (C)	Sakmarian–Artinskian	Río Genoa Group	Aguada Loca, Betancourt (SP XVI), Ferrarotti IIB and Pique Carbón localities, Tepuel-Genoa Basin, Chubut Province, Argentina	Slender obovate to broad rectangular margin feeding (DT15)	<i>Glossopteris wilsonii</i>
Gallego <i>et al.</i> , 2014, figs 3.1–3.3. (C)	Sakmarian–Artinskian	Río Genoa Group	Aguada Loca, Betancourt (SP XVI, XIX), Ferrarotti IIB and Pique Carbón localities, Tepuel-Genoa Basin, Chubut Province, Argentina	Elliptical round-ended hole feeding scars tracking secondary veins (DT78)	<i>Glossopteris wilsonii</i>
Gallego <i>et al.</i> , 2014, fig. 3.4. (C)	Sakmarian–Artinskian	Río Genoa Group	Aguada Loca, Betancourt (SP XVI, XIX), Ferrarotti IIB and Pique Carbón localities, Tepuel-Genoa Basin, Chubut Province, Argentina	Circular hole feeding damage on both sides of the lamina (DT02)	<i>Glossopteris wilsonii</i>
Gallego <i>et al.</i> , 2014, fig. 4.1. (C)	Sakmarian–Artinskian	Río Genoa Group	Betancourt (SP II, XVI) locality, Tepuel-Genoa Basin, Chubut Province, Argentina	Small circular mostly interveinal surface feeding scars (DT29)	<i>Ginkgoites eximia</i>
Gallego <i>et al.</i> , 2014, fig. 4.2. (C)	Sakmarian–Artinskian	Río Genoa Group	Betancourt (SP II, XVI) locality, Tepuel-Genoa Basin, Chubut Province, Argentina	Large, roughly circular mostly interveinal surface feeding scars (DT29)	<i>Glossopteris wilsonii</i>
Gallego <i>et al.</i> , 2014, fig. 4.3. (C)	Sakmarian–Artinskian	Río Genoa Group	Betancourt (SP II, XVI) locality, Tepuel-Genoa Basin, Chubut Province, Argentina	(1) Circular surface feeding damage (DT29); (2) Elliptical oviposition scars transverse to venation (DT137)	<i>Ginkgoites feruglioi</i>
Gallego <i>et al.</i> , 2014, fig. 4.4. (C)	Sakmarian–Artinskian	Río Genoa Group	Betancourt (SP II, XVI) locality, Tepuel-Genoa Basin, Chubut Province, Argentina	Slender interveinal surface feeding damage (DT28)	<i>Noeggerathopsis</i> sp.
Gallego <i>et al.</i> , 2014, fig. 5.1, 5.2. (C)	Sakmarian–Artinskian	Río Genoa Group	Betancourt (SP II, XIX) and La Casilda localities, Tepuel-Genoa Basin, Chubut Province, Argentina	Multiple elliptical oviposition scars parallel to veins, flanking lamina margin (DT102)	<i>Gangamopteris obovata</i>
Gallego <i>et al.</i> , 2014, fig. 5.3. (C)	Sakmarian–Artinskian	Río Genoa Group	Betancourt (SP XIX) locality, Tepuel-Genoa Basin, Chubut Province, Argentina	Solitary oviposition scars near midrib	<i>Gangamopteris obovata</i>
Gallego <i>et al.</i> , 2014, fig. 5.4. (C)	Sakmarian–Artinskian	Río Genoa Group	Betancourt (SP II, XIX) locality, Tepuel-Genoa Basin, Chubut Province, Argentina	Small elliptical oviposition scars parallel to venation on inner portion of lamina	<i>Gangamopteris</i> sp.
Gallego <i>et al.</i> 2014, fig. 6. (C)	Sakmarian–Artinskian	Río Genoa Group	Ferrarotti IIB locality, Tepuel-Genoa Basin, Chubut Province, Argentina	Multiple bulbous U-shaped oviposition scars located on basal zone of midrib	<i>Glossopteris wilsonii</i>

Guerra-Sommer, 1995, pl. 1, fig. b-e. (C)	Sakmarian–Artinskian	Rio Bonito Formation	Paraná Basin, Rio Grande do Sul, Brazil	(1) Simple scalloped apical feeding; (2) crenulate deeply embayed marginal feeding	<i>Rubidgea</i> and <i>Glossopteris</i> sp. (5 of 90 specimens with damage)
Guerra-Sommer & Cazzullo-Klepzig, 2000, fig. 2E. (C)	Sakmarian–Artinskian	Rio Bonito Formation	Roof-shale, Faxinal mine, Paraná Basin, Rio Grande do Sul, Brazil	Deep, crenulate-margined excision	<i>Glossopteris</i> sp.
Harrington 1934, pl. 1, fig. 4. (C)	Cisuralian	Bonete Series?	Sierra Australes, Buenos Aires Province, Argentina	Elliptical oviposition scars along proximal portion of midrib	cf. <i>Glossopteris decipiens</i>
Jasper <i>et al.</i> , 2003, fig. 3A, B. (C)	Sakmarian–Artinskian	Rio Bonito Formation	Faxinal or Base of Morro Papaléo section, Paraná Basin, Rio Grande do Sul, Brazil	Small (<2 mm), circular, mid-lamina hole feeding with thin reaction rim	<i>Botrychopsis plantiana</i>
Kurtz, 1921, figs 27, 34, 4, 53. (C)	Permian	uncertain	Argentina	(1) Possible simple notched margin feeding; (2) Possible hole feeding	(1) <i>Noeggerathopsis hislopti</i> ; (2) <i>Rhipidopsis densinervis</i>
Labandeira & Curran, 2013, fig. 2.	Sakmarian–Artinskian	Rio Bonito Formation	Northeast of Minas (Lauro Müller), Paraná Basin, Santa Catarina, Brazil	Scattered elliptical oviposition scars parallel to secondary veins (DT100)	<i>Glossopteris</i> sp.
Leguizamon, 1979, fig. 5. (C)	Asselian–Sakmarian	Bajo de Veliz Formation	Bajo de Veliz, San Luis Province, Argentina	Deep rounded-rectangular apical incision	<i>Euryphyllum whittianum</i>
Melchor & Césari, 1997, fig. 4.3. (C)	Lopingian	Carapacha Formation	Curacó River, Carapacha Basin, La Pampa, Argentina	Irregularly lobed deep marginal feeding to midrib	<i>Glossopteris browniana</i>
Melchor & Césari, 1997, fig. 7.3. (C)	Lopingian	Carapacha Formation	Curacó River, Carapacha Basin, La Pampa, Argentina	Series of possible elliptical oviposition scars marginal to midrib	<i>Glossopteris wilsonii</i>
Melchor & Césari, 1997, fig. 8.1. (C)	Lopingian	Carapacha Formation	Carapacha Basin, La Pampa, Argentina	Indented apical feeding	<i>Glossopteris</i> sp. cf. <i>G. pandurata</i>
Melchor & Césari, 1997, fig. 8.5, 8.8. (C)	Lopingian	Carapacha Formation	Curacó River, Carapacha Basin, La Pampa, Argentina	Rectangular margin feeding to midrib	<i>Glossopteris pumpeana</i>
Menendez, 1962, figs 1, 2. (C)	Cisuralian	Bonete Series	Arroyo Piedra Azul, Sierra de Pillahuincó, Buenos Aires Province, Argentina	Possible circular oviposition scars	glossopterid scale leaf (= <i>Lanceolatus bonairensis</i>)
Millan & Dolianiti, 1982 (C)	Asselian	Itararé Group	Itapema, bairro Cerquillo Velho, município de Cerquillo, São Paulo, Brazil	Deeply scalloped apical feeding	<i>Rubidgea obovata</i>
Perinotto & Rösler, 1984, fig. 1, pl. 1, fig. 1. (C)	Kungurian–Roadian	Serra Alta or Teresina Formation	Iguaçu River near Fluvioópolis, Paraná Basin, Paraná, Brazil	Rectangular margin incision	<i>Glossopteris</i> sp. cf. <i>G. occidentalis</i>
Pinheiro <i>et al.</i> , 2012a, pl. 1, fig. 1. (C)	Sakmarian?	Basal to middle part of the Rio Bonito Formation	Rio da Estiva, Paraná Basin, Santa Catarina, Brazil	Extensive margin feeding forming irregular lobes and narrow rounded embayments	<i>Gangamopteris obovata</i>
Pinheiro <i>et al.</i> , 2012a, pl. 1, fig. 2. (C)	Sakmarian?	Basal to middle part of the Rio Bonito Formation	Rio da Estiva, Paraná Basin, Santa Catarina, Brazil	(1) Deep rectangular margin feeding embayments; (2) Small elliptical hole feeding; (3) narrow slit-like hole feeding between secondary veins	<i>Glossopteris</i> sp.
Pinheiro <i>et al.</i> , 2012a, pl. 1, fig. 1. (C)	Sakmarian?	Basal to middle part of the Rio Bonito Formation	Rio da Estiva, Paraná Basin, Santa Catarina, Brazil	Elliptical mid-lamina hole feeding	<i>Glossopteris communis</i>

Pinheiro <i>et al.</i> , 2012a, pl. 1, figs 4–7; Pinheiro <i>et al.</i> 2012b, pl. 1, figs 12, 13. (C)	Sakmarian?	basal to middle part of the Rio Bonito Formation	Rio da Estiva, Paraná Basin, Santa Catarina, Brazil	Linear hole feeding between secondary veins (DT08)	<i>Glossopteris communis</i> , <i>Glossopteris</i> sp., <i>G.</i> <i>occidentalis</i> (said to also occur on <i>Gangamopteris burtadica</i> , <i>Ga. obovata</i>)
Pinheiro <i>et al.</i> , 2012b, pl. 1, figs 1, 4. (C)	Cisuralian	Itararé Group	Morro do Papaléo (Faxinal), Mariana Pimentel, Paraná Basin, Rio Grande do Sul, Brazil	Deep, scalloped margin feeding (DT12)	<i>Glossopteris communis</i> (said to also occur on <i>Glossopteris</i> sp., <i>G. indica</i> , <i>G. brasiliensis</i> , <i>G. browniana</i> , <i>G. angustifolia</i> , <i>Gangamopteris</i> sp., <i>Ga.</i> <i>obovata</i> ; <i>Noeggerathopsis</i> <i>histolpii</i>)
Pinheiro <i>et al.</i> , 2012b, pl. 1, fig. 2, 5. (C)	Cisuralian	Itararé Group	Morro do Papaléo (Faxinal), Mariana Pimentel, Paraná Basin, Rio Grande do Sul, Brazil	Deep rectangular margin feeding embayments (DT15)	<i>Glossopteris</i> sp. (said to also occur on <i>Glossopteris</i> <i>communis</i>)
Pinheiro <i>et al.</i> , 2012b, pl. 1, figs 3, 10. (C)	Cisuralian	Itararé Group	Morro do Papaléo (levels N3/4), Mariana Pimentel, Paraná Basin, Rio Grande do Sul, Brazil	Possible leaf mine near lamina margin (DT99)	<i>Glossopteris communis</i>
Pinheiro <i>et al.</i> 2012b, pl. 1, figs 6, 9. (C)	Cisuralian	Itararé Group	Morro do Papaléo (levels N3/4), Mariana Pimentel, Paraná Basin, Rio Grande do Sul, Brazil	Small circular to reniform hole feeding (DT01, DT02)	<i>Glossopteris communis</i> (said to also occur on <i>Glossopteris</i> sp.)
Pinheiro <i>et al.</i> , 2012b, pl. 1, figs 7, 8. (C)	Cisuralian	Itararé Group	Morro do Papaléo (levels N3/4), Mariana Pimentel, Paraná Basin, Rio Grande do Sul, Brazil	Elliptical surface feeding spanning several secondary veins (DT103)	<i>Glossopteris indica</i>
Pinheiro <i>et al.</i> , 2012b, pl. 1, fig. 11. (C)	Sakmarian– Artinskian	Siderópolis Member, upper Rio Bonito Formation	Morro do Papaléo (levels L7/8), Mariana Pimentel, Paraná Basin, Rio Grande do Sul, Brazil	Circular hole feeding (DT01, DT02)	<i>Noeggerathopsis histolpii</i>
Pinheiro <i>et al.</i> , 2015, figs 1A–E, H, J; 2A–C. (C)	late Asselian– Sakmarian	Taciba Formation, uppermost Itararé Group	Morro do Papaléo (levels L7/8), Mariana Pimentel, Paraná Basin, Rio Grande do Sul, Brazil	(1) Shallow multi-lobed margin feeding (DT12) to deep simple- scalloped margin feeding; (2) Circular hole feeding (DT02)	<i>Botrychiopsis plantiana</i>
Pinheiro <i>et al.</i> , 2015, fig. 11.	Asselian– Sakmarian	Bajo de Véliz Formation	Bajo de Véliz, Paganzo Basin, San Luis Province, Argentina	Shallow multi-lobed margin feeding (DT12)	<i>Botrychiopsis plantiana</i>
Pinheiro <i>et al.</i> , 2015, figs 1F, G; 2D, E.	Asselian– Sakmarian	Arroyo Totoral Formation	Arroyo Totoral, Paganzo Basin, La Rioja Province, Argentina	(1) Shallow multi-lobed margin feeding (DT12); (2) Circular hole feeding (DT02)	<i>Botrychiopsis plantiana</i>
Read, 1941, pl. 3, fig. 9. (C)	Permian (probably Cisuralian)	Tubarão Supergroup	Cambuly, Rio das Pedras, Paraná Basin, Paraná, Brazil	Possible pinnule apex truncation	<i>Pecopteris cambulyensis</i>
Read, 1941, pl. 4, figs 3, 5. (C)	Permian (probably Cisuralian)	Tubarão Supergroup	Rio Ferreira near Treviso, Paraná Basin, Santa Catarina, Brazil	Possible circular oviposition scar adjacent to midrib	<i>Glossopteris</i> sp. cf. <i>G. ampla</i>
Read, 1941, pl. 5, figs 3, 6. (C)	Cisuralian	Itararé Group	Teixeira Soares, Paraná Basin, Paraná, Brazil	Possible interveinal surface feeding	<i>Glossopteris browniana</i>

Rohn, 1984, pl. 1, fig. 2a, b. (C)	Wordian	Serrinha Member, Rio do Rasto Formation	Dorizon, Paraná Basin, Paraná, Brazil	Broadly scalloped margin feeding	<i>Glossopteris leptoneura</i>
Rohn, 1984, pl. 2, fig. 1a, b. (C)	Wordian	Serrinha Member, Rio do Rasto Formation	Dorizon, Paraná Basin, Paraná, Brazil	Shallow scalloped margin feeding	<i>Glossopteris grafi</i>
Rohn & Rösler, 1989a, pl. 1, fig. 15. (C)	Wordian–Wuchiapingian	Rio do Rasto Formation	Highway BR373, km 103.8, Paraná Basin, Paraná or Santa Catarina, Brazil	Possible narrow marginal slot feeding	<i>Glossopteris riorastensis</i>
Rohn & Rösler 1989b, pl. 1, figs 2, 3. (C)	Wordian–Wuchiapingian	Rio do Rasto Formation	Reserva-Cândido de Abreu, Paraná Basin, Brazil	Possible scalloped marginal and apical feeding	<i>Ilexoidephyllum permicum</i>
Rohn <i>et al.</i> , 1997, pl. 1, figs 4, 5. (C)	Kungurian–Roadian	Teresima Formation	Prudentópolis area, Paraná Basin, Paraná, Brazil	Large elliptical hole feeding adjacent to midrib	<i>Glossopteris</i> sp.
Tybusch <i>et al.</i> , 2003, fig. 3; Tybusch, 2005, pl. 1, fig. E, pl. 4, figs A, B. (C)	Sakmarian–Artinskian	Rio Bonito Formation	Morro do Papaléo Mine, Paraná Basin, Rio Grande do Sul, Brazil	Possible linear to broad patches of surface feeding from midrib to margin	<i>Gangamopteris obovata</i> and <i>Gangamopteris</i> sp. 2
White, 1908, pl. 7, fig. 2; Tybusch & Iannuzzi, 2010, fig. 4A. (C)	Sakmarian–Artinskian	Siderópolis Member, top of Rio Bonito Formation	Lauro Müller, Paraná Basin, Santa Catarina, Brazil	Possible elliptical oviposition scars adjacent to midrib	<i>Glossopteris occidentalis</i>
White, 1908, pl. 5, figs 1, 1a. (C)	Sakmarian–Artinskian	Rio Bonito Formation (225 m below Irati Formation)	Northeast of Minas (Lauro Müller), Paraná Basin, Santa Catarina, Brazil	<i>Rosellinites gangamopteroides</i> : possible small circular fungal germings, galls or piercing and sucking damage	<i>Gangamopteris obovata</i>
White, 1908, p. 5, fig. 2. (C)	Sakmarian–Artinskian	Rio Bonito Formation (225 m below Irati Formation)	Northeast of Minas (Lauro Müller), Paraná Basin, Santa Catarina, Brazil	<i>Hysterites brasiliensis</i> : possible lorate oviposition scars or scattered short interveinal surface feeding scars	<i>Noeggerathopsis hislopii</i>
White, 1908, pl. 9, fig. 7. (C)	Sakmarian–Artinskian	Probably Rio Bonito Formation	Uncertain: various possible sources in the Paraná Basin, Santa Catarina and Rio Grande do Sul, Brazil	Possible small circular interveinal oviposition scars or piercing and sucking damage	<i>Noeggerathopsis hislopii</i>
This study, Fig. 4J. (C)	Lopingian	Egg Harbour Member, Bay of Harbours Formation	Dos Lomas, East Falkland Islands	Solitary elliptical oviposition scar (DT76) on leaf midline	<i>Gangamopteris cyclopteroides</i> var <i>major</i>
Africa, Arabia					
Abu Hamad <i>et al.</i> , 2008, pl. 3, figs 1B, 2, 3B. (C)	latest Permian or earliest Triassic	Um Irma Formation	Wadi Himara, Dead Sea, Jordan	Small circular hole feeding (DT02)	<i>Dicroidium irnensis</i>
Anderson & Anderson, 1985 (C)				See Table 2	
Anderson & McLachlan, 1976, pl. 1, fig. 5. (C)	Artinskian	Whitehill Formation	South-western Karoo Basin, South Africa	Oviposition scars on midrib (DT76)	<i>Gangamopteris</i> sp.
Archangelsky & Wagner, 1983, figs 9, 10. (C)	Lopingian?	Coal-bearing succession of the Gomanimbrik Formation	750 m SSW of Dadaş village, western part of Hazro mlter, Anatolia, southeast Turkey	Possible mining: linear trace parallel to margin, <1 mm wide, c. 2 mm from margin	<i>Glossopteris stricta</i>
Araújo <i>et al.</i> , 2018, fig. 1A, B. (AP)	Lopingian	Unit uncertain	Chicóa-Mucutuê Basin, Mozambique	Tree hollows (probably fungal rather than arthropod damage)	<i>Australoxylon teixeirae</i>
Benecke, 1976, figs 33, 41. (C)	Lopingian	Normandien Formation	Mooi River, Karoo Basin, KwaZulu-Natal, South Africa	Possible margin feeding, arching of polysperm (DT12?)	<i>Fetura natalensis</i>

Bernardes de Oliveira & Pons, 1975, pl 1, fig. 3. (C)	Artinskian	Ecca Group equivalents,	Zambezi Basin, Mozambique	Possible deeply embayed margin feeding	<i>Glossopteris</i> sp. cf. <i>G. longicaulis</i>
Berthelin <i>et al.</i> 2006, pl. 4A, C. (C)	Roadian	unit A of the Gharif Formation	North cliff, Gharif, Oman	Possible deeply embayed margin feeding (DT14 / 15)	<i>Glossopteris anatolica</i>
Berthelin <i>et al.</i> 2003, fig. 3C, D. (C)	Roadian	Upper Gharif Formation	Haushi-Huqf area, Oman	(1) Probable elliptical, 1-2 mm, hole feeds (DT02); (2) possible polylobate surface feeding across midrib (DT30); (3) C-shaped marginal feeding (DT12); (4) Possible cluster of <1 mm circular oviposition scars on mid-lamina (DT100)	<i>Glossopteris</i> sp. (DTs 02, 12, 30); <i>Glossopteris damudica</i> (DT100)
Botha <i>et al.</i> , 2020, fig. 4A, B, D. (C)	Changhsingian	Lowermost Palingkloof Member, Balfour Formation	Nooitgedacht Farm, western Karoo Basin, Free State Province, South Africa	Ovipositions on midrib (DT76), linear ranks of spindle-shaped oviposition scars in midlamina, to either side of midrib (cf. DTs 54, 102), scattered, isolated oviposition scars on lamina (DT101)	<i>Glossopteris</i> sp.
El-Khayal <i>et al.</i> , 1980, fig. 2a. (C)	Lopingian?	Khuff Formation	Unayzah, Saudi Arabia	Possible pair of oviposition scars on leaf midline	<i>Contaites</i> sp. cf. <i>C. principalis</i>
Gastaldo <i>et al.</i> , 2017, fig. 7B, D. (C)	Changhsingian (earliest Triassic?)	Palingkloof Member, Balfour Formation	Blaaufontein Farm (Old Lootsberg Pass), Eastern Cape Province, South Africa	Oviposition scars on lamina (DT101), U-shaped necrotic lesion, possibly surface feeding (DT 97), possible oviposition on lamina (DT101), possible DT136	<i>Trizygia speciosa</i> (DT101); <i>Glossopteris</i> sp. (DTs 97, 101, 136)
Gordon-Gray <i>et al.</i> , 1976, pl. II, fig. 11; pl. IV, figs 26, 27; van Dijk <i>et al.</i> , 1978, fig. 8i; van Dijk, 1981, figs 15, 21, 23, 56-62. (C)	Lopingian	Normandien Formation	Lidgettton, Karoo Basin, KwaZulu-Natal, South Africa	Spindle-shaped oviposition scars with a strong mediolongitudinal groove, both scattered (DT101) and in linear longitudinal rows between stem ridges (cf. DT100, DT72) of sphenopsid stem; possible hole feed in scale leaf (DT01); leaves with scalloped continuous margin feeding traces (D12) and large cusped excision to midrib (DT14), and elliptical to trullate lesion on lamina and across midrib, with surface feeding, partial skeletonisation and pronounced reaction rim (cf. DT31)	<i>Paracalamites australis</i> (DTs 101, 100, 72); <i>Glossopteris</i> spp. (DTs 12, 14, 31, 101); scale leaf (DT01); possible leaf/bract crypsis (?homopteran and plecopteran wings)
Hoeg & Bose, 1960, pl. VII, figs 1, 5. (C)	Asselian-Artinskian	Lukuga Group	Greinerville, Katanga, Democratic Republic of the Congo	C-shaped margin feeding (DT12)	<i>Noeggerathiopsis hislopii</i>
Hoeg & Bose, 1960, pl. XII, fig. 3. (C)	Asselian-Artinskian	Lukuga Group	Walikale, North Kivu, Democratic Republic of the Congo	Possible apical truncation (DT13)	<i>Gangamopteris cyclopteroides</i>

<p>Kovács-Endrődy, 1976, pl. II, figs a, c; pl. III, figs a, b; 1977, pl. X, fig. 1; 1981, pl. 3, fig. 4; 1991, pl. 5.4, figs 4; 7; pl. 5.6, fig. 5; pl. 5.9, figs 2–4; pl. 5.10, fig. 2; pl. 5.11, figs 5, 7, 8, 13, 14; pl. 5.12, figs 1–4, 6; pl. 5.16, fig. 6 pl. 5.17, fig. 5; pl. 5.18, figs 1, 4–6; pl. 5.19, fig. 1; pl. 5.20, figs 1, 2; pl. 5.20, figs 1, 2; pl. 5.21, figs 3, 4, 6, 7; pl. 5.22, fig. 2; pl. 5.23, fig. 2; pl. 5.26, figs 6, 8, 9, 12. (C)</p>	<p>Artinskian–Kungurian</p>	<p>Hamamskraal Formation (Vryheid Formation equivalent)</p>	<p>Hamamskraal, outlier of northern Karoo Basin, Gauteng, South Africa</p>	<p>Hole feeding: very small, circular hole feeding (DT01); circular hole feeding (DT02); polylobate hole feeding Margin feeding: C-shaped, U-shaped and continuous, trenched, cusped/scalloped, polylobate margin feeding (DT12) Surface feeding: U-shaped necrotic lesion from margin across lamina, following vein course, possibly fungal or surface feeding damage (DT97); rectangular region of surface feeding with little alteration of tissues, perpendicular to venation (cf. DT130); surface feeding or fungal damage along leaf margin, with scalloped margin (cf. DT27, but with scalloped damage margin), discrete lesions at margin (cf. DT29); <i>Piercing & sucking</i>: linear rows of circular punctures along one or both sides of midrib, or on the midrib (DT138) <i>Oviposition</i>: circular, elliptical to spindle-shaped oviposition scars on midrib, may be single or evenly spaced in a row, in one case becoming progressively smaller and more closely spaced acropetally (DT76), distinct row of ovipositions immediately adjacent to midrib, spaced at equal intervals (cf. DT76), circular, elliptical to spindle-shaped, scattered oviposition scars on lamina, mostly parallel to venation (DT101), rows of oviposition scars, end-to-end, in some cases with shared reaction rim (new DT), scars of various sizes, circular, elliptical, spindle-shaped, with margins ranging from crisp to ragged, mostly parallel to venation, may be clustered in small groups, or closely spaced and abundant over larger areas, in some cases of higher concentration near midrib and may cause regional disruption of tissues (DT100) <i>Seed predation</i>: single central boring (DT73) <i>Fungal</i>: V-shaped necrotic lesion on margin, partially constrained by venation (cf. DT97)</p>	<p><i>Glossopteris pseudocommunis</i> (DTs 54, 12, 76); <i>G. taeniopteroides</i> (DTs 03, 12, 15, 76, 100, 101); <i>G. angustifolia</i> (DTs 76, 101); <i>G. ampla</i> (DTs 76, 97, 101); <i>G. browniana</i> (DTs 101, 01); <i>G. elliptica</i> (DTs 12, 101); <i>G. flabellivenosa</i> (DT101); <i>G. divergens</i> (DTs 02, 76, 101, 130); <i>G. indica</i> (DTs 12, 100, 101, 138); <i>Glossopteris</i> spp. (DT76; 101); scale leaf (DT100); <i>G. maccayi</i> (DTs 12, cf. 27, 76, 101); <i>G. andreamszki</i> (DTs 12, 15, 76, 101, 138); <i>G. stricta</i> (DTs 02, 12, 76, 101); <i>G. clarkii</i> (DTs 03, 12, 97, 100, 101, 138); <i>G. ferrugistratum</i> (DTs 03, 12, 76, 97, 101); <i>Condaicarpus</i>sp. (DT73)</p>
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Kovács-Endrődy, 1977, pl. XII, fig. 3, 4, pl. XV, fig. 2; Kovács-Endrődy, 1991, pl. 5, 15, fig. 1, 2, pl. 5, 17, fig. 1, (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng, South Africa	Possible piercing and sucking scars over veins, scattered (DT46); possible hole-feeding on lamina (DT01); possible margin feeding (DT12) or surface feeding with associated necrotic lesion (cf. DT30); scalloped continuous margin feeding (DT12); oviposition scars on midrib (DT76), and lamina (DT101); C-shaped lesions on margin, could be surface feeding or fungal/bacterial disease (cf. DT97).	<i>Glossopteris tortuosa</i> (DT76), <i>G. maccayi</i> (DT12), <i>Glossopteris</i> spp. (DTs 01, 12, cf. 30, 46, 76, cf. 97, 101)
Labandeira <i>et al.</i> , 2007, p. 8, DT12, p. 10, DTs 101, 102, p. 15, DT10; Prevec <i>et al.</i> , 2009, pl. IV, figs 5–9, pl. V, figs 1, 3, 4, pl. XI, figs 1–10, pl. XII, figs 1–10, pl. XII, figs 1–11, (C)	Wuchiapingian	Normandien Formation	Clouston Farm, northeastern Karoo Basin, KwaZulu-Natal, South Africa	DTs 22 distinctive damage types (DTs 01, 02, 03, 07, 12, 13, 14, 15, 16, 17, 29, 30, 31, 33, 46, 48, 75, 76, 101, 102, 103, 106) on 137 plant organs, of 9972 specimens surveyed	<i>Glossopteris</i> spp.: hole feeding (DTs 01, 02, 03, 07); margin feeding (DTs 12, 13, 14, 15); skeletonization (DTs 16, 17); surface feeding (DTs 29, 30, 31, 75, 103, 106); galling (DT33); piercing and sucking (DTs 46, 48); oviposition (DTs 76, 101, 102). Glossopterid scale leaves: hole feeding (DT07); margin feeding (DT12); surface feeding (DTs 30, 75); oviposition (DT76). Lycophyte axis: margin feeding (DT12). Sphenophyte roots: hole feeding (DT01); margin feeding (DT12) Sphenophyte axis: oviposition (DT101)
Labandeira <i>et al.</i> , 2007, p. 9, DT97; Bordy & Prevec, 2008, pl. I, fig. I; pl. II, figs D, E, F, H, I, J; Labandeira & Prevec, 2014, fig. 6B–K; Prevec, 2016, figs 13, 4B, 13, 15B, (C)	Lopingian	Emakwezini Formation (Normandien Formation equivalent)	Kwa Yaya, Lebombo Basin, KwaZulu-Natal, South Africa	Oviposition scars on lamina (DT101, DT100, cf. DT54) and midrib (DT76); dense oviposition scars with associated regional necrosis in apical region (DT136); margin feeding: continuous (with inverted cusps), C- and U-shaped (DT12); hole feeding (DT02); fungal damage affecting surface tissues adjacent to apical foliar damage (DT13); elongate-ellipsoidal, full-depth galls (new DT); tiny, circular galls (cf. DT80); lenticular to trench-shaped necrotic areas (possibly fungal) approximately parallel to venation (cf. DT97)	<i>Glossopteris</i> spp.

Lacey <i>et al.</i> , 1975, pp. 364, 366, 369, 370, 395.	Lopingian	Normandien Formation (formerly Estcourt Formation)	Mooi River, Karoo Basin, KwaZulu-Natal, South Africa	Small, circular, carbonised features, possible galls (cf. DT80); transversely elliptical oviposition scars on midrib (DT76); hole feed (DT01); continuous and C-shaped margin feeding (DT12); margin feeding to midrib (DT14)	<i>Glossopteris</i> spp.
Le Roux, 1970, pl. 3, figs 1, 2. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng Province, South Africa	(1) C- to U-shaped apical feeding (DT13); (2) keyhole-type margin feeding (DT15); (3) Polylobate hole feeding (DT05); (4) possible oviposition scars (DT101)	<i>Psynophyllum kidstonii</i>
Le Roux, 1976, pl. 1, fig. 6. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng Province, South Africa	Pinnule apex truncation and removal	<i>Pecopteris singeri</i>
Le Roux, 1976, pl. 2, fig. 10. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng Province, South Africa	C-shaped apical feeding (DT13)	<i>Sphenophyllum</i> sp. cf. <i>S. thonii</i>
Leslie, 1921, pl. 1, fig. 1. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng Province, South Africa	Polylobate hole feeding (DT03)	<i>Glossopteris stricta</i>
Pant, 1958, fig. 7A. (C)	Cisuralian?	upper coals of the Ecce Group equivalents	Mhukuru Coalfield, Songea district, Tanzania	Possible C-shaped margin feeding	<i>Glossopteris colpodes</i>
Plumstead, 1961, pl. 10, fig. 1. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng Province, South Africa	C-shaped margin feeding (DT12)	<i>Taeniopteris gemmina</i>
Plumstead, 1962; 1963 pl. B, fig. 5; 1969, pl. XIII, fig. 8; Melville, 1983a, 1983b, fig. 3B. (C)	Artinskian–Kungurian	Vryheid Formation	Breyton Colliery, Karoo Basin, Mpumalanga Province, South Africa	Possible isolated galls	<i>Breytenia plumsteadiae</i>
Plumstead, 1963, pl. A, figs 1–6; van Amerom, 1966, figs 1–3; Stephenson & Scott, 1992, fig. 11–M; 1969, pl. XIV, fig. 3, 4; Scott <i>et al.</i> , 1992, fig. 11B; Prevec, 2016, fig. 13.15A. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng Province, South Africa	Continuous margin feeding with convex and concave scallops (DT12); deep arcuate margin feeding to the midrib (DT14), and across the leaf apex (DT13); hole feeding (DT02); spindle-shaped oviposition scars of various sizes on lamina, parallel to venation (DT101), clusters of linear grooves parallel to venation, possibly representing failed ovipositions/exploratory probing by insect ovipositor (new DT)	<i>Glossopteris</i> spp.
Plumstead, 1966, fig. 8. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng Province, South Africa	Small hole feeding (DT02)	<i>Glossopteris</i> sp.
Plumstead, 1970, pl. III, figs E, F; Bordy & Prevec, 2008, pl. III, figs E, F. (C)	Lopingian	Emakwezini Formation	Somkele Borehole core, Lebombo Basin, KwaZulu-Natal, South Africa	Closely spaced oviposition scars (DTs 76, 101)	<i>Glossopteris</i> sp.
Plumstead, 1969, Pl. XII, fig. 2; Anderson & Anderson, 1985, pl. 54, figs 1–7; McLoughlin, 2011, fig. 2A–H; This study, Fig. 4B. (C)	Artinskian–Kungurian	Vryheid Formation	Vereeniging, Karoo Basin, Gauteng, South Africa	Galls on base of midrib	<i>Palaeovittaria kurtzii</i>

Prevec <i>et al.</i> , 2010, figs 8E, G, H, K, L, 9C; Labandeira <i>et al.</i> , 2007, p. 11, DT136; Prevec 2012, fig. 15; Labandeira & Prevec, 2014: fig. 6A. (C)	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass, southern Karoo Basin, Eastern Cape Province, South Africa	Necrotic legion (possibly fungal) associated with extensive oviposition damage (DT136) Ovipositions on midrib (DT76), large ovipositions with prominent reaction rims on lamina (101), ovipositions in ranks along the leaf margin (DT102), rectangular margin feeding with prominent reaction rims, C-shaped margin feeding (DT12), piercing and sucking (DT138)	<i>Glossopteris</i> sp. (DTs 12, 76, 101, 102, 136, 138); <i>Trizygia speciosa</i> (DTs 101, 29)
Rayner & Coventry, 1985, fig. 1b, e. (C)	Kungurian?–Guadalupian?	Volksrust Formation equivalent	Lawley, Gauteng, South Africa	Polylobate hole feeding (DT03)	<i>Glossopteris taenioides</i> , <i>G. indica</i>
Seward, 1897, pl. XXI, fig. 1. (C)	?Artinskian–Kungurian	?Vryheid Formation	Boschmans Fontein, Middleburg, Mpumalanga, South Africa	Probable oviposition scars regularly spaced along mid-lamina (cf. DT102)	<i>Glossopteris</i> sp.
Tate, 1867, pl. V, fig. 8. (C)	Permian	Ecce Group or Adelaide Subgroup	Buffalo River mouth, Eastern Cape Province, South Africa	Probable oviposition scars	<i>Rubidgea mackayi</i>
van Dijk, 2011, figs 3, 4. (C)	Lopingian	Normandien Formation (Beaufort Group)	Wagondrift Quarry, near Estcourt, KwaZulu-Natal, South Africa	Possible galls (DT34) and surface feeding (cf. DT79)	<i>Glossopteris</i> sp.
Wagner, 1962, pl. 24, figs 2, 2a. (C)	Lopingian?	Coal-bearing succession of the Gomanimbrik Formation	800 m SW of Dadaş village, western part of Hazro inlier, Anatolia, southeast Turkey	Mid-pinnule circular ?hole feeding	<i>Gigantopteris</i> sp.
Wagner, 1962, pl. 25, figs 5, 6. (C)	Lopingian?	Coal-bearing succession of the Gomanimbrik Formation	800 m SW of Dadaş village, western part of Hazro inlier, Anatolia, southeast Turkey	U-shaped margin feeding	<i>Glossopteris</i> sp. cf. <i>G. stricta</i>
Zavada & Mentis, fig. 5B, C. 1992 (AP)	Artinskian–Changhsingian	Vryheid–Normandien formations	Various sites, Karoo Basin, South Africa	Arthropod borings in late-season wood	<i>Agathoxylon</i> (= <i>Dadoxylon</i>)
Zeiller, 1896, pl. XVI, fig. 5A; pl. XVIII, fig. 3. (C)	?Artinskian–Kungurian	Probably Vryheid Formation	northern Karoo Basin, Gauteng Province, South Africa	C-shaped margin feeding (DT12); oviposition scars (DT102)	<i>Glossopteris browniana</i> (DT12); <i>Glossopteris angustifolia</i> (DT102)
Madagascar					
Appert, 1977, pl. 3, figs 5, 6. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Possible interveinal surface feeding	<i>Gangamopteris cyclopteroides</i>
Appert, 1977, pl. 3, figs 3, 4. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Possible gall or oviposition scars	<i>Gangamopteris cyclopteroides</i>
Appert, 1977, pl. 4, fig. 4. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Shallow continuous margin feeding	<i>Gangamopteris cyclopteroides</i>
Appert, 1977, pl. 6, figs 4, 5. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Deep U-shaped margin feeding	cf. <i>Lesleya</i> (= <i>Glossopteris</i> sp.)
Appert, 1977, pl. 6, figs 4, 5. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Possible C-shaped apical feeding	<i>Sphenophyllum sakoense</i>
Appert, 1977, pl. 22, figs 1, 2. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Possible mid-lamina hole feeding	<i>Glossopteris communis</i>
Appert, 1977, pl. 25, figs 1, 4. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Possible V-shaped margin feeding	<i>Glossopteris communis</i>
Appert, 1977, pl. 28, figs 1-6. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	Possible elliptical oviposition scars on midrib	<i>Glossopteris indica</i> & <i>Glossopteris</i> type C
Appert, 1977, pl. 31, figs 1, 2. (C)	Artinskian	Sakoa Group	Sakoa Basin, Madagascar	C-shaped margin feeding	<i>Glossopteris</i> sp.

India									
Agashe <i>et al.</i> , 1983, fig. 5. (C)	Permian	uncertain	Umrer Colliery, Nagpur district, Maharashtra	Elliptical hole feeding mostly following veins	<i>Euryphyllum obovatum</i>				
Banerjee, 1978, pl. 8, fig. 19; Chandra & Surange, 1979, pl. 4, fig. 6. (C)	Artinskian	Karharbari Formation	Pnaora, South Rewa Basin, Madhya Pradesh	V-shaped marginal feeding	<i>Glossopteris taenitoides</i>				
Banerjee & Bera, 1998, figs 1, 2. (C)	Lopingian	Raniganj Formation	Jharia Coalfield, Mohuda Basin, West Bengal	Crater-like galls	<i>Glossopteris</i> sp.				
Brongniart, 1830, pl. 62, fig. 2. (C)	Kungurian–Wordian or Lopingian	Barakar or Raniganj Formation,	Raniganj Coalfield, West Bengal, India	Possible oviposition scars parallel to lamina margin	<i>Glossopteris indica</i> holotype (equivocal based on illustrations by Chandra & Surange, 1979 and Rigby <i>et al.</i> , 1980)				
Bunbury, 1861, pl. 8, figs 1, 4. (C)	Permian	Unit uncertain	Silewādā, Satpura Basin, Nagpur, Maharashtra, India	Circular oviposition scars or small hole-feeding scars	<i>Glossopteris</i>				
Bunbury, 1861, pl. 12, fig. 3. (C)	Permian	Unit uncertain	Silewādā, Satpura Basin, Nagpur, Maharashtra, India	Possible large circular gall	Unidentified axis				
Chandra & Singh, 1992, pl. 1, fig. 5. (C)	Changhsingian	Kamthi Formation	Mahanadi Graben, Dhenkanal, Odisha	Paired elliptical oviposition scars flanking midrib	<i>Glossopteris communis</i>				
Chandra & Singh, 1992, pl. 12, fig. 3. (C)	Changhsingian	Kamthi Formation	Mahanadi Graben, Dhenkanal, Odisha	Possible C-shaped margin-feeding near apex	<i>Glossopteris</i> sp.				
Chandra & Singh, 1996, pl. 1, fig. D. (C)	Asselian	Talchir Formation	Talchir Coalfield, Mahanadi Basin, Odisha	Broadly scalloped apical feeding	<i>Gangamopteris clarkeana</i>				
Chandra & Singh, 1996, pl. 2, fig. B. (C)	Asselian	Talchir Formation	Talchir Coalfield, Mahanadi Basin, Odisha	Circular oviposition scars clustered near base of lamina	<i>Gangamopteris major</i>				
Chandra & Singh, 1996, pl. 4, fig. A–E. (C)	Asselian	Talchir Formation	Talchir Coalfield, Mahanadi Basin, Odisha	Circular galls?, densely covering axis	unidentified axes				
Chandra & Singh, 1996, pl. 6, figs F, G. (C)	Asselian	Talchir Formation	Talchir Coalfield, Mahanadi Basin, Odisha	Possible seed predation: circular markings on integument	<i>Cordaicarpus</i> sp.				
Edirisooriya <i>et al.</i> , 2018, fig. 4a, c. (C)	Lopingian?	Unit undefined	Tabbowa Basin, western Sri Lanka	Hole feeding	<i>Glossopteris raniganjensis</i>				
Edirisooriya <i>et al.</i> , 2018, fig. 4b, f. (C)	Lopingian?	Unit undefined	Tabbowa Basin, western Sri Lanka	(1) U-shaped and (2) V-shaped margin feeding	<i>Glossopteris raniganjensis</i>				
Edirisooriya <i>et al.</i> , 2018, 4d. (C)	Lopingian?	Unit undefined	Tabbowa Basin, western Sri Lanka	Elliptical oviposition scars adjacent to midrib	<i>Glossopteris raniganjensis</i>				
Edirisooriya <i>et al.</i> , 2018, fig. 4e. (C)	Lopingian?	Unit undefined	Tabbowa Basin, western Sri Lanka	Possible skeletization of mid-lamina area	<i>Glossopteris raniganjensis</i>				
Edirisooriya <i>et al.</i> , 2018, fig. 4g, h. (C)	Lopingian?	Unit undefined	Tabbowa Basin, western Sri Lanka	Possible piercing-and-sucking scars on secondary veins	<i>Glossopteris raniganjensis</i>				
Feistmantel, 1880, pl. 12A, fig. 2. (C)	Kungurian–Wordian	Barakar Formation	Talchir Coalfield, Mahanadi Basin, Odisha	Possible scalloped apical feeding on leaves	<i>Trizygia speciosa</i>				

Maheshwari & Bajpai, 1990, fig. 5. (C)	Kungurian-Wordian	Lalmatia coal seam, Barakar Formation	Hura Coalfield, Rajmahal Basin, Bihar, India	Inferred leaf mines (but probably imprints of burrows in underlying sediment)	<i>Saportaea</i> sp.
Maheshwari & Bajpai, 1992, text-fig. 10, pl. 3, fig. 2, 3. (C)	Kungurian-Wordian	Lalmatia coal seam, Barakar Formation	Hura Coalfield, Rajmahal Basin, Bihar, India	(1) Possible shallow margin feeding, base of leaf segment; (2) Deep U-shaped apical feeding	<i>Rhipidopsis densinervis</i>
Maheshwari & Tewari, 1986, text-fig. 1, pl. 1, figs 1-4. (C)	Artinskian	Karharbari Formation,	Shahdol district, Madhya Pradesh, India	Possible zoochory	<i>Maheshwariella spinicornuta</i> seeds (6 × 2.5 mm) with 0.75 mm long micropylar horns bearing reverse-orientated epidermal barbs
Maithy, 1965, pl. 1, fig. 5, pl. 2, fig. 8; Maithy, 1977, pl. 1, fig. 2. (C)	Artinskian	Karharbari Formation	Giridh Coalfield, Damodar Basin, Bihar, India	Possible galls, or oviposition scars	Indeterminate axis (previously assigned to cf. <i>Cyclodendron</i> sp. and <i>Buriadia</i> sp.)
Pal <i>et al.</i> , 2010, pl. 2, fig. 13. (C)	Changhsingian	Maitur Formation (lowermost Panchet Group)	Raniganj Coalfield, Damodar Basin, West Bengal	Rectangular hole feeding delimited by secondary veins	<i>Glossopteris indica</i>
Pal <i>et al.</i> , 2010, pl. 2, fig. 3. (C)	Changhsingian	Maitur Formation (lowermost Panchet Group)	Raniganj Coalfield, Damodar Basin, West Bengal	Apical feeding leaving veinal extensions	<i>Glossopteris retifera</i>
Pal <i>et al.</i> , 2010, pl. 2, fig. 14. (C)	Changhsingian	Maitur Formation (lowermost Panchet Group)	Raniganj Coalfield, Damodar Basin, West Bengal	C-shaped margin feeding	<i>Glossopteris emarginata</i>
Pant & Choudhury, 1977, pl. 5, fig. 31. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	C-shaped margin feeding	<i>Belemnopteris pellucida</i>
Pant & Misra, 1976, pl. 2, fig. 6. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Pinnule removal or margin feeding	<i>Asansolia phegopteroides</i>
Pant & Misra, 1977, pl. 3, fig. 1. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Possible gall on pinnule	<i>Trithecopteris gondwanensis</i> (= <i>Dichotomopteris lindleyi</i>)
Pant & Singh, 1987, pl. 10, fig. 93. (AP)	Lopingian	Raniganj Formation	New Kenda, Raniganj Coalfield, West Bengal	Possible arthropod borings (or fungal pocket rot) in latewood	<i>Catervoxylon raniganjensis</i>
Pant & Srivastava, 1995, figs 1.5, 1.6, 7.10-7.12. (C)	?Kungurian	Mamal Formation	Mamal Nala Section, Pahaligam, Kashmir Himalaya, India	Circular galls on lamina	<i>Glossopteris taeniopteroides</i>
Pant & Verma, 1964, pl. 12, fig. 15. (C)	Kungurian-Wordian	Barakar Formation	Manendragarh Coalfield, Rewa Basin	Possible hole feeding, proximal lamina	<i>Noeggerathiopsis fibrosa</i>
Saksena, 1962, pl. 1, figs 4, 7, 8. (C)	Changhsingian	"Pali-Daigaon beds"	Karkati, South Rewa Gondwana Basin, Madhya Pradesh	Possible deep, narrow margin feeding (to quarter to half lamina width)	<i>Glossopteris indica</i> , <i>Glossopteris angustifolia</i>
Sen, 1955, figs 1, 2. (C)	Kungurian-Wordian	Barakar Formation	Sohagpur Coalfield, Son Basin, Madhya Pradesh, India	Possible circular piercing and sucking damage, galls or mineral staining on secondary veins	<i>Glossopteris</i> sp.
Sen, 1963, figs 1, 2. (C)	?Kungurian	lower Barakar Formation;	Pachwara Coalfield, Bihar, India	Possible large elliptical gall on midrib	<i>Glossopteris</i>
Srivastava, 1979, text-fig. 10, pl. 2, fig. 12. (C)	Lopingian	Raniganj Formation	Auranga Coalfield, Damodar Basin, Bihar, India	Possible U-shaped apical feeding	Glossopterid scale leaf

Srivastava, 1988, pl. 1, figs 9, 10; Srivastava & Srivastava, 2016, pl. 1, figs 9, 10. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal	Possible galls with circular or spiral pattern on leaf	<i>Glossopteris</i> sp.
Srivastava, 1988, pl. 1, figs 4, 5. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal	Continuous extensive margin feeding, series of irregular scallops	<i>Glossopteris</i> sp.
Srivastava, 1988, pl. 1, fig. 8; Srivastava & Srivastava, 2016, pl. 1, fig. 8. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal	Numerous fine pustules over lamina (possibly abiotic)	<i>Glossopteris</i> sp.
Srivastava, 1988, pl. 1, figs 6, 7. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal	Paired elliptical oviposition scars flanking midrib	<i>Glossopteris</i> sp.
Srivastava, 1988, 1996, 2008; Srivastava & Agnihotri, 2011. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal, India	Apical and margin feeding embayments between veins	<i>Noeggerathopsis</i> sp.
Srivastava, 1992, pl. 4, figs 5, 6. (C)	Kungurian–Wordian	Barakar Formation	Raniganj Coalfield, West Bengal	Possible deeply notched (rectangular) apical feeding	<i>Cordaites</i> (<i>Noeggerathopsis</i>) sp.
Srivastava, 1996; 1998, fig. 4; 2008, fig. 1; Srivastava & Srivastava, 2016, pl. 1, figs 4, 5; Srivastava & Agnihotri, 2011, fig. 1A, B. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal, India	Continuously scalloped margin	<i>Glossopteris indica</i>
Srivastava, 1998b, figs 5, 6; Srivastava & Srivastava, 2016, pl. 1, fig. 7. (C)	Kungurian–Wordian	Barakar Formation	Raniganj Coalfield, Damodar Basin, West Bengal	Rows of small oviposition scars flanking midrib	<i>Glossopteris</i> sp.
Srivastava & Agnihotri, 2011, fig. 1C–E. (C)	Kungurian–Wordian	Barakar Formation	Raniganj Coalfield, Damodar Basin, West Bengal	Broadly scalloped margin feeding	<i>Glossopteris communis</i>
Srivastava & Agnihotri, 2011, fig. 1I, J. (C)	Kungurian–Wordian	Barakar Formation	Raniganj Coalfield, Damodar Basin, West Bengal	C-shaped isolated margin feeding	<i>Glossopteris indica</i>
Srivastava & Agnihotri, 2011, fig. 1K–N. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal, India	Deeply incised narrow (trench) margin feeding or possible surface feeding following secondary veins	<i>Glossopteris stenoneura</i>
Srivastava & Agnihotri, 2011, fig. 1O, P. (C)	?Kungurian	lower Barakar Formation	Raniganj Coalfield, West Bengal, India	Isolated oviposition scar near midrib; C-shaped margin feeding	<i>Glossopteris indica</i>
Srivastava <i>et al.</i> , 2010, pl. 1, fig. 1. (C)	Kungurian–Wordian	Barakar Formation	Raniganj Coalfield, Damodar Basin, West Bengal	Irregular continuous margin feeding	<i>Glossopteris stenoneura</i>
Surange & Lele, 1955, pl. 1, figs 3, 4. (C)	Asselian	lower Talchir Formation	Giridih Coalfield, Bihar	Apex feeding	<i>Noeggerathopsis hislopii</i>
Saksena, 1962, pl. 1, figs 4, 6. (C)	Changhsingian	"Pali-Daigaon beds"	Karkati, South Rewa Gondwana Basin, Madhya Pradesh	Possible hole feeding	<i>Glossopteris browitiana</i>
Maheshwari & Prakash, 1965, pl. 3, fig. 21. (C)	Lopingian	Damuda Group	Bansloi River, Rajmahal Hills, Bihar	Possible broad shallow margin feeding	<i>Glossopteris reitjfera</i>
Maheshwari, 1965, pl. 3, figs 20, 21. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Possible narrow V-shaped margin feeding	<i>Glossopteris retusa</i>
Maheshwari, 1967, pl. 4, fig. 21. (AP)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Possible boring in latewood	<i>Megaporoxylon krauselii</i>

Banerji <i>et al.</i> , 1976, pl. 2, fig. 19. (C)	latest Changhsingian	?basal Panchet Group equivalents	Gopad River, Nidpur, Madhya Pradesh	Hole feeding adjacent to midrib	<i>Glossopteris taeniopteroides</i>
Bose <i>et al.</i> , 1977, text-fig. 4, pl. 2, fig. 21. (C)	latest Changhsingian	?basal Panchet Group	Ramkola-Tatapani Coalfield, Madhya Pradesh	Narrow V-shaped margin feeding	<i>Glossopteris retifera</i>
Maithy, 1978, pl. 2, fig. 12. (C)	Lopingian	Raniganj Formation	East Raniganj Coalfield, West Bengal	Small circular ?galls over secondary veins	<i>Parasphenophyllum crenulatum</i> (= <i>Trizygia speciosa</i>)
Singh <i>et al.</i> , 1982, pl. 9, fig. 62. (C)	?Kungurian	Mamal Formation	Marhoma, Kashmir	Possible narrow V-shaped margin feeding	<i>Glossopteris</i> sp.
Li & Rigby, 1995, pl. 2, figs 2, 3. (C)	?Cisuralian	Qubu Formation	southern Xizang (Tibet), China	Circular gall-like structure on leaf lamina	<i>Glossopteris xizangensis</i>
Chandra <i>et al.</i> , 1990, pl. 1, fig. 5. (C)	Lopingian	Raniganj Formation equivalent	Marhwas, Sidhi district, Madhya Pradesh	Possible oviposition scars around midrib at base of leaf	<i>Glossopteris spatulata</i>
Singh & Chandra, 1999, pl. 3, fig. 2. (C)	Kungurian-Wordian	Barakar Formation	Brijraj Nagar, Ib-River Coalfield, Mahanadi Basin, Odisha	Elliptical hole feeding on pinnules	<i>Neomariopteris hughesii</i>
Singh & Chandra, 2000, pl. 1, fig. 1. (C)	Changhsingian	Kamthi Formation	Madhupur Village, Talchir Coalfield, Odisha	Possible small elliptical hole feeding	<i>Glossopteris indica</i>
Singh & Chandra, 2000, pl. 3, fig. 2. (C)	Changhsingian	Kamthi Formation	Madhupur Village, Talchir Coalfield, Odisha	Elliptical oviposition scar on midrib	<i>Glossopteris tenuifolia</i>
Singh & Chandra, 2000, pl. 5, fig. 3. (C)	Changhsingian	Kamthi Formation	Madhupur Village, Talchir Coalfield, Odisha	C-shaped and continuous irregularly notched margin feeding	<i>Glossopteris tortuosa</i>
Singh & Maheshwari, 2000, pl. 4, fig. 5. (C)	Kungurian-Wordian	Barakar Formation	Religara Colliery, South Karanpura Coalfield, Bihar	Notched apical feeding	<i>Glossopteris obovata</i>
Singh, 2002b, pl. 2, figs 1-4. (C)	Kungurian-Wordian	Barakar Formation	Jharkand Colliery, West Bokaro Coalfield, Jharkand	" <i>Bokarospermum maheshwari</i> " (= gall on median part of midrib)	<i>Glossopteris</i> sp.
Pillai, 2012, fig. 3, pl. 1, figs 1-3. (C)	Kungurian-Wordian	Barakar Formation	Pench Valley Coalfield, Satpura Basin	Possible long interveinal surface feeding	<i>Cheirophyllum maithyi</i>
Singh <i>et al.</i> , 2012, pl. 1, fig. 1. (C)	Roadian-Wordian?	upper Barakar Formation equivalent	Manikpur Colliery, Korba Coalfield, Son-Mahanadi Master Basin, Chhattisgarh	Possible C-shaped margin feeding	<i>Gangamopteris cyclopteroides</i>
Singh <i>et al.</i> , 2012, pl. 4, fig. 4. (C)	Kungurian?	lower Barakar Formation equivalent	Dipika Colliery, Korba Coalfield, Son-Mahanadi Master Basin, Chhattisgarh	Possible V- to C-shaped apical feeding	<i>Gangamopteris clarkeana</i>
Gautam <i>et al.</i> , 2013, pl. 2, fig. 9. (C)	Artinskian	upper Karharbari to lower Barakar Formation equivalent	Johilla-Ganjra Nala confluence, South Rewa Gondwana Basin, Madhya Pradesh	Possible gall on midvein, mid-leaf	<i>Gangamopteris major</i>
Srivastava & Maheshwari, 1973, text-fig. 1, pl. 1, figs 1-4, 6. (C)	latest Changhsingian or earliest Triassic	Nidpur beds'	Wet bank, Gopad River, near Nidpur, Sidhi District, Madhya Pradesh	Possible 0.5 mm diameter oviposition scars spread over lamina	<i>Satsangia campanulata</i> (=possible ginkgoalean leaf)
Singh & Chandra, 1987, pl. 3, figs 2, 6. (C)	Changhsingian	Kamthi Formation	Hinjrida Ghati, near Handapa Village, Dhenkanal District, Mahanadi Basin, Odisha	Possible deeply notched margin feeding	<i>Glossopteris dhenkanalensis</i>

Singh & Chandra, 1996, pl. 1, fig. 2. (C)	Kungurian–Wordian	Barakar Formation	Gopal Prasad Village, Talchir Coalfield, Mahanadi Basin, Odisha	Narrow V-shaped apical feeding	<i>Glossopteris stenoneura</i>
Srivastava & Tewari, 1996, pl. 1, fig. 2. (C)	Kungurian–Wordian	Barakar Formation	Auranga Coalfield, Bihar	V-shaped apical feeding	<i>Gangamopteris major</i>
Srivastava & Tewari, 1996, pl. 1, fig. 3. (C)	Kungurian–Wordian	Barakar Formation	Auranga Coalfield, Bihar	C-shaped scallops - continuous margin feeding	<i>Glossopteris angustifolia</i>
Chauhan <i>et al.</i> , 2011, text-fig. 2A, B, pl. 2, figs 1, 4. (C)	Lopingian	Raniganj Formation	Damra Colliery, Raniganj Coalfield, West Bengal	V-shaped apical and V-shaped marginal feeding	<i>Glossopteris sessilis</i>
Chauhan <i>et al.</i> , 1985, text-fig. 1A, pl. 1, figs 2–4. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Irregular continuous margin feeding	<i>Belemnopteris sagittifolia</i>
Chauhan <i>et al.</i> , 1985, text-fig. 1B, pl. 1, fig. 1. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	C-shaped and V-shaped margin feeding	<i>Glossopteris conspicua</i>
Chauhan <i>et al.</i> , 1985, pl. 1, figs 5, 6. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Putative coprolites on leaf surface	<i>Belemnopteris sagittifolia</i>
Mukherjee <i>et al.</i> , 1966, pl. 39, figs 26, 27. (C)	Changhsingian	Roof of Mahuda coal seam, Raniganj Formation	Murulidih Colliery, Jharia Coalfield, Bihar	Asymmetrical apex feeding	<i>Glossopteris angustifolia</i>
This study, Fig. 3I. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Elliptical hole feeding on leaflets	<i>Trizygia speciosa</i>
This study, Fig. 3N. (C)	Changhsingian	Kamthi Formation	Hinjrida Ghati, near Handapa Village, Dhenkanal District, Mahanadi Basin, Odisha	Polylobate area of surface feeding damage (DT30)	<i>Glossopteris</i> sp.
This study, Fig. 3R. (C)	Changhsingian	Kamthi Formation	Hinjrida Ghati, near Handapa Village, Dhenkanal District, Mahanadi Basin, Odisha	Possible mucivory scars over secondary vein junctions	<i>Glossopteris</i> sp.
This study, Fig. 4L. (C)	Lopingian	Raniganj Formation	Raniganj Coalfield, West Bengal	Series of elliptical oviposition scars (DT76?) on and adjacent to midrib	<i>Glossopteris intermedia</i>
Srivastava, 1995, pl. 2, fig. A. (C)	Permian	Unit uncertain (possibly Barakar Formation)	Location uncertain (possibly Auranga or Raniganj coalfields), India	Irregular margin feeding	<i>Glossopteris</i> sp.
Srivastava, 1995, pl. 2, fig. B, C. (C)	Permian	Unit uncertain (possibly Barakar Formation)	Location uncertain (possibly Auranga or Raniganj coalfields), India	Small oviposition scars in outer lamina	<i>Glossopteris</i> sp.
Srivastava, 1995, pl. 2, fig. D, E. (C)	Permian	Unit uncertain (possibly Barakar Formation)	Location uncertain (possibly Auranga or Raniganj coalfields), India	Possible C-shaped margin feeding	<i>Glossopteris</i> sp.
Srivastava, 1995, pl. 2, fig. B. (C)	Permian	Unit uncertain (possibly Barakar Formation)	Location uncertain (possibly Auranga or Raniganj coalfields), India	Possible seed herbivory (corrugated surface)	<i>Condaicarpus</i> sp.
Tewari <i>et al.</i> 2017, pl. 3, fig. 2. (C)	Kungurian–Wordian	Barakar Formation	Mauguru area, Godavari Graben, India	Possible large circular gall on mid-lamina	<i>Glossopteris cordatifolia</i>
Pillai <i>et al.</i> 2018, pl. 1, fig. 4. (C)	Lopingian	Pali Formation	Johilla Coalfield, South Rewa Gondwana Basin, Madhya Pradesh	Deeply embayed margin feeding	<i>Glossopteris gondwanensis</i>

Antarctica									
Cridland, 1963, fig. 18. (C)	Lopingian	Mount Glossopteris Formation	Ohio Range		Possible hole feeding	Glossopterid scale leaf (<i>Eremonia</i>)			
Cúneo <i>et al.</i> , 1993, pl. 1, fig. 4; Taylor <i>et al.</i> 1989, fig. 3. (C)	Lopingian	Weller Coal Measures	Aztec Mountain, southern Victoria Land		Possible gall or oviposition scar	<i>Glossopteris</i> sp. (gangamopteroid appearance) (on base of midrib)			
Cúneo <i>et al.</i> , 1993, pl. 3, fig. 1. (C)	Changhsingian	upper Buckley Formation	Skaar Ridge, central Transantarctic Mountains		Hole feeding	<i>Glossopteris</i> sp. (mid-lamina)			
Cúneo <i>et al.</i> , 1993, pl. 3, fig. 1, 3. (C)	Changhsingian	upper Buckley Formation	Skaar Ridge, central Transantarctic Mountains		Margin feeding (simple scallops)	<i>Glossopteris</i> sp.			
Decombeix <i>et al.</i> , 2012, fig. 3B, C. (AP)	Changhsingian	upper Buckley Formation	Coalsack Bluff, central Transantarctic Mountains		Coprolites in lacunae within primary wood	<i>Kaokoxydon</i> sp.			
DeWitt <i>et al.</i> , 2018, pl. 1, figs 3, 4; pl. 2, fig. 3. (C)	Changhsingian	upper Buckley Formation	Skaar Ridge, central Transantarctic Mountains		(1) Possible margin feeding (simple scallops); (2) Possible hole feeding (mid-lamina circular holes); (3) Apical feeding (simple scallop)	1) <i>Glossopteris</i> sp.; (2) <i>Glossopteris</i> sp.; (3) glossopterid scale leaf			
Harper, 2015; pl. 12, fig. 156; Harper <i>et al.</i> , 2016, fig. 3g. (AP)	Changhsingian	upper Buckley Formation	Skaar Ridge, central Transantarctic Mountains		Galleries in secondary wood containing spherical coprolites (orbitatid mites)	<i>Vertebraria</i> sp. (glossopterid root)			
Kellogg & Taylor, 2004, fig. 1.2. (AP)	Changhsingian	upper Buckley Formation	Skaar Ridge, Beardmore Glacier region, Queen Alexandra Range, central Transantarctic Mountains		Coprolites containing tracheid fragments (attributed to orbitatid mites)	?glossopterid stem wood			
Klavins <i>et al.</i> , 2001, pls 1, 2. (AP)	Changhsingian	upper Buckley Formation	Skaar Ridge, Beardmore Glacier region, Queen Alexandra Range, central Transantarctic Mountains		Expansion of seed sarcotesta interpreted as a possible equivalent of an elaiosome for arthropod dispersal	<i>Choanostoma verruculosum</i>			
Lambrecht <i>et al.</i> , 1972, pl. 1, figs 3, 4. (C)	Lopingian?	unit uncertain	Law Glacier area, central Transantarctic Mountains		(1) Possible oviposition scars (DT101); (2) Possible apex feeding (DT13)	cf. <i>Gangamopteris angustifolia</i> ; <i>Glossopteris</i> sp. cf. <i>G. orbicularis</i>			
Maheshwari, 1972, pl. 14, fig. 2. (AP)	Lopingian	Mount Glossopteris Formation	Terrace Ridge, Ohio Range, Transantarctic Mountains		Cavities in secondary xylem (possibly fungal damage or orbitatid mite borings)	<i>Polysolenoxylon krauselii</i>			
Maheshwari, 1972, pl. 1, fig. 2. (AP)	Lopingian?	Unit uncertain	Mercer Ridge, Mount Schopf, Ohio Range, Horlick Mountains		Cavities with thickened rims in secondary xylem (possibly fungal damage or orbitatid mite borings)	<i>Araucarioxylon bengalense</i>			
McLoughlin <i>et al.</i> , 1997; Holdgate <i>et al.</i> , 2005, fig. 14i; Slater <i>et al.</i> , 2012, pl. 1, figs 1-4; pl. 2, figs 2, 3; Slater <i>et al.</i> , 2015, fig. 7B; Slater, 2014, fig. 5A-C; This study, Fig. 4H. (AP)	Capitanian-Wuchiapingian	Topmost Toploje Member, Baimnedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica		Isolated small oblong or cylindrical coprolites containing pollen and spore fragments, and in some cases cell walls, fungi (palynophagy to generalist ?detritivory)	Dispersed in permineralized peat matrix			
McLoughlin <i>et al.</i> , 2005, fig. 4B, C, F. (C)	Guadalupian	Undefined shale unit	Fossilryggen, Vestfjella, Dromming Maud Land		Possible notched margin feeding	<i>Glossopteris</i> sp. cf. <i>G. spatulata</i>			
Plumstead, 1962a, pl. 3, figs 5, 6; pl. 4, fig. 5; pl. 5, fig. 3; This study, Fig. 1F. (C)	Permian	Unit uncertain	(1) Allan Nunatak; (2, 3) Whichaway Nunataks		(1) Possible margin feeding (V-shaped notch); (2) crenulate margin; (3) deep embayment	(1) <i>Glossopteris</i> sp. (listed as <i>Palaeovittaria</i> sp.); (2) <i>Glossopteris indica</i> ; (3) <i>Glossopteris communis</i>			

Slater <i>et al.</i> , 2012, pl. 5, 1–6; Slater <i>et al.</i> 2015, fig. 6C; Slater, 2014, figs 5F, 8D–H; This study, Fig. 4F, G. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Coprolites with tracheid fragments in secondary wood, and locally in peat matrix (boring and/or saproxylophagy)	<i>Vertebraria</i> and <i>Australoxylon</i> sp.
Slater <i>et al.</i> , 2012, pl. 4, figs 1–4. This study, Fig. 4I. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Sub-rounded to angular coprolites containing densely packed mesophyll cell wall fragments in cavities within mesophyll (leaf mining or detritivory)	<i>Glossopteris</i> sp.
Slater <i>et al.</i> , 2012, pl. 3, fig. 5; pl. 4, fig. 5; Slater, 2014, fig. 5E. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Ovoid coprolite in fern sporangium; and ovoid coprolites filled with spores (palynophagy)	Unidentified fern sporangium, and dispersed in permineralized peat
Slater <i>et al.</i> , 2012, pl. 2, fig. 4; pl. 4, fig. 6. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Isolated large ellipsoid to spherical coprolites with amorphous contents in leaf debris (?detritivory)	Dispersed between glossopterid leaf debris in permineralized peat
Slater <i>et al.</i> , 2012, pl. 6, figs 3, 4; Harper <i>et al.</i> , 2016, fig. 3E. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Spherical to ovoid coprolites containing fungal spores (fungivory)	Dispersed in permineralized peat matrix
Slater <i>et al.</i> , 2012, pl. 3, fig. 4. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Squat ellipsoidal to spherical coprolites containing glossopterid pollen (palynophagy)	Dispersed in permineralized peat matrix
Slater <i>et al.</i> , 2012, pl. 2, figs 1–3; pl. 3, figs 2, 3; Slater <i>et al.</i> 2015, fig. 5D. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Spherical to ellipsoidal coprolites containing coarse constituents (folivory or detritivory)	Dispersed in permineralized peat matrix
Slater <i>et al.</i> , 2012, pl. 3, fig. 1. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Oblong spiral ornamented coprolite with amorphous contents	Dispersed in permineralized peat matrix
Taylor & Taylor, 1989, fig. 4; Pigg 1990, pl. 5, figs 2, 4. (AP)	Changhsingian	upper Buckley Formation	Skaar Ridge, central Transantarctic Mountains, Antarctica	Possible hole feeding	<i>Glossopteris skaarensis</i>
Tewari <i>et al.</i> , 2015, figs 8G, 9C, 12G. (C)	Changhsingian	upper Weller Formation	Allan Hills, South Victoria Land	(1) Possible piercing-and-sucking damage or small oviposition scar on midrib; (2) broad V-shaped margin feeding; (3) broad embayment following secondary veins to midrib.	(1) <i>Glossopteris arberi</i> ; (2) <i>Glossopteris bucklandensis</i> ; (3) <i>Glossopteris damudica</i>
White, 1969, figs 1–4; Weaver <i>et al.</i> , 1997, fig. 10A–G; ?fig. 11C; McLoughlin, 2011b, fig. 5C; Harper <i>et al.</i> 2016, fig. 3f; This study, Fig. 4E. (AP)	Capitanian–Wuchiapingian	Topmost Toploje Member, Bainmedart Coal Measures, Amery Group	Radok Lake area, Lambert Graben, East Antarctica	Borings in late wood of secondary xylem of trunk wood (attributed to oribatid mites or possibly beetles)	<i>Australoxylon mondii</i>

Australasia									
Beattie, 2007, fig. 7A, C; This study, Figs 3E, G. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Notched, C-shaped scalloped and deeply to shallowly embayed (U- and V-shaped) isolated and continuous margin feeding	<i>Glossopteris</i> sp.			
Beattie, 2007, fig. 7D. This study, Figs 3B-D. (C)	Changhsingian	Croudace Bay Formation, upper Newcastle Coal Measures	Belmont, northern Sydney Basin, New South Wales	Belmont, northern Sydney Basin, New South Wales	Isolated U-, V- and C-shaped marginal excisions and continuous margin feeding	<i>Glossopteris</i> sp.			
Beattie, 2007, fig. 7B. (C)	Changhsingian	Croudace Bay Formation, upper Newcastle Coal Measures	Belmont, northern Sydney Basin, New South Wales	Belmont, northern Sydney Basin, New South Wales	Small (<1 mm) circular clustered oviposition scars on axis	<i>Paracalamites australis</i>			
Begg <i>et al.</i> , 1986, fig. 19B. (C)	Kungurian-Guadalupian	Mangarewa Formation	Productus Creek, South Island, New Zealand	Productus Creek, South Island, New Zealand	Elliptical, mid-lamina hole feeding	<i>Glossopteris</i> sp.			
Carruthers, 1872, p. 354 (no figures). (C)	Permian (?Lopingian)	Uncertain	Uncertain, probably Bowen Basin, Queensland	Uncertain, probably Bowen Basin, Queensland	Mention of sori-like structures running along secondary veins (=possible interveinal surface feeding)	<i>Glossopteris</i> sp.			
Chaloner <i>et al.</i> , 1991, fig. 5; Scott <i>et al.</i> , 1992, fig. 3. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Continuous scalloped margin and apical feeding	<i>Glossopteris</i> sp.			
David, 1891, pp. 424-425 (no figures). (C)	Artinskian	Greta Coal Measures	Richmond Vale, northern Sydney Basin, New South Wales	Richmond Vale, northern Sydney Basin, New South Wales	Mention of symmetrically arranged, dark oval spots (= possible oviposition scars)	<i>Gangamopteris</i> sp.			
Feistmantel, 1890, pl. 20, fig. 5. (C)	Lopingian	Illawarra Coal Measures	Bowenfels, western Sydney Basin, New South Wales	Bowenfels, western Sydney Basin, New South Wales	V-shaped apical notch (possible apex feeding)	<i>Glossopteris spatulatocordata</i>			
Holmes, 1995, fig. 15. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Possible apex feeding on pinnules	<i>Cooyalopteris dimorpha</i>			
Holmes, 1995, fig. 53. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Possible interveinal hole feeding	<i>Glossopteris parallela</i>			
Holmes, 1995, fig. 54. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Deep (to midrib), irregular margin feeding	<i>Glossopteris parallela</i>			
Holmes, 1995, figs 55, 56. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Linear arrays of possible galls over secondary veins	<i>Glossopteris parallela</i>			
Holmes, 1995, fig. 57. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Clusters of small, rod-like, ?oviposition scars on mid-lamina	<i>Glossopteris ampla</i>			
Holmes, 1995, figs 59, 60. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Cooyal, Sydney Basin, New South Wales	Small to large, circular galls or oviposition scars on proximal half of midrib	<i>Glossopteris ampla</i>			
Mitchell, 1872, fig. 1. (C)	Changhsingian	Newcastle Coal Measures	Lake Macquarie Road near Charlestown, northern Sydney Basin, New South Wales	Lake Macquarie Road near Charlestown, northern Sydney Basin, New South Wales	Possible circular oviposition or hole-feeding scars parallel to lamina margin	<i>Glossopteris</i> sp.			

McLoughlin, 1990a, pl. 5, figs 1, 5, 8, text-fig. 14; McLoughlin, 1994a, pl. 3, fig. 5; pl. 4, figs 1, 3; McLoughlin, 2011a, fig. 4A, B; This study, Fig. 4M. (C)	late Wuchiapingian–early Changhsingian	Black Alley Shale, Blackwater Group	Inglis Dome, southwestern Bowen Basin, Queensland	Roughly circular oviposition scars flanking each side of midrib	<i>Glossopteris bucklandensis</i>
McLoughlin, 1990a, pl. 5, figs 2, 6; McLoughlin, 1994a, pl. 3, fig. 4; pl. 4, figs 8, 9; McLoughlin, 2011a, fig. 4C, G. (C)	late Wuchiapingian–early Changhsingian	Black Alley Shale, Blackwater Group	Inglis Dome, southwestern Bowen Basin, Queensland	Small elliptical gall or solitary oviposition scar on base of midrib	<i>Glossopteris bucklandensis</i>
McLoughlin, 1990b, pl. 2, figs 7, 8; McLoughlin, 2011a, fig. 4D, F. (C)	late Wuchiapingian–early Changhsingian	Black Alley Shale, Blackwater Group	Inglis Dome, southwestern Bowen Basin, Queensland	Small ovate gall or solitary oviposition scar on proximal part of midrib	<i>Glossopteris xiphophylla</i>
McLoughlin, 1992a, pl. 8, figs 7, 10. (AP)	Wuchiapingian	McMillan Formation	Shirt Creek, Comet Platform, central Bowen Basin, Queensland	Arthropod borings or fungal pocket rot cavities in both early- and late-season wood	<i>Araucarioxylon</i> (= <i>Agathoxylon</i>)
McLoughlin, 1992b, pl. 6, figs 7, 11. (C)	Artinskian	Irwin River Coal Measures	Irwin River and Woolaga Creek, northern Perth Basin, Western Australia	Possible small (c. 1 mm) circular oviposition scars on axes	<i>Paracalamites australis</i>
McLoughlin, 1994a, pl. 1, fig. 4. (C)	Changhsingian	Bandanna Formation, Blackwater Group	Reids Dome, southwestern Bowen Basin, Queensland	U-shaped scallop, margin feeding	<i>Glossopteris browniana</i>
McLoughlin, 1994a, pl. 3, fig. 9. (C)	late Wuchiapingian–early Changhsingian	Black Alley Shale, Blackwater Group	Inglis Dome, southwestern Bowen Basin, Queensland	Broad, wavy margin feeding in proximal part of leaf	<i>Glossopteris bucklandensis</i>
McLoughlin, 1994a, pl. 4, fig. 6. (C)	late Wuchiapingian–early Changhsingian	Kaloola Formation, Blackwater Group	Theodore, southeast Bowen Basin, Queensland	Possible interveinal hole or surface feeding	<i>Glossopteris burngrovensis</i>
McLoughlin, 1994a, pl. 5, fig. 5. (C)	late Wuchiapingian–early Changhsingian	Burngrove Formation	Rubina Station, Dawson Tectonic Zone, central Bowen Basin, Queensland	Elliptical hole feeding spanning secondary veins	<i>Glossopteris burngrovensis</i>
McLoughlin, 1994a, pl. 6, figs 1, 5; This study, Fig. 3O. (C)	late Wuchiapingian–early Changhsingian	Black Alley Shale, Blackwater Group	Inglis Dome, southwestern Bowen Basin, Queensland	Possible surface feeding between secondary veins (raised areolae)	<i>Glossopteris chevronata</i>
McLoughlin, 1994a, pl. 8, fig. 12. (C)	late Wuchiapingian–early Changhsingian	Black Alley Shale, Blackwater Group	Inglis Dome, southwestern Bowen Basin, Queensland	Possible C-shaped margin feeding	<i>Glossopteris denisonensis</i>
McLoughlin, 1994a, pl. 11, fig. 7. (C)	Changhsingian	Rangal Coal Measures, Blackwater Group	Blackwater Mine, Comet Platform, central Bowen Basin, Queensland	Broadly rounded excision to midrib near base of lamina	<i>Glossopteris grandis</i>
McLoughlin, 1994b, pl. 8, figs 2, 6; pl. 9, figs 1, 2; text-fig. 16. (C)	Changhsingian	Rangal Coal Measures, Blackwater Group	Blackwater Mine, Comet Platform, central Bowen Basin, Queensland	C-shaped, V-shaped, and deep (extending to midrib) and broad marginal feeding scallops	<i>Glossopteris truncata</i>

McLoughlin, 1994b, pl. 1, fig. 8. (C)	late Wuchiapingian–early Changhsingian	Kaloola Formation, Blackwater Group	Theodore, southeast Bowen Basin, Queensland	C-shaped marginal feeding scallop	<i>Glossopteris indicoides</i>
McLoughlin, 1994b, pl. 3, fig. 11. (C)	late Wuchiapingian–early Changhsingian	Kaloola Formation, Blackwater Group	Theodore, southeast Bowen Basin, Queensland	Possible shallow V-shaped marginal feeding notches in distal portion of leaf	<i>Glossopteris linguiforma</i>
McLoughlin, 1994b, pl. 4, fig. 2. (C)	late Wuchiapingian–early Changhsingian	Burngrove Formation	Minnie Creek, Comet Platform, central Bowen Basin, Queensland	Truncate apical feeding	<i>Glossopteris</i> sp. cf. <i>G. schoppfi</i>
McLoughlin, 1994b, pl. 5, fig. 12. (C)	late Wuchiapingian–early Changhsingian	Burngrove Formation	Minnie Creek, Comet Platform, central Bowen Basin, Queensland	Shallowly scalloped margin feeding	<i>Glossopteris</i> sp. cf. <i>G. schoppfi</i>
McLoughlin, 1994b, pl. 7, figs 7, 8. (C)	Changhsingian	Black Alley Shale and Bandanna Formation, Blackwater Group	Inglis Dome, southwestern Bowen Basin, Queensland	C-shaped to broadly scalloped margin feeding	<i>Glossopteris rhombimaculata</i>
McLoughlin, 2011a, fig. 2A, B; Slater, 2014, fig. 2H; This study, Fig. 3A. (C)	Capitanian-Wuchiapingian	Cullen Bullen Subgroup, Illawarra Coal Measures	Ulan Coal Mine, northwestern Sydney Basin, New South Wales	Large gall on proximal midrib	<i>Glossopteris acutifolia</i>
McLoughlin, 2012, pl. 2, figs 2, 4. (C)	mid-Sakmarian–late Artinskian	Reids Dome beds	GSQ Taroom 11 stratigraphic bore, south-western Bowen Basin, Queensland	Broad area of pitted damage to lamina (possible arthropod, fungal, physical, or diagenetic damage)	<i>Glossopteris</i> sp.
McQueen, 1954, pl. 12, fig. 9; Begg <i>et al.</i> , 1986, fig. 8. (C)	Wuchiapingian	Arthurton Group	Balclutha-Gore district, South Island, New Zealand	Possible C-shaped margin feeding	<i>Noeggerathopsis hislopii</i>
Naugolnykh 2016, pl. 1, fig. 2. (C)	Lopingian	Dunedoo Formation, Illawarra Coal Measures	Notis Quarry, Cobborah, Gunnedah Basin, New South Wales	undulate margin feeding	<i>Glossopteris</i> sp.
Rigby, 1966, pl. 34, fig. 42; Rigby <i>et al.</i> , 1988, fig. 3; Rigby, 1993, pl. 87, fig. 2. (C)	Artinskian	Mingenev Formation	Errugulla Springs Station, Mingenev, northern Perth Basin, Western Australia	Deeply embayed (to midrib) margin feeding	<i>Glossopteris erregullanus</i>
Rigby, 1966, pl. 34, fig. 43; Rigby, 1993, pl. 88, fig. 4. (C)	Wordian–Wuchiapingian	Wagina Sandstone	South branch of Irwin River, northern Perth Basin, Western Australia	Elliptical hole feeding, inner to middle lamina	<i>Glossopteris waginanus</i>
Rigby, 1967, pl. 25, fig. 2; White, 1986, fig. 131; This study, Fig. 3Q. (C)	Lopingian	Lithgow Coal, Illawarra Coal Measures	Duncans Pass, near Katoomba, western Sydney Basin, New South Wales	Possible oviposition or mucivory scars: numerous small circular raised scars over secondary veins	<i>Gangamopteris walkomii</i>
Rigby, 1996, pl. 2, figs 5, 9; Rigby, 2001, fig. 4C. (C)	Kungurian–Roadian	Aifiam Group	Mimika Regency, Papua Province, Indonesia	Deep (to midrib), V-shaped embayment: margin feeding	<i>Glossopteris</i> sp. F, H
Rigby, 1996, pl. 2, fig. 7. (C)	Kungurian–Roadian	Aifiam Group	Mimika Regency, Papua Province, Indonesia	C-shaped margin feeding	<i>Glossopteris</i> sp. C

Walkom, 1928, pl. 22, fig. 7. (AP)	Artinskian	Ravensfield Sandstone Member, Farley Formation	Near Farley, Sydney Basin, New South Wales	Cavity in secondary wood containing coprolites	<i>Dadoxylon (=Agathoxylon) farleyense</i>
White, 1961, figs 8, 9. (C)	Cisuralian	Agate Creek Volcanic Group	Headwaters of Agate Creek, Kennedy Igneous Association, north Queensland	Small elliptical solitary oviposition scar on proximal part of midrib	<i>Glossopteris angustifolia</i> and <i>G. sp. cf. G. intermittens</i> (probably synonymous)
White, 1961, fig. 13. (C)	Cisuralian	Agate Creek Volcanic Group	Headwaters of Agate Creek, Kennedy Igneous Association, north Queensland	Narrow, slit-like margin feeding (to midrib)	<i>Glossopteris indica</i>
White, 1962, pl. 1, fig. 3. (C)	Asselian-Sakmarian	Lizzie Creek Volcanics	3.2 km NW of Bowen River Hotel, Bowen Basin, Queensland	Possible large linear longitudinal mid-lamina hole feeding damage	" <i>Cordaites australis</i> " (= <i>Noeggerathopsis sp.</i>)
White, 1964, pl. 11, fig. 1. (C)	Lopingian	Undifferentiated Blackwater Group	3.2 km SW of Kammiss Creek homestead, Bowen Basin, Queensland	Possible apex feeding (irregular truncation with reaction tissue)	<i>Glossopteris angustifolia</i>
White, 1978, fig. 60. (C)	Changhsingian	Croudace Bay Formation, upper Newcastle Coal Measures	Belmont, northern Sydney Basin, New South Wales	Narrow, slit-like margin feeding	glossopterid scale leaf?
White, 1986, fig. 130. (C)	Lopingian	Dunedoo Formation, Illawarra Coal Measures	Notts Quarry, Cobborah, Gunnedah Basin, New South Wales	Truncate to V-shaped possible apex feeding	<i>Glossopteris sp.</i>
White, 1986, fig. 184. (C)	Lopingian	Newcastle Coal Measures	Shepherds Hill, Newcastle, Sydney Basin, New South Wales	Possible circular oviposition scars on axis internodes	<i>Phyllothea etheridgei</i>
This study, Fig. 3H. (C)	Changhsingian	Croudace Bay Formation, upper Newcastle Coal Measures	Belmont, northern Sydney Basin, New South Wales	Truncate apex feeding	<i>Glossopteris xiphophylla</i>
This study, Fig. 3I. (C)	Guadalupian-Lopingian	Whittingham Coal Measures	Saxonvale Mine, Sydney Basin, New South Wales	V-shaped apical feeding	<i>Glossopteris browniana</i>
This study, Fig. 3K. (C)	Wuchiapingian	Moranbah Coal Measures	Rosella Creek, Bowen Basin, Queensland	Isolated elliptical interveinal hole feeding	<i>Belemnopteris elongata</i>
This study, Fig. 3L. (C)	Artinskian	Koogah Formation	Mount Wingen, Gunnedah Basin, New South Wales	Elliptical hole feeding	<i>Glossopteris sp.</i>
This study, Fig. 4D. (C)	Artinskian	Koogah Formation	Mount Wingen, Gunnedah Basin, New South Wales	C-shaped and irregular margin feeding (and pseudodamage from root penetration)	<i>Glossopteris sp.</i>
This study, Fig. 3M. (C)	Artinskian	Koogah Formation	Mount Wingen, Gunnedah Basin, New South Wales	Elliptical zones of skeletonization	<i>Glossopteris sp.</i>
This study, Fig. 3P. (C)	Changhsingian	upper Illawarra Coal Measures	Cooyal, Sydney Basin, New South Wales	Polylobate area of roughened surface feeding damage	<i>Glossopteris sp.</i>
This study, Fig. 4K. (C)	Permian (Lopingian?)	Unit uncertain	Bowen Basin, Queensland	Series of elliptical oviposition scars (DT76) on midrib	<i>Glossopteris sp. cf. G. browniana</i>

Table 2—Compendium of arthropod damage on plants illustrated by Anderson & Anderson (1985) from the Permian of the Karoo Basin, South Africa. Damage identification has utilized the functional feeding groups of Labandeira *et al.* (2007), and has followed their classification scheme as closely as possible. Additional descriptions have been included in cases where damage did not fit comfortably within existing DTs. The taxonomy used by the original authors has been followed, and does not necessarily represent the views of the current authors. Recognition of incidents of damage, and accuracy in classification was highly dependant on the quality of the illustrations in the original publications. Identifications were conservative, and only recorded if reasonably clear diagnosis was possible. Rigorous identifications would require careful microscopic examination and rotation.

Stratigraphic unit; age; locality	Plant taxon	Plant organ	Figure number	Margin feeding	Hole feeding	Surface feeding	Skeletonization	Piercing and sucking	Oviposition	Galling	Seed predation
Normandien Formation; Wuchiapingian; Bergville	Glossopteri-dales: <i>Estcourtia vandijkii</i>	leaves	pl. 97, figs 1, 7, 8, 9		Small, circular hole feed (DT01)				Circular to elliptical oviposition scars scattered on lamina (DT101), ?dense cluster of oviposition scars leading to tissue disruption (cf. DT136), small elliptical oviposition on midrib (DT76)		
As above	Glossopteri-dales: <i>Estcourtia bergvillensis</i>	leaves	pl. 99, figs 2, 4, 6, 7	Shallow, V-shaped margin feeding (DT12); feeding across leaf apex (DT13), causing distortion of leaf lamina					Circular to elliptical oviposition scars scattered on lamina (DT101), larger oviposition scars perpendicular to venation, more diffuse reaction rim (DT101)		
Normandien Formation; Wuchiapingian; Loskop	Glossopteri-dales: <i>Plumsteadia gibbosa</i>	leaves	pl. 93, figs 1, 2, 3, 7	C-shaped and cusped margin feeding (DT12)	Very small holes in lamina (DT01)	Lesion at margin, with ragged tissue from reaction rim to diffuse leaf margin; wedge-shaped lesion at apex, with very dark staining (DT75), and possible cluster of oviposition scars (cf. DT136)		Possible clusters of circular punctures causing tissue disruption (DT46);	Small, elliptical ovipositions scattered on lamina, parallel to venation (DT101), and on midrib (DT76)		

As above	Glossopteri- dales: <i>Estcourtia</i> <i>vandijkii</i>	leaves	pl. 98, figs 1, 2, 4, 5, 6	Hole feeding adjacent to midrib (DT02)	Necrotic lesion (DT29) with indistinct reaction rim	Although leaf in pl. 98, fig. 6 has apparent skeletoni- zation, there are no convincing reaction rims. Removal of primary vein may point to post- senescence detritivory		circular to elliptical oviposition scars on lamina (DT101) and midrib (DT76)		
As above	Glossopteri- dales: <i>Estcourtia</i> <i>bergvillensis</i>	leaves	pl. 100, figs 1, 3					Small, circular oviposition scars on lamina (DT101) and midrib (DT76)		
As above	Glossopteri- dales: <i>Lidgetttonia</i> <i>inhluzanensis</i>	leaves	pl. 122, fig. 17					Elliptical oviposition scars on lamina (DT101) and midrib (DT76)		
As above	Glossopteri- dales: <i>Glossopteris</i> <i>lostopenensis</i>	leaves	pl. 132, figs 1, 4, 7	Shallow C-shaped and cusped margin feeding (DT12), margin feeding to midrib (DT14) and across leaf apex (DT13)			rows of puncture marks along veins (DT138)	Spindle-shaped and elliptical oviposition scars scattered on lamina (DT101) and on the midrib (DT76)		
Normandien Formation; Wuchiapingian; Estcourt area (Rondedraai, Sheba's Breast, Indian school, Wagondrift, Lowlands)	Glossopteri- dales: <i>Glossopteris</i> <i>symmetrifolia</i>	leaves	pl. 140, figs 3, 6		Elliptical/ polylobate region of surface feeding (DT29)			Oviposition scars on midrib (DT46) and on lamina (DT101)		
Normandien Formation; Wuchiapingian; Estcourt	Incertae sedis: <i>Taeniopteris</i> <i>estcourtitana</i>	leaves	pl. 166, figs 1, 2	Small, elliptical hole feeding (DT02)				Oviposition scars on midrib (DT46) and on lamina (DT101)		

Normandien Formation; Wuchiapingian; Mooi River area (National Rd., Far End quarry, Far End west, Rosetta)	Glossopteri- dales: <i>Plumsteadia natalensis</i>	leaves	pl. 92, fig. 1a	C-shaped margin feeding (DT12)	Small, elliptical hole feeding (DT02), tiny hole feeding (DT01)	Darkly stained necrotic lesion with well-defined reaction rim (DT30)	Tiny punctures, some with dark staining, scattered across lamina (DT46)			
Normandien Formation; Wuchiapingian; Mooi River	Glossopteri- dales: <i>Estcourtia vandijkii</i>	leaves	pl. 96, figs 1, 2, 3, 4, 5, 6, 8, 10	Undulating, scalloped and V-shaped margin feeding (DT12); very broad discoloured band adjacent to arcuate margin feed, possible secondary fungal infection; apex feeding leading to distorted leaf growth (DT13)	Small circular hole feeding (DT01), hole feeding (DT02)					
As above	Glossopteri- dales: <i>Rigbya arbertoides</i>	leaves	pl. 101, figs 14, 15, 16, 17,	Cusped, deeply incised margin feed (DT15); undulating continuous margin feeding, C-shaped margin feeds (DT12)	Small circular hole feeding (DT01), hole feeding (DT02)	Necrotic, polylobate surface feeding with well-defined reaction rim (DT30)		Narrowly elliptical oviposition scars on lamina (DT101) and midrib (DT76)		
As above	Glossopteri- dales: <i>Lidgettonia mootriverensis</i>	scale leaves	pl. 115, fig. 3					Elliptical oviposition scars on lamina (DT101)		
As above	Glossopteri- dales: <i>Lidgettonia mootriverensis</i>	leaves	pl. 117, figs 1, 2, 4, 5, 7, 8; pl. 118, figs 3, 5, 7	V-shaped, C-shaped, shallow, scalloped margin feeding (DT12)	Elliptical hole feeding (DT02); cluster of tiny holes in lamina (DT01), associated with leaf chlorosis	Necrotic zones of possible surface feeding (DT29)		Circular to elliptical oviposition scars on lamina (DT101) and midrib (DT76)		

As above	Glossopteri- dales: <i>Lidgettonia</i> <i>inhluzanensis</i>	leaves	pl. 119, fig. 31					Abundant elliptical punctures, in rows along midrib and scattered on lamina (DT48)	Narrowly elliptical ovipositions on midrib (DT76)		
As above	Glossopteri- dales: <i>Lidgettonia</i> <i>lidgetto-</i> <i>nioides</i>	leaves	pl. 126, fig. 4, 6, 8; pl. 127, figs 4, 11		Necrotic zone in base of leaf, no venation visible (DT30)	Tiny, circular hole feeds (DT01)		Small, circular punctures over veins (DT46)	Elliptical oviposition scars on lamina (DT101), narrowly elliptical ovipositions on midrib (DT76)	Very small galls (DT80), or piercing damage	
As above	Glossopteri- dales: <i>Lidgettonia</i> <i>elegans</i>	leaves	pl. 131, figs 11, 13, 14	Shallow, cusped continuous margin feeding (DT12), deep, U-shaped to rectangular excisions to margin (DT14)				Tiny punctures, some with dark staining, scattered on lamina (DT46)	Oviposition scars on midrib (DT76), and lamina (DT101)		
As above	Glossopteri- dales: <i>Glossopteris</i> <i>symmetrifolia</i>	leaves	pl. 138, figs 3, 4; pl. 139, figs 3						Small, circular oviposition scars on lamina (DT101)		
As above	Sphenopsida: <i>Benligtfootia</i> <i>mooiensis</i>	leaf	p. 148	Possible C-shaped margin feeding (DT12)					Scattered elliptical oviposition scars parallel to veins (DT101)		
Normandien Formation; Wuchiapingian; Lidgetton	Sphenopsida: <i>Phyllothecca</i> <i>australis</i>	stems	pl. 39, figs 14, 15						Rare, scattered, elliptical oviposition scars between ribs		
As above	Glossopteri- dales: <i>Lidgettonia</i> <i>africana</i>	leaves	pl. 114, figs 1, 4, 7	C-shaped, cusped, and undulating, continuous margin feeding (DT12)		Circular hole feed (DT02)			Oviposition scars on midrib (DT76)		
As above	Glossopteri- dales: <i>Lidgettonia</i> <i>africana</i>	scale leaves	pl. 113, fig. 7			Elliptical hole feed (DT02)				Possible stained circular gall on vein (DT32)	

Normandien Formation; Wuchiapingian; Inhluzani (and Glandsrock, Boschhoek)	Glossopteri- dales: <i>Lidgettonia inhluzanensis</i>	leaves	pl. 119, fig. 31					Abundant elliptical punctures, in rows along midrib and scattered on lamina (DT48)	Narrowly elliptical ovipositions on midrib (DT76)		
Normandien Formation; Wuchiapingian; Bulwer	Sphenopsida: <i>Sphenophyllum spectosum</i>	leaves	pl. 32, fig. 1, 2, 3, 4		Possible surface feeding (DT29) or fungal lesion; necrotic lesion with feathered edge, near apex	Small, polylobate hole feed (DT03)			Elliptical oviposition scars (DT101), parallel to venation		
As above	Glossopteri- dales: <i>Rigbya arbertoides</i>	leaves	pl. 102, figs 8, 10, 11, 12, 13, 14, 16	C-shaped, undulating, and cusped, continuous margin feeding (DT12), deeply incised, trenched and keyhole feeding (DT15), distortion of surrounding tissue; feeding across apex (DT13), deeply incised margin feeding, reaching midrib (DT14)		Circular to polylobate hole feeds, of various sizes (DT01, DT02)	Regions of skeletonization with an undulating margin, mostly along leaf edges (DT22), and small polylobate areas (DT24); reaction rim very pronounced.	Tiny, darkly stained punctures in lines along midrib (DT138)			
As above	Glossopteri- dales: <i>Lidgettonia lidgettonioides</i>	leaves	pl. 128, figs 13, 15, 17, 19, 20	Cusped continuous margin feeding (DT12), cusped margin feeding across apex of leaf (DT13)		Circular to polylobate hole feeds, of various sizes (DT01, DT02)			Small elliptical ovipositions on midrib (DT76), and lamina (DT101)		
?Geological outlier; ?Wordian –Wuchiapingian; Lawley, Gauteng Province	Sphenopsida: <i>Ramiganjia rayneri</i>	foliar shoots	pl. 34, figs 3, 4								

As above	Sphenopsida: <i>Ramiganjia lanceolata</i>	foliar shoots	pl. 35, figs 1, 5	Possible margin feeding (DT12)															
As above	Glossopteri- dales: <i>Arberia alweyensis</i>	leaves	pl. 110, figs 1, 2	C-shaped margin feeding (D12); deeply incised, very narrow trench feeding (DT15)															Elliptical oviposition scars on lamina (DT101) and midrib (DT76)
As above	Glossopteri- dales: <i>Lidgettonia lavleyensis</i>	scale leaves	pl. 123, figs 7, 15, 17	Arcuate margin feed (DT12)															Possible ovipositions on a rhombic scale leaf (DT101)
As above	Glossopteri- dales: <i>Lidgettonia lavleyensis</i>	leaves	pl. 124, figs 1, 2, 3, 4	Deeply incised keyhole feeding (DT15)															Elliptical oviposition scars on lamina (DT101) and midrib (DT76)
As above	Glossopteri- dales: <i>Glossopteris</i> sp. cf. <i>G. damudica</i>	leaves	pl. 135, figs 1, 2																Elliptical oviposition scars on lamina, parallel to veins (DT101) and midrib (DT76)
? Volkstrust Formation; Kungurian-Wordian; Cedara	Glossopteri- dales: <i>Hirsutum acadarensis</i>	leaves	pl. 77, figs 1, 2, 7	C-shaped margin feeding, scalloped, deeply incised, continuous margin feeding (DT12); keyhole margin feeding (DT15)															Circular oviposition scars on midrib, or to each side of midrib (DT76), or scattered across lamina (101)
As above	Glossopteri- dales: <i>Escourtia bergvillensis</i>	leaves	pl. 100, fig. 5																Circular oviposition scars on midrib, or to each side of midrib (DT76), or scattered across lamina (101)
As above	Glossopteri- dales: <i>Arberia cedarensis</i>	leaves	pl. 109, figs 1, 2, 3	Arcuate, cuspedate and v-shaped margin feeds (DT12)															Oviposition scar on lamina (DT101)
																			Oviposition scars on lamina (DT101), oviposition scars on midrib (DT76)
																			Possible gall, small, circular, densely stained (DT32)

Hamanskraal Formation (Vryheid Formation equivalent); Kungurian-Roadian; Hamanskraal	Sphenopsida: <i>Sphero-phyllum hamman-skraalensis</i>	leaf	pl. 31, fig. 7						Scattered, elliptical oviposition scars parallel to veins on lamina (DT101)			seed with circular boring (DT74)
As above	Polypodio-psida: <i>Asterotheca hammans-kraalensis</i>	pinnule	pl. 45, fig. 1					Possible piercing & sucking; tiny punctures on rachis, some in rows (DT138)	Possible elliptical oviposition on rachis (DT76)			
As above	Glossopteri-dales: <i>Ottokaria hammans-kraalensis</i>	leaves	pl. 60, figs 8, 14	C-shaped margin feeding (DT12)					Elliptical scars scattered on lamina (DT101) and on midrib (DT76)			
As above	Glossopteri-dales: <i>Hirsutum lestii</i>	leaves; seed	pl. 81, figs 4, 10; pl. 82, figs 1-3	C-shaped margin feeding (DT12)	Small, circular hole feeding (DT01)	Repeating, V-shaped lesions along leaf margin, very diffuse reaction rims, possibly surface feeding, or fungal infection.		Possible piercing and sucking in lines along midrib (DT138) and scattered across midrib	Circular, elliptical and spindle-shaped scars scattered on lamina (DT101), orientated parallel to venation and across venation, in vertical rows parallel to leaf margin (cf. DT54), and on midrib (DT76)			
As above	Glossopteri-dales: <i>Arberia madag-scarlensis</i>	leaves	pl. 106, fig. 1			Blunt v-shaped necrotic regions extending from margin to midrib (DT97), may be fungal in nature			Elliptical oviposition scars scattered on lamina (DT101), orientated parallel to venation			

Vryheid Formation; Artinskian–Roadian; Ermelo	Glossopteri–dales: <i>Ottokaria</i> sp. cf. <i>O. obovata</i>	leaves	pl. 59, figs 2, 3, 6			U- to V-shaped lesions partially constrained by venation, possibly surface feeding, or fungal infection (DT97)		Elliptical oviposition scars, between veins, parallel to venation (DT101), and on 'midrib' (DT76)		Seed with circular boring (DT74)
As above	Glossopteri–dales: <i>Hirsutum leslii</i>	leaves, seeds	pl. 84, figs 1–6; pl. 85, fig. 11; pl. 86, fig. 22	Cusped margin feeding (DT12);	Small, polylobate hole feed (DT03)		Elliptical oviposition scars, between veins, parallel to venation (DT101), and on 'midrib' (DT76)			
As above	Cordaitales: <i>Noeggerathia-opsis hislopii</i>	leaves	pl. 156, figs 2, 4, 5, 6				Elliptical oviposition scars, between veins, parallel to venation (DT101)			
Vryheid Formation; Artinskian–Roadian; Vereeniging	Lycopsida: <i>Cyclodendron leslii</i>	micro-phyll	pl. 25, fig. 2				Possible elliptical to lanceolate oviposition scar (DT101)			
As above	Glossopteri–dales: <i>Palaeovittaria kuitzi</i>	leaves	pl. 54; figs 1–8; pl. 55, fig. 1	Scalloped continuous margin feeding; (DT12)	Deeply incised, polylobate hole feeding	Small, elliptical, in vertical rows on veins in 'midrib' (DT138)	Elliptical oviposition scars, between veins, parallel to venation (DT101), and on 'midrib' (DT76)	Large, single (one double) gall in basal portion of leaf, on 'midrib', lanceolate to spindle-shaped (cf. DT85)		
As above	Glossopteri–dales: <i>Ottokaria buritadica</i>	leaves	pl. 56, figs 1, 2; pl. 58, fig. 6	Arcuate margin feed (DT12)			Elliptical oviposition scars, between and parallel to venation (DT101), and on midrib (DT76)			

As above	Glossopteri- dales: <i>Ottokaria</i> sp. cf. <i>O. obovata</i>	leaves	pl. 59, figs 2, 3, 6			U- to V-shaped lesions partly constrained by veins, possibly surface feeding, or fungal infection (DT97)			Elliptical oviposition scars, between veins, parallel to venation (DT101), and on midrib' (DT76)		
As above	Glossopteri- dales: <i>Ottokaria</i> <i>transvaalensis</i>	leaves	pl. 63, fig. 1, pl. 64, fig. 3	Margin feeding across most of apex (DT13); deeply incised, narrow trench feeding between veins (or alternatively a pre- senescence tear in the leaf)				Elliptical oviposition scars, between veins, parallel to venation (DT101), and on midrib (DT76); row of oviposition scars on midrib, decreasing in size acropetally (new DT)			
As above	Glossopteri- dales: <i>Ottokaria</i> <i>ferrugistratum</i>	leaves	pl. 66, figs 1, 3a	C-shaped margin feeding (DT12)				Elliptical oviposition scars, between veins, parallel to venation (DT101), and on midrib (DT76)			
As above	Glossopteri- dales: <i>Scutum</i> <i>rubidgeum</i>	leaves	pl. 67, fig. 22; pl. 68, fig. 12; pl. 69, figs 1, 2; pl. 70, fig. 6	Arcuate, C- and V-shaped margin feeding (DT12)	Small, elliptical hole feeding (DT02)						
As above	Glossopteri- dales: <i>Scutum</i> <i>draperium</i>	leaves	pl. 71, fig. 2; pl. 72, fig. 1		Possible polylobate hole feeding on midrib (DT03)	U-shaped lesion of disrupted tissue (DT97); (possibly fungal damage linked to oviposition scar)		Oviposition scars on midrib (DT76)			
As above	Glossopteri- dales: <i>Hirsutum</i> <i>duitoitides</i>	leaves	pl. 75, figs 1, 2, 6; pl. 76, figs 1, 2, 5	Arcuate, scalloped and C-shaped margin feeding (DT12)		Polylobate lesions with well-defined reaction rim, possibly surface feeding (DT30)	Possible punctures, over veins of midrib (DT53)	Scattered oviposition scars (DT101)			

As above	Glossopteri- dales: <i>Hirsutum</i> <i>intermittens</i>	leaves	pl. 78, figs 18, 19; pl. 79, figs 1, 3, 4, 5; pl. 80, figs 1–8	Assorted margin feeding styles, with very pronounced reaction rims; deeply incised, polylobate feeds and keyhole feeding (DT15), scalloped continuous feeding traces, C-shaped feeding (DT12); feeding across leaf apex (DT13); deeply incised arcuate feeding, to midrib (DT14)	Small, elliptical hole feed (DT02)	C-shaped and polylobate regions with diffuse reaction rims (DT29); necrotic, polylobate lesions with pronounced reaction rim (DT30); almost rectangular region with edges constrained by venation and sharp reaction rim, but very broad, diffuse reaction tissue	Possible punctures, over veins of midrib (DT53) and on loamina	Scattered, elliptical and tiny circular oviposition scars on lamina (DT101) orientated parallel to venation, and on midrib (DT76)	
As above	Glossopteri- dales: <i>Lanceolatus</i> <i>lerouxides</i>	leaves	pl. 87, figs 1, 2, 5, 7; pl. 88, figs 1, 2, 3, 4, 5	U-shaped, deeply incised margin feeding (DT15); C-shaped and cusped margin feeding (DT12) with associated necrotic tissue; feeding across apex of leaf (DT13)		Large, U-shaped to polylobate lesions extending from leaf margin, with clear reaction rim and little interior disruption of tissues (cf. DT130)	Possible piercing and sucking in cluster (DT 46) from midrib onto lamina, and scattered on midrib	Circular and narrowly elliptical oviposition on lamina, orientated parallel to venation (DT101) and on midrib (DT76)	
As above	Glossopteri- dales: <i>Lanceolatus</i> <i>strictus</i>	leaves	pl. 89, fig. 1, pl. 91, fig. 3	V-shaped margin feed (DT12)				Circular oviposition scars on lamina (DT101) and on midrib (DT76)	
As above	Glossopteri- dales: <i>Arberia</i> <i>leukitensis</i>	leaves	pl. 107, figs 1, 3, 4, 5; pl. 108, fig. 3, 6	V-shaped margin feed (DT12)	Polylobate hole feeding (DT03)			Elliptical oviposition scars, parallel to venation (DT101), oviposition on midrib (DT76)	
As above	Ginkgoales: <i>Sphenobaiera</i> <i>eccensis</i>	leaves	pl. 148, figs 6--8	C-shaped margin feed (DT12)				Small, circular punctures over a vein (DT46)	Very small, elliptical oviposition scars, between veins, in rows or scattered (DT101)

As above	Ginkgoales?: <i>Metreophyllum lerouxii</i>	Leaves	pl. 149, figs 1, 2; pl. 150, fig. 5						Small, circular punctures over a vein, in linear arrangement (DT138)	Elongate-elliptical oviposition scars in cluster (DT100), and scattered on lamina (DT101), most parallel to veins, but some subparallel		
As above	Ginkgoales: <i>Ginkgo-phyllum kidstonii</i>	leaves and stems	pl. 152, fig. 4	Large, triangular, apical margin feed (DT12)	Deeply incised, polylobate hole feeding (DT15)					Small, elliptical oviposition scars (DT101)		
As above	Ginkgoales: <i>Flabellifolium</i> sp. A	leaf	pl. 154, fig. 6							Circular to elliptical oviposition scars (DT101)		
As above	Cordaitales: <i>Noeggerathioopsis elongata</i>	leaf	pl. 157, fig. 2						Cluster of circular punctures (DT46)	Elliptical to spindle-shaped oviposition scars parallel to venation (DT101)		
As above	Incertae sedis: <i>Taeniopteris gemmina</i>	leaf	pl. 165, figs 3, 5, 7		Possible C-shaped margin feeding; DT12					Scattered oviposition, elliptical and parallel to venation (DT101), possible oviposition on midrib (DT76)		
As above	Incertae sedis: <i>Botrychiopsis valida</i>	leaves/ fronds	pl. 167, fig. 4	Arcuate margin feeding (DT12), and deeply incised trench feeding (DT15)								
Vryheid Formation; Artinskian-Roadian; Hlobane C.	Glossopteri- dales: <i>Arberia hlobanensis</i>	leaves, seeds	pl. 103, figs 10, 11; pl. 104, figs 3, 6b	Broad, deeply incised trench feeding (DT15) with diffuse discoloured band near margin, flanking feeding trace; large, deeply incised V-shaped margin feed (DT15), extending almost to midrib	Darkly-stained, polylobate lesion (DT38) against margin of leaf					Elliptical oviposition scars on lamina, parallel to venation (DT101); Possible oviposition on midrib (DT76)		
As above	Comifers: <i>Podocamites hlobanensis</i>	leaves	pl. 162, figs 11, 17, 18, 20	Arcuate margin feeding (DT12); feeding across apex (DT13) with necrotic lesion (possibly secondary fungal or bacterial infection)	Small, elliptical hole feeds (DT01)				Dense aggregation of punctures with associated necrotic lesion			

Table 3—Compendium of published records of insect and other terrestrial arthropod body fossils from the Permian of Gondwana, sorted according to geographic region and taxonomic order.

Authors, year and figure	Age	Stratigraphic unit	Locality, Basin, Country	Species/taxon	Order and/or Family	Inferred feeding style
Africa						
Zeuner, 1955	Lopingian	Lower Beaufort Group	Madzivadzido, Serami River, Sebungu District, Zimbabwe	<i>Rhodesiomylacris bondi</i>	Order Blattodea, Family Mylacridae (Cockroaches)	Where preserved, Blattodea typically possess generalized chewing mandibles, and comparable modern forms exhibit omnivorous diets, including widespread herbivory and detritivory.
Riek, 1976a, fig. 1.	Cisuralian	Hammanskraal Formation (Vryheid Formation equivalent)	Hammanskraal, South Africa	<i>Syrciophlebia kovacsae</i>	Order Blattodea, Family Spiloblattinidae (Cockroaches)	
Miller, 1952; Schlüter, 1997	Lopingian	Maji ya Chumvi Formation	Core, 60 km west of Mombasa, Kenya	Undescribed Blattodea	Order Blattodea, Family Mesoblattinidae (Cockroaches)	
Riek, 1976b, pl. 3, figs 3, 5.	Permian, Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Phyllelytron aeminatum</i>	Order Protelytroptera, Family Protoleidae (Extinct Order, resemble cockroaches, probable stem-group earwigs)	
Riek, 1976b, pl. 1, fig. 8.	Permian, Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Paolekia penditae</i>	Order Protoblattodea, Family Paoliidae (Cockroaches)	
Geertsema & van den Heever, 1996; Geertsema <i>et al.</i> , 2002, fig. 6.	Cisuralian	Whitehill Formation	Worcester, Western Cape Province, South Africa	<i>Afrocupes firmae</i>	Order Coleoptera (Beetles)	Extant Coleoptera have an extremely broad range of feeding styles. In fossil examples, unless the mouthparts are preserved it is difficult to assess the feeding ecology. Permian Coleopterans are likely responsible for various signs of leaf damage (direct herbivory), wood boring and detritivory.
Oelofsen, 1981	Cisuralian	Whitehill Formation	Northwestern part of Karoo Basin, South Africa	Undescribed Coleopteran wing	Order Coleoptera (Beetles)	
Prevec <i>et al.</i> 2009, pl. 14, figs 1, 2.	Lopingian	Normandien Formation	Clouston Farm Locality, Colenso, South Africa	Unidentified Grylloblattid	Order Grylloblattida (Rock crawlers)	Though diverse during the Permian, there is only one known extant family of Grylloblattida. Modern Grylloblattida are omnivorous, with a preference for carnivory and scavenging other arthropod remains. However, they can also consume plant matter via herbivory or detritivory, particularly as nymphs. Many extinct forms may have been predators.
Riek, 1976a, figs 2, 3.	Cisuralian	Hammanskraal Formation (Vryheid Formation equivalent)	Haakdoornfontein, South Africa	<i>Thaumatophora pronotalis</i> (Nymph)	Order Grylloblattida (Rock crawlers)	

Riek, 1973; van Dijk, 1997	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Liomopteroides similis</i>	Order Grylloblattida <i>incertae sedis</i> (Rock crawlers)	
Aristov <i>et al.</i> , 2009, fig. 2A.	Lopingian	Emakwezini Formation	Kwa Yaya, KwaZulu-Natal, Lebombo Basin, South Africa	<i>Iphikozulu kwayaywaensis</i>	Order Grylloblattida, Family Chaulioditidae (Rock crawlers)	
Riek, 1976b, pl. 1, fig. 7; Aristov <i>et al.</i> , 2009, fig. 2C.	Lopingian	Emakwezini Formation (Normandien Formation equivalent)	Emakwezini Railway Station locality, South Africa	<i>Neoliomopterum picturatum</i>	Order Grylloblattida, Family Liomopteridae (Rock crawlers)	
van Dijk, 1981, fig. 54; van Dijk, 1997.	Lopingian	Normandien Formation	Lidgettton Locality, South Africa	<i>Mioptera stuckenbergi</i>	As above	
Riek, 1976b; van Dijk, 1997	Lopingian	Normandien Formation	Lidgettton Locality, South Africa	<i>Miopteroideis andrei</i>	As above	
Riek, 1976b, pl. 1, fig. 5; van Dijk, 1997	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Miopteroideis andrei</i>	As above	
Riek, 1973; Riek, 1976b, pl. 1, figs 2, 3; van Dijk, 1997	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Mioptera stuckenbergi</i>	As above	
Riek, 1976b	Lopingian	Normandien Formation	Bulwer Locality, South Africa	<i>Miopterina tenuipennis</i>	Order Grylloblattida, Family Megakhosaridae (Rock crawlers)	
Riek, 1976b, pl. 1, fig. 4; van Dijk, 1997	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Miopterina tenuipennis</i>	As above	
Pretorius <i>et al.</i> , 2021, fig. 3.	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass Locality, Southern Karoo Basin, South Africa	<i>Mioptera stuckenbergi</i>	Order Grylloblattodea, Family Liomopteridae (Rock crawlers)	
Pretorius <i>et al.</i> , 2021, fig. 4.	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass Locality, Southern Karoo Basin, South Africa	<i>Mioptera</i> sp.	As above	
Prevec <i>et al.</i> , 2010, fig. 6C	Changhsingian	<i>Dicynodon Assemblage Zone</i> of the Beaufort Group	New Wapadsberg Pass Locality, South Africa	Hemipteran nymph	Order Hemiptera (Bugs)	Most extant hemipterans are phytophagous, and employ their distinctive piercing and sucking mouthparts to puncture holes in vegetation and extract plant sap. Some Hemiptera are also predatory. During the Permian, hemipterans may have been responsible for many of the signs of mucivory in fossil plant remains.
Riek, 1976b, pl. 5, fig. 5.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	Unidentified Hemipteran nymph	Order Hemiptera, Homoptera (Bugs)	
Riek, 1976b, pl. 4, fig. 4.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Neurobole ramosa</i>	Order Hemiptera, Homoptera, Family Cicadopsobolidae (Bugs)	

Riek, 1973; Riek, 1976b, pl. 4, fig. 5.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Austroprosboleoides vandijki</i>	Order Hemiptera, Homoptera, Family Cicadoprosoboldae (Bugs)	
Riek, 1973; Riek, 1976b, pl. 5, fig. 2.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Dysmorphosearella lobata</i>	Order Hemiptera, Homoptera, Family Eoscartarellidae (Bugs)	
Riek, 1973	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Ignotala miriflora</i>	Order Hemiptera, Homoptera, Family Ignotalidae (Bugs)	
Riek, 1973; Riek, 1976b, pl. 4, fig. 1.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Megoniella multinerva</i>	As above	
Riek, 1976b, pl. 4, fig. 2.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Perissovena heidiae</i>	Order Hemiptera, Homoptera, Family Pereboriidae? (Bugs)	
Riek, 1974; Riek, 1976b; Geertsema <i>et al.</i> , 2002, fig. 5	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Aleuromyropa bibulla</i> (Nymph)	Order Hemiptera, Homoptera, Family Permaleurodidae, Sternorrhynchan nymph (Bugs, aphids)	
Riek, 1976b, pl. 5, figs 1, 3.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Beaufortiseus dixi</i>	Order Hemiptera, Homoptera, Family Prosoboldae (Bugs)	
Riek, 1976b, pl. 5, fig. 4.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Protopsyllidium lynae</i>	Order Hemiptera, Homoptera, Family Protopsyllidiidae (Bugs)	
Riek, 1976b, pl. 4, fig. 3.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Orthoseytina dubitata</i>	Order Hemiptera, Homoptera, Family Scytinopteridae (Bugs)	
Riek, 1973	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Redaetinaura aequinata</i>	Order Hemiptera, Homoptera, Family Uninervidae (Bugs)	
Pretorius <i>et al.</i> , 2021, fig. 6.	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass, southern Karoo Basin, South Africa	Unidentified immature nymph	Order Hemiptera, Suborder Auchenorrhyncha (Bugs)	
Pretorius <i>et al.</i> , 2021, fig. 5.	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass, southern Karoo Basin, South Africa	<i>Permocicada</i> sp.	Order Hemiptera, Suborder Auchenorrhyncha, Family Prosoboldae (Bugs)	
van Dijk & Geertsema, 1999, fig. 32.	Lopingian	Normandien Formation	Mount West, Mooi River Locality, South Africa	<i>Afrostenivicia rediae</i>	Order Hemiptera, Suborder Homoptera, Family Ipsviciidae (Bugs)	
van Dijk & Geertsema, 1999, fig. 23.	Lopingian	Normandien Formation	Lidgetton Locality, South Africa	<i>Permocicada thompsoni</i>	Order Hemiptera, Suborder Homoptera, Family Prosoboldae (Bugs)	
van Dijk & Geertsema, 1999, fig. 31.	Lopingian	Normandien Formation	Balgowan, near Lidgetton Locality, South Africa	<i>Stenotegmocicada triclades</i>	As above	
Prevec <i>et al.</i> , 2009, pl. 14, figs 3, 4.	Lopingian	Normandien Formation	Clouston Farm Locality, Colenso, South Africa	Sternorrhynchan nymphs	Order Hemiptera, Suborder Sternorrhyncha (Bugs, aphids)	

McLachlan & Anderson, 1977, fig. 2.	Cisuralian	Whitehill Formation	Modderdrift Locality, Southern Karoo Basin, South Africa	Undescribed fragmentary Mecopteran wings	Order Mecoptera (Scorpionflies)	Many extant Mecoptera have long beak-shaped rostra, which they use for predation or scavenging. Some Palaeozoic Mecoptera may have played a role as pollinators of gymnosperms.
Pinto & De Omellas, 1978c	Cisuralian	Whitehill Formation	Worcester, Western Cape Province, South Africa	<i>Afrochoristella maclachlani</i>	Order Mecoptera (Scorpionflies)	
Riek, 1976b	Lopingian	Normandien Formation	Mooi River Locality, South Africa	Unidentified	Order Mecoptera, Family Nannochoiristidae? (Scorpionflies)	
Riek, 1973	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Agetochoiristella similis</i>	Order Mecoptera, Family Agetopanorpidae (Scorpionflies)	
Riek, 1976b, pl. 6, figs 4, 5, 7.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Prochoristella hartmani</i>	Order Mecoptera, Family Mesopanorpididae (Scorpionflies)	
van Dijk & Geertsema, 1999, fig. 51.	Lopingian	Normandien Formation	Balgowan, near Lidgetton Locality, South Africa	<i>Prochoristella balgowanensis</i>	As above	
van Dijk & Geertsema, 1999, fig. 53.	Lopingian	Normandien Formation	Bulwer Locality, South Africa	<i>Prochoristella bulwerensis</i>	As above	
van Dijk & Geertsema, 1999, fig. 57.	Lopingian	Normandien Formation	Bulwer Locality, South Africa	<i>Neochoristella goodalli</i>	Order Mecoptera, Family Nannochoiristidae (Scorpionflies)	
Riek, 1976b, pl. 6, figs 1, 2.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Mesochorista australica</i>	Order Mecoptera, Family Permochoiristidae (Scorpionflies)	
Riek, 1976b, pl. 6, fig. 3.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Mesochorista channingi</i>	As above	
van Dijk & Geertsema, 1999, fig. 47.	Lopingian	Normandien Formation	Bulwer Locality, South Africa	<i>Calliethira granthami</i>	Order Mecoptera, Family Permochoiristidae (Scorpionflies)	
Riek, 1973, pl. 3 figs 2, 4.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Permonka bifida</i>	Order Miomoptera, Family Permosialidae (Extinct Order)	Where preserved, the mouthparts of Miomoptera consist of unspecialised chewing mandibles. Evidence from gut contents has indicated palynophagy, and feeding on gymnosperm strobili Novokshonov & Zhuzhgovva (2004).
Riek, 1976b, pl. 6, fig. 6	Lopingian	Normandien Formation	Mooi River Locality, South Africa	Unidentified	Order Neuroptera, Family Archeosmylidae (Lacewings)	Extant Neuroptera typically possess simple chewing mandibles. The larvae of extant Neuroptera are usually predatory, and possess elongate mandibles specialized for piercing and sucking insect prey. Many living adult Neuroptera are also predators, however, some also consume nectar.

Riek, 1976b, pl. 6, fig. 8	Permian, Lopingian	Beaufort Group, Normandien Formation	Mooi River Locality, South Africa	<i>Sismeroobius pusillus</i>	Order Neuroptera, Family Palaeomerobidae (Lacewings)	Extant Orthoptera are major plant herbivores, and possess mandibulate mouthparts adapted for biting and chewing leaf matter. Orthopterans or stem-orthopterans may have been responsible for many of the signs of leaf-margin feeding on fossil leaves from the Permian.
McLachlan & Anderson, 1978, fig. 3.	Cisuralian	Ecce Group, Whitehill Formation	Krantzpoort Locality, southern Karoo Basin, South Africa	Undescribed Protorthopteran wings	Order Protorthoptera (Paraphyletic, basal Neoptera)	
Riek 1974b, fig. 1.	Earliest Permian	Dwyka Series	Zimbabwe	<i>Hadentomoides dwykensis</i>	Order Protorthoptera, Family Hadentomoidae (Paraphyletic, basal Neoptera)	
Pruvost, 1934	Cisuralian	Base of Ecce Group	Democratic Republic of Congo	<i>Boutakovia saleei</i>	As above	
Pretorius <i>et al.</i> , 2021, fig. 2a.	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass Locality, Southern Karoo Basin, South Africa	Genus and species unidentified	Order Orthoptera (Grasshoppers, crickets)	
Riek, 1976b, pl. 2, fig. 2.	Permian, Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Eolocustopsis primitiva</i>	Order Orthoptera, Family Locustopsidae (Grasshoppers, crickets)	
Geertsema & van Dijk, 1999; Geertsema <i>et al.</i> , 2002, fig. 7.	Cisuralian	Laingsburg Formation	Laingsburg, Western Cape Province, South Africa	<i>Afrodoeschia oosthuizeni</i>	Order Orthoptera, Family Oedischidae (long-horned orthopteran, Grasshoppers, crickets)	
Riek, 1976b, pl. 2, fig. 1.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Protettavus exilis</i>	Order Orthoptera, Family Tettavidae (Grasshoppers, crickets)	
Riek, 1976b, pl. 1, fig. 1.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Karoohymen delicatulus</i>	Order Palaeodictyopteroidea, Suborder Megaseoptera, Family Scythohymenidae (Paraphyletic)	Where preserved, the mouthparts of Palaeodictyoptera comprise distinctive elongate piercing-and-sucking mouthparts.
van Dijk & Geertsema, 1999, fig. 1.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Karoohymen minutus</i>	Order Palaeodictyopteroidea, Suborder Megaseoptera, Scythohymenidae (Paraphyletic)	
Pretorius <i>et al.</i> , 2021, fig. 2b.	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass Locality, southern Karoo Basin, South Africa	Genus and species unidentified	Order Paoliida, Family Anthracoptilidae (Extinct neopteran sister group of Dictyoptera)	
Pinto & De Ornellas, 1978c	Cisuralian	Whitehill Formation	Worcester, Western Cape Province, South Africa	<i>Sharovia permiafricana</i>	Order Paraplecoptera (Stoneflies)	Modern Plecoptera (stoneflies) usually comprise aquatic nymphs and terrestrial adults. They possess simple chewing mandibles. The nymphs may feed on submerged vegetation, or engage in active predation. In extant forms, many of the adults do not feed, but some are herbivorous.

Riek, 1973; Riek, 1976b, pl. 1, fig. 6.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Liomopterina clara</i>	Order Paraplecoptera, Family Liomopteridae (Stoneflies)	
Paulian, 1965, fig. 2; Pinto & De Ornellas, 1978	Cisuralian	'Serie à Charbon'	Mavonono River, Madagascar	<i>Narkemina</i> sp. 'D'	Order Paraplecoptera, Family Narkemocacurgidae (Stoneflies)	
Riek, 1973; Riek, 1976b, pl. 2, fig. 3.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Euxenoperla simplex</i>	Order Plecoptera, Family ?Gripopterygidae (Stoneflies)	
Riek, 1973; Riek, 1976b, pl. 2, fig. 4.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Euxenoperla similis</i>	Order Plecoptera, Family ?Gripopterygidae (Stoneflies)	
Riek, 1976b, pl. 2, fig. 5.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Euxenoperla oliveri</i>	Order Plecoptera, Family ?Gripopterygidae (Stoneflies)	
Riek, 1976b, pl. 3, fig. 1.	Lopingian	Normandien Formation	Mooi River Locality, South Africa	<i>Euxenoperla jaequesi</i>	Order Plecoptera, Family ?Gripopterygidae (Stoneflies)	
van Dijk & Geertsema, 2004, fig. 1.	Lopingian	Normandien Formation	Bulwer Locality, South Africa	<i>Afroperla permiana</i>	Order Plecoptera, Family Palaeonemouridae (Perlaria, Stoneflies)	
Pretorius <i>et al.</i> , 2021, fig. 7.	Changhsingian	Elandsberg Member, Balfour Formation	Wapadsberg Pass Locality, southern Karoo Basin, South Africa	Unidentified abdomen of an insect	Order unknown	
Riek, 1976c, figs 1–4.	Cisuralian	Hammanskraal Formation (Vryheid Formation equivalent)	Haakdoorn-fontein, South Africa	<i>Permobrya mirabilis</i>	Order Collembola, Family Entomobryidae (Hexapod, Collembolan)	Extant collembolans are generally omnivorous, and engage in active herbivory and detritivory.
Antarctica						
Plumstead, 1962a	Permian		Theron Mountains, Filchner Ice Shelf	Homopterous insect wing	Order Hemiptera, Suborder Homoptera (Bugs)	Most extant hemipterans are phytophagous, and employ their distinctive piercing and sucking mouthparts to puncture holes in vegetation and extract plant sap. Some Hemiptera are also predatory. During the Permian, hemipterans may be responsible for many of the signs of hole-feeding in fossil plant remains.
Tasch & Riek, 1969	Permian	Polar-Star Formation	Polestar Peak, Sentinel Mountains, Antarctica	Homopterous insect wing	Order Hemiptera, Suborder Homoptera, Family Stenoviciidae? (Bugs)	
Carpenter, 1969, figs. 4, 5; Tasch, 1972, fig. 1.	mid-late Permian	Mount Glossopteris Formation	Leaia Ledge, Ohio Range, Antarctica	<i>Uralonympha schopfi</i> (Nymph)	Order Perlaria (Stoneflies)	<i>Uralonympha schopfi</i> was likely a generalist/ herbivore. Found on same bedding plane as conchostrachans, and in association with <i>Glossopteris</i> fragments.
Slater <i>et al.</i> , 2012, fig. 2; Slater <i>et al.</i> , 2015, fig. 6G.	Guadalupian (Roadian-Wordian)	Toploje Member of the lower Baimmedart Coal Measures	Prince Charles Mountains, Antarctica	Unknown - acid-macerated arthropod cuticle fragments	Order unknown	

Australia Tillyard, 1924; Jell, 2004	Lopingian (?early Changhsingian)	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Permosyne belmontensis</i>	Order Coleoptera (beetles)	Extant Coleoptera exhibit an extremely broad range of feeding styles. In fossil examples, unless the mouthparts are preserved it is difficult to assess the feeding ecology. Permian Coleopterans are likely responsible for various signs of leaf damage (direct herbivory), wood boring and detritivory.
Tillyard, 1924; Jell, 2004	Lopingian (?early Changhsingian)	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Permosyne affinis</i>	As above	
Tillyard, 1924; Jell, 2004	Lopingian (?early Changhsingian)	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Permosyne mitchelli</i>	As above	
Tillyard, 1924; Jell, 2004	Lopingian (?early Changhsingian)	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Permosyne pincombeae</i>	As above	
Yan <i>et al.</i> , 2017, figs 1, 3.	Lopingian (?early Changhsingian)	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Ponomarenkia belmonthensis</i>	Order Coleoptera, family Ponomarenkiidae (beetles)	
Ponomarenko <i>et al.</i> , 2020, fig. 2.	Lopingian (?early Changhsingian)	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Gondwanocoleus chikatunovi</i>	Order Coleoptera, suborder Archostemata, family Asiocoleidae (Beetles)	
Riek, 1953; Bethoux <i>et al.</i> , 2007	Lopingian (?early Changhsingian)	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Eoglosselytrum perplexa</i>	Order Glosselytrodea (Extinct Order)	Unknown
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation, Newcastle Coal Measures	Australia, Sydney Basin	<i>Austroscytina imperfecta</i>	Order Hemiptera (Bugs)	Most extant hemipterans are phytophagous, and employ their distinctive piercing and sucking mouthparts to puncture holes in vegetation and extract plant sap. Some Hemiptera are also predatory. During the Permian, hemipterans may be responsible for many of the signs of hole-feeding in fossil plant remains.
Evans, 1958; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Bekkerscytina primitiva</i>	As above	
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Eopsyllidium delicatulum</i>	As above	
Evans, 1958; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Eoscytina migdisovae</i>	As above	
Evans, 1958; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Eoscytina incompleta</i>	As above	
Evans, 1963; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Tychiticoloides belmontensis</i>	As above	

Evans, 1958; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Belmontocarta perfecta</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Eochiloiocycla angusta</i>	As above
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Paraknightia magnifica</i>	As above
Tillyard, 1922; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Pincombea mirabilis</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Eupincombea postica</i>	As above
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Protopincombea obscura</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Anomaloscytina metapteryx</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Anomaloscytina incompleta</i>	As above
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Austroprosbole maculata</i>	As above
Tillyard 1921; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Michelloneura permiana</i>	As above
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permodiphthera robusta</i>	As above
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Belpsylla reticulata</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Clavopsyllidium minutum</i>	As above
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permosyllidium mitchelli</i>	As above
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permosyllidium affine</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permosyllidops stanleyi</i>	As above
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permosyloides insolita</i>	As above
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permothea latipennis</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permotheella scytinopteroides</i>	As above
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Protopsyllidium australe</i>	As above
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Protopsyllidium sinuatum</i>	As above
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Protopsyllops minuta</i>	As above

Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Psocopsyllidium media</i>	As above	
Davis, 1942; Jell, 2004	Permian, Lopingian (?early Changhsingian)	Croudace Bay Formation	Australia, Sydney Basin	<i>Psocoscytina bifida</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Psyllidella magna</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Psyllidiana davisia</i>	As above	
Evans, 1956; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Tripsyllidium wadei</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Elliptoscarta ovalis</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Homaloscytina plana</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina mitchelli</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina quinquemedia</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina indistincta</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina subcostalis</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina irregularis</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina belmontensis</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina obliqua</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina pincombei</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Orthoscytina tetraeneura</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permobrachus dubia</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permobrachus magnus</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permoglyphis belmontensis</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permojassus australis</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permojassus dubius</i>	As above	

Evans, 1947; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Stenoglyphis kimblensis</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Stenoscytina australiensis</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Palaeoviccia incerta</i>	As above	
Evans, 1943a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permagra distincta</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permocentrus trivenulatus</i>	As above	
Tillyard, 1918; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permoscarta mitchelli</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permoviccia obscura</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Stanleyana pulchra</i>	As above	
Evans, 1943b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Stenoviccia angustata</i>	As above	
Beattie, 2007	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	undescribed protopsyllid	As above	
Chapman, 1932; Pickett, 1984	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Pincombella belmontensis</i> (originally described as a limuloid chelicerate arthropod)	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Aphryganoneura anomala</i>	Order Mecoptera (scorpionflies)	Many extant Mecoptera have long beak-shaped rostra, which they use for predation or scavenging. Some Palaeozoic Mecoptera may have played a role as pollinators of gymnosperms.
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Agetochoristella adscita</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Neoaegeta elongata</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Neopetromantis australis</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Phipoides elegans</i>	As above	
Tillyard, 1919; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Belmontia mitchelli</i>	As above	
Tillyard, 1922; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Parabelmontia permiana</i>	As above	

Tillyard, 1918; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Mesochorista austratica</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Mesochorista jucunda</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Mesochorista dubia</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Mesochorista phipa</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Parachorista pincombeae</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Parachorista splendida</i>	Order Mecoptera (scorpionflies)	
Tillyard, 1922; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Parachorista bairdae</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Parachorista warrenensis</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Mesopanorpodes belmontensis</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Mesopanorpodes robustus</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Prochoristella megaloprepia</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Prochoristella anagaura</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Prochoristella exilis</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Prochoristella pusilla</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Prochoristella belli</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Prochoristella concinna</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Nannochoristella reducta</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Neochoristella optata</i>	As above	
Martynova, 1948; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Robinjohnia tillyardi</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permomerpe australis</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permomerpe nanus</i>	As above	

Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permotamyderus ableptus</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Choristotamyderus nanus</i>	As above	
Tillyard, 1929; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permotipula patricia</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Xenochorista splendida</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Xenochorista sobrina</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Archeosmylus pectinatus</i>	Order Neuroptera (Lacewings)	Extant Neuroptera typically possess simple chewing mandibles. The larvae of extant Neuroptera are usually predatory, and possess elongate mandibles specialised for piercing and sucking insect prey. Many living adult Neuroptera are also predators, however, some also consume nectar.
Tillyard, 1922; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permithone belmontensis</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permithone oliarcooides</i>	As above	
Riek, 1953; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permithone neoxenus</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permithone pincombeae</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permotpsychops belmontensis</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permorapisma biserialis</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permorapisma triserialis</i>	As above	
Tillyard, 1935b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Polytaxineura stanleyi</i>	Order Odonata (Dragonflies)	All larvae, nymphs and adults of living Odonata (and likely extinct Protodonata) are predatory.
Tillyard, 1935c; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Stenoperlidium permianum</i>	Order Plecoptera (Perlaria) (Stoneflies)	Modern Plecoptera (stoneflies) usually comprise aquatic nymphs and terrestrial adults. They possess simple chewing mandibles. The nymphs may feed on submerged vegetation, or engage in active predation. In extant forms, many of the adults do not feed, but some are herbivorous.
Tillyard, 1935c; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Stenoperlidium anomala</i>	Order Plecoptera (Perlaria) (Stoneflies)	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Austrelyron tillyardi</i>	Order Protelytroptera (Order extinct)	Extant Dermaptera are omnivorous scavengers and predators

Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Phyllelytron folium</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Phyllelytron granulatum</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Phyllelytron melinum</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Phyllelytron petalon</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Chanoselytron gingiva</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Dermelytron conservativum</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Dermelytron pigmentatum</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Psychelelytron progressivum</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Elythrathrix hirsuta</i>	As above	
Tillyard, 1924; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permophilus pincombei</i>	As above	
Tillyard, 1924; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permophilus minor</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permophilus hirtus</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permophilus capulus</i>	As above	
Tillyard, 1918; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permophilgor belmontensis</i>	As above	
Tillyard, 1922; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Permophilgor indistinctus</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Labidelelytron enervatum</i>	As above	
Kukalová, 1966; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Xenelelytron ligula</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Megapsocidium australe</i>	Order Psocoptera (Psocids, Barklice, Barkflies)	Living Psocoptera typically possess chewing mandibles, and often feed on fungi, algae, lichen and organic detritus.
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Stenopsocidium australe</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Zygopsocus permianus</i>	As above	

Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Austrocypha abrupta</i>	Order Thysanoptera (Thrips)	Extant thrips are tiny (<1 mm) and possess distinctive asymmetrical mouthparts used to pierce plant tissues suck up the sap. Some extant thrips are also predatory, and others feed on pollen (and are involved in pollination), or on fungal spores. It has been hypothesised that their ancestral diet was fungivorous. Some extant thrips are also known to produce plant galls.
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Austrocypha baretti</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Lophiocypha permiana</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Lophiocypha stanleyi</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Lophiocypha thysanella</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Lophiocypha maxima</i>	As above	
Tillyard, 1921; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Lophioneura ustulata</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Lophioneura angusta</i>	As above	
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Lophioneura conjuncta</i>	As above	
Tillyard, 1935a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Zoropsocus delicatulus</i>	As above	
Davis, 1942; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Zoropsocus stanleyi</i>	As above	
Tillyard, 1926b; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Cladochorista belmontensis</i>	Order Trichoptera (caddisflies)	In living forms, the aquatic larvae display a range of feeding strategies, including predation, herbivory/detrivory of plant leaves, algal grazing, or filter feeding in water (often using a silk net-like contraption). Among extant trichopterans the majority of adult forms do not feed, but some are nectivorous.
Tillyard, 1926a; Jell, 2004	?early Changhsingian	Croudace Bay Formation	Australia, Sydney Basin	<i>Actinoscytina belmontensis</i>	Order Hemiptera, Suborder Heteroptera (True/Typical Bugs)	Most extant hemipterans are phytophagous, and employ their distinctive piercing and sucking mouthparts to puncture holes in vegetation and extract plant sap. Some Hemiptera are also predatory. During the Permian, hemipterans may be responsible for many of the signs of mucivory in fossil plant remains.

India	Earliest Permian	Talchir Formation	Borehole core, Daltongunj Coalfield in Bihar, India	<i>Rajiharablatta laskarii</i>	Order Blattodea (cockroaches)	Where preserved, Blattodea typically possess generalized chewing mandibles, and comparable modern forms have omnivorous diets, including widespread herbivory and detritivory.
Pinto <i>et al.</i> , 1992, fig. 5; Kapoor <i>et al.</i> , 1993	Cisuralian	Mamali Formation	Baliarpatti Spur, Kashmir Basin		As above	
Pant & Srivastava, 1995, fig. 7.	Cisuralian	Mamali Formation	Mamali Nala Section, Liddar Valley, Kashmir	<i>Triassoblatta natalensis</i>	As above	
Pant & Srivastava, 1995, fig. 8.	Cisuralian	Kamthi Formation/ Mamali Formation	Handappa Bed, Hinjrida Ghati, Orissa, Kashmir	<i>Aisoblatta</i> sp.	As above	
Srivastava 1988a, figs. 1, 2; Pinto <i>et al.</i> , 1992, fig. 4; Srivastava, 1998b, fig. 3	Guadalupian	Barakar Formation	Raniganj Coalfield, India	Unnamed insect wing	Order Blattodea, Family Archimyliacridae (cockroaches)	
Hislop, 1861	Permian	Kota-Maleri beds	Maharashtra, India	Unnamed wing covers of Blattidae	Order Blattodea, Family Blattidae (cockroaches)	
Handlirsch, 1906; Pinto <i>et al.</i> , 1992, fig. 1.	Cisuralian	Gangamopteris Beds	Risin Spur, Srinagar, Kashmir Basin	<i>Gondwanoblatta reticulata</i>	As above	
Bana, 1964; Pinto <i>et al.</i> , 1992, fig. 2.	Cisuralian	Mamali Formation	Risin Spur, near Srinagar, Kashmir Basin	<i>Prognoblattina columbina</i>	As above	
Verma, 1967; Pinto <i>et al.</i> , 1992, figs. 14, 15.	Cisuralian	Mamali Formation	Baliarpatti, near Marahom, Kashmir Basin	<i>Kashmiroblatta marahaomensis</i>	As above	
Srivastava, 1988b; Srivastava, 1996; Srivastava, 1998b, fig. 2.	Guadalupian	Barakar Formation	Raniganj Coalfield, India	<i>Kaltanicupes</i> sp.	Order Coleoptera (beetles)	Extant Coleoptera exhibit an extremely broad range of feeding styles. In fossil examples, unless the mouthparts are preserved it is difficult to assess the feeding ecology. In the Permian, Coleopterans are likely responsible for various signs of leaf damage (direct herbivory), wood boring and detritivory.
Srivastava, 1988b; Srivastava, 1996; Srivastava, 1998b, fig. 1.	Guadalupian	Barakar Formation	Raniganj Coalfield, India	<i>Probolepicada gondwanica</i>	Order Hemiptera, suborder Homoptera (Bugs)	Most extant hemipterans are phytophagous, and employ their distinctive piercing and sucking mouthparts to puncture holes in vegetation and extract plant sap. Some Hemiptera are also predatory. During the Permian, hemipterans may be responsible for many of the signs of hole-feeding in fossil plant remains.
Srivastava, 1988b; Srivastava, 1996	Guadalupian	Barakar Formation	Raniganj Coalfield, India	<i>Probole irattiensis</i>	Order Hemiptera, suborder Homoptera (Bugs)	

Srivastava, 1988b; Srivastava, 1996	Guadalupian	Barakar Formation	Raniganj Coalfield, India	<i>Asiachorista beuburgae</i>	Order Mecoptera (scorpionflies)	Many extant Mecoptera have long beak-shaped rostra, which they use for predation or scavenging. Some Palaeozoic Mecoptera may have played a role as pollinators of gymnosperms.
Srivastava, 1988b; Srivastava, 1996	Guadalupian	Barakar Formation	Raniganj Coalfield, India	<i>Petromantis evansi</i>	Order Mecoptera (scorpionflies)	
Chandra & Singh, 1996	Lowermost Permian	Talchir Formation	Talchir Coalfield, India	Unnamed insect wing	Order unknown	
Rao & Shah, 1959	Permian	Kota-Maleri beds	Pranhita, Godawari Basin, India	Unnamed dorsal impression of insect wing	Order unknown	
Feistmantel, 1880	Permian	Talchir Formation	West Bengal, Deogarh Basin, India	Unnamed insect wing	Order unknown	
Kumar <i>et al.</i> 2011, figs. 2, 3.	Cisuralian	Manjir Formation	Chamba Valley, Himachal Pradesh, India	<i>Acarus indicus</i>	Order Sarcoptiformes, suborder Oribatida, Astigmatina (arachnid mites)	Extant oribatid mites are exceptionally numerous in soil environments and leaf litter. They comprise a diverse clade of arachnid arthropods, and are among the major detritivores and fungivores of forest soils. Some Oribatid mites also inhabit the woody tissues of plants. Oribatid mites likely fulfilled a similar role in the Permian, and may be responsible for many of the smaller microcoprolites found among permineralized plant tissues and peats, and extracted by acid digestion.
South America						
Calisto & Piñeiro, 2019, fig. 3a, b, fig. 5.	Artinskian	Mangrullo Formation	El Baron locality, Cerro Largo county, Paraná Basin, Uruguay	<i>Barona arcuata</i>	Order Blattodea (Cockroaches)	Where preserved, Blattodea typically possess generalized chewing mandibles, and comparable modern forms have omnivorous diets, including widespread herbivory and detritivory.
Halle, 1911	Lopingian	Gondwana Series	Falkland Islands	Undescribed Blattodea	Order Blattodea (Cockroaches)	
Pinto & Sedor, 2000; Ricetti <i>et al.</i> , 2016, fig. 4, A1, B1, C1.	Asselian	Lontras Shale, Campo Moarão Formation, and Maíra Formation, Itararé Group	Campáleo outcrop, Santa Catarina, Paraná Basin, Brazil	<i>Anthracoblattina mendesi</i>	Order Blattodea, Family Phylloblattidae (Cockroaches)	
Pinto, 1972	Kungurian-early Kazanian	Irati Formation	Rio Grande do Sul, Paraná Basin, Brazil	<i>Aissoblatta</i> sp.	Order Blattodea, Family Spiloblattidae (Cockroaches)	
Pinto & Purper, 1979	Gzhelian-Asselian	Teixeira Soares Formation, Itararé Group	Teixeira Soares, Paraná State, Brazil	<i>Phylloblatta Paranáensis</i>	Order Blattodea, Family Archimiliacridae (Cockroaches)	
Pinto & Purper, 1979, Pl. 2 photo 5.	Gzhelian-Asselian	Teixeira Soares Formation, Itararé Group	Teixeira Soares, Paraná State, Brazil	<i>Phylloblatta sommeri</i>	As above	

Pinto & Purper, 1979, Pl. 2 photo 1.	Gzhelian-Asselian	Teixeira Soares Formation, Itarare Group	Teixeira Soares, Paraná State, Brazil	<i>Anthracoblattina oliveirai</i>	As above	As above
Petri, 1945; Pinto & Purper, 1979, Pl. 2 photo 2.	Gzhelian-Asselian	Teixeira Soares Formation, Itarare Group	Teixeira Soares, Paraná State, Brazil	<i>Phylloblatta roxoi</i>	As above	As above
Pinto & Purper, 1979, Pl. 2 photo 3.	Gzhelian-Asselian	Teixeira Soares Formation, Itarare Group	Teixeira Soares, Paraná State, Brazil	<i>Phylloblatta pauloi</i>	As above	
Pinto & Purper, 1979, Pl. 2 photo 6.	Gzhelian-Asselian	Teixeira Soares Formation, Itarare Group	Teixeira Soares, Paraná State, Brazil	<i>Anthracoblattina langei</i>	As above	
Pinto, 1972a	Gzhelian-Asselian	Rio Genoa Formation	Betancourt, Chubut Province, Argentina	<i>Archangelskyblatta vishniakovae</i>	As above	
Pinto & Mendez, 2002, Fig. 1a, b.	Gzhelian-Asselian	Rio Genoa Formation	Betancourt, Chubut Province, Argentina	<i>Anthracoblattina archangelski</i>	Order Blattodea, Family Phylloblattidae (Cockroaches)	
Pinto, 1987a; Adami-Rodrigues <i>et al.</i> , 2004, fig. 3A.	Kungurian-early Kazanian	Irrati/Serra Alta Formation	Brazil, Rio Grande do Sul, Minas do Leão municipality, Paraná Basin	<i>Kaltanicupes pomonarenkoi</i>	Order Coleoptera (Beetles)	Extant Coleoptera exhibit an extremely broad range of feeding styles. In fossil examples, unless the mouthparts are preserved it is difficult to assess the feeding ecology. In the Permian, Coleopterans are likely responsible for various signs of leaf damage (direct herbivory), wood boring and detritivory.
Pinto, 1987a; Adami-Rodrigues <i>et al.</i> , 2004b, fig. 3E.	Kungurian-early Kazanian	Irrati/Serra Alta Formation	Brazil, Rio Grande do Sul, Minas do Leão municipality, Paraná Basin	<i>Protocupoides rohdendorfi</i>	Order Coleoptera (Beetles)	
Martins-Neto <i>et al.</i> , 2007, fig. 10.	Gzhelian-Asselian	Itararé Sub-group, upper part of the Rio do Sul Formation	Taió municipality, State of Santa Catarina	<i>Taiophlebia niloriclasodae</i>	Order Grylloblattida (=Eoblattida), Family Protophasmatidae (Taiophlebiidae), (Rock crawlers)	Though diverse during the Permian, there is only one known extant family of Grylloblattida. Modern Grylloblattida are omnivorous, with a preference for carnivory and scavenging other arthropod remains. However, they can also consume plant matter via herbivory or detritivory, particularly as nymphs. Many extinct forms may have been predators.
Martins-Neto <i>et al.</i> , 2007, fig. 5.	Gzhelian-Asselian	Bajo de Véliz Formation	Argentina	<i>Velizphlebia cruzi</i>	Order Grylloblattida, Family Proedischidae (Rock crawlers)	
Martins-Neto <i>et al.</i> , 2007, fig. 9.	Gzhelian-Asselian	Bajo de Véliz Formation	Argentina	<i>Paganzophlebia polyclata</i>	Order Grylloblattida, Family Proedischidae (Rock crawlers)	
Pinto & De Ornellas, 1978a, pl. I, figs 4, 5, pl. II, figs 2, 3; Martins-Neto <i>et al.</i> , 2007	Gzhelian-Asselian	Bajo de Véliz Formation	Argentina	<i>Irajanarkemina rohdendorfi</i>	Order Grylloblattida, Family Proedischidae (Rock crawlers)	

Martins-Neto <i>et al.</i> , 2007	Gzhelian-Asselian	Bajo de Véliz Formation	Argentina	<i>Argentino-narkemina amosi</i>	Order Grylloblattida, Family Proedischidae (Rock crawlers)	
Pinto & Adami-Rodrigues, 1995, pl. 2.	Gzhelian-Asselian	Itararé Sub-Group, base of Tubarão Group	Core number 2-I.G.G, São Paulo State, Paraná Basin, Brazil	<i>Cacurgulopsis sanguinettiae</i>	Order Grylloblattida/Eoblattida, Family Protophasmatidae (Rock crawlers)	
Wüdrig <i>et al.</i> , 1998	Gzhelian-Asselian	Itararé Sub-Group, base of Tubarão Group	Core number 2-I.G.G, São Paulo State, Paraná Basin, Brazil	<i>Pintopinna martinsetoi</i>	Order Grylloblattida/Eoblattida, Family Protophasmatidae (Rock crawlers)	
Martins-Neto & Rohn, 1996	Capitanian-?Lopingian	Rio do Rasto Formation	Santa Catarina, Paraná Basin, Brazil	<i>Proboldinella riorastensis</i>	Order Hemiptera, Family Prosbolidae (Bugs)	Most extant hemipterans are phytophagous, and employ their distinctive piercing and sucking mouthparts to puncture holes in vegetation and extract plant sap. Some Hemiptera are also predatory. During the Permian, hemipterans may be responsible for many of the signs of mucivory in fossil plant remains.
Pinto & De Ornelas, 1981b; Adami-Rodrigues <i>et al.</i> , 2004, fig. 3D.	Kungurian-early Kazanian	Irrati/Serra Alta Formation	Brazil, Rio Grande do Sul, Minas do Leão municipality, Paraná Basin	<i>Gondwanoptera capsii</i>	Order Hemiptera, Suborder Homoptera (Bugs)	
Pinto <i>et al.</i> , 2000, fig. 6.	Permian	Mangrullo Member of Melo Formation	El Baron Ranch, Uruguay	<i>Paracicadopsis mendezalzoi</i>	Order Hemiptera, Suborder Homoptera, Family Cicadopsyllidae, (Bugs)	
Pinto, 1990b, fig. 6; Adami-Rodrigues <i>et al.</i> , 2004, fig. 3C.	Kungurian-early Kazanian	Irrati/Serra Alta Formation	Brazil, Rio Grande do Sul, Minas do Leão municipality, Paraná Basin	<i>Fulgoringrui kukalovae</i>	Order Hemiptera, Suborder Homoptera, Family Fulgoringruidae (Bugs)	
Pinto, 1987b, pl. 2 fig. 1; Adami-Rodrigues <i>et al.</i> , 2004, fig. 3B.	Kungurian-early Kazanian	Irrati/Serra Alta Formation	Brazil, Rio Grande do Sul, Minas do Leão municipality, Paraná Basin	<i>Prosbollecicada gondwanica</i>	Order Hemiptera, Suborder Homoptera, Family Prosbollecicadidae (Bugs)	
Pinto, 1987b, pl. 2 fig. 2.	Kungurian-early Kazanian	Irrati/Serra Alta Formation	Brazil, Rio Grande do Sul, Minas do Leão municipality, Paraná Basin	<i>Prosbollecicada iratienensis</i>	Order Hemiptera, Suborder Homoptera, Family Prosbollecicadidae (Bugs)	
Pinto, 1972b, pl. 3 fig. 1a, b.	Kungurian-early Kazanian	Irati Formation	Rio Grande do Sul, Paraná Basin, Brazil	<i>Petromantis rieki</i>	Order Mecoptera, Family Permochoristidae (Scorpionflies)	Many extant Mecoptera have long beak-shaped rostra, which they use for predation or scavenging. Some Palaeozoic Mecoptera may have played a role as pollinators of gymnosperms.
Pinto, 1972b, pl. 3 fig. 2a, b.	Kungurian-early Kazanian	Irati Formation	Rio Grande do Sul, Paraná Basin, Brazil	<i>Petromantis evansi</i>	Order Mecoptera, Family Permochoristidae (Scorpionflies)	

Pinto 1972b, pl. 3 fig. 3a, B.	Kungurian– early Kazanian	Iratí Formation	Rio Grande do Sul, Paraná Basin, Brazil	<i>Asiachorista beckermigdisovae</i>	Order Mecoptera, Family Permochoristidae (Scorpionflies)	Extant Neuroptera typically possess simple chewing mandibles. The larvae of extant Neuroptera are usually predatory, and possess elongate mandibles specialized for piercing and sucking insect prey. Many living adult Neuroptera are also predators, however, some also consume nectar.
Pinto & De Ornellas, 1980, fig. 1.	Kungurian– early Kazanian	Iratí/Serra Alta Formation	Brazil, Rio Grande do Sol, Minas do Leão municipality, Paraná Basin, Brazil	<i>Permipsythone pauflorovi</i>	Order Neuroptera, Family Permopsychopsidae (Lacewings)	All larvae, nymphs and adults of living Odonata (and likely extinct Protodonata) are predatory.
Tillyard, 1928	Lopingian	?Upper Permian	Falkland Islands	<i>Protagrion/ Permagrion falklandicum</i>	Order Odonata (Dragonflies and damselflies)	
Rösler <i>et al.</i> , 1981	Lopingian	Iratí Formation	Amaral Machado quarry, São Paulo State, Paraná Basin, Brazil	<i>Gondwanoptilon brasiliensis</i>	Order Odonata/ Megasinoptera, Family Permaeschnidae (Dragonflies and damselflies)	
Fossa-Manzini, 1941	Lopingian	?Upper Permian	Falkland Islands	Undescribed Palaeodictyoptera	Order Palaeodictyoptera (Paraphyletic)	Where preserved, the mouthparts of Palaeodictyoptera comprise distinctive elongate piercing-and-sucking mouthparts.
Pinto, 1994, pl. 2.	Gzhelian- Asselian	Piedra Shotle Formation	Chubut, Argentina	<i>Archaeomegaptilus ferreirai</i>	Order Palaeodictyoptera, Family Archaeomegaptilidae (Paraphyletic)	
Pinto, 1992, fig. 2.	Gzhelian- Asselian	Piedra Shotle Formation	Argentina	<i>Breyeria brauckmanni</i>	Order Palaeodictyoptera, Family Breyeriidae (Paraphyletic)	
Pinto, 1995, pl. 2.	Gzhelian- Asselian	Bajo de Véliz Formation	Provincia de San Luis, Argentina	<i>Sphecorydaloides lucchesei</i>	Order Palaeodictyoptera, Suborder Megasecoptera, Family Sphecorydaloididae (Paraphyletic)	
Pinto, 1986, pl. 2.	Gzhelian- Asselian	Malanzan Formation	Cuestita de la Herradura, Sierra de los Llanos at la Rioja, Argentina	<i>Xenoptera riojaensis</i>	Order Palaeodictyoptera, Suborder Megasecoptera, Family Xenopteridae (Paraphyletic)	
Pinto & De Ornellas, 1978b, pl. 1, fig. 1, 2.	Gzhelian- Asselian	Bajo de Véliz Formation	Provincia de San Luis, Argentina	<i>Philiaspilon huentickeni</i>	Order Palaeodictyopteroidea/ Megasecopteroidea, Suborder Diaphanopteroidea, Family Diaphanopteridae (Paraphyletic)	Diaphanopteroidea are known as 'beaked insects' from examples where the head is preserved.
Pinto & Adami- Rodríguez, 1997, pl. 1 & 2.	Gzhelian- Asselian	Bajo de Véliz Formation	Argentina	<i>Velisoptera taschi</i>	Order Palaeodictyopteroidea, Suborder Diaphanopteroidea, Family Velisopteridae (Extinct Order)	.

Pinto & De Ornellas, 1981a	Gzhelian-Asselian	Bajo de Veliz Formation	Argentina	Undescribed	Order Paraplecoptera (stem-Stoneflies)	Modern Plecoptera (stoneflies) usually comprise aquatic nymphs and terrestrial adults. They possess simple chewing mandibles. The nymphs may feed on submerged vegetation, or engage in active predation. In extant forms, many of the adults do not feed, but some are herbivorous.
Pinto, 1990a, fig. 7.	Gzhelian-Asselian	Itarare Sub-Group, base of Tubarão Group	Paraná Basin, Brazil	<i>Carpenteroptera onzii</i>	Order Paraplecoptera, Family Cacurgonarkemidae (Stoneflies)	
Pinto & De Ornellas, 1978a, pl. I, figs. 4, 5, pl. II, figs. 2, 3.	Gzhelian-Asselian	Itarare Sub-Group, base of Tubarão Group	Core number 2-I.G.G, São Paulo State, Paraná Basin, Brazil	<i>Narkemina rodendorfi</i>	Order Paraplecoptera, Family Narkemocacurgidae (Stoneflies)	
Pinto & De Ornellas, 1978a	Gzhelian-Asselian	Bajo de Veliz Formation	Paganzo Basin, Argentina	<i>Narkemina</i> sp.	As above	
Pinto & De Ornellas, 1978a, pl. I, fig. 6, pl. II, figs. 4a, 4b.	Gzhelian-Asselian	Base of Itarare Sub-Group, base of Tubarão Group	Durasnal Locality, Rio Grande do Sol, Brazil	<i>Carpenteroptera (Narkemina) rochacamposi</i>	As above	
Pinto & De Ornellas, 1978a, pl. I, fig. 7, pl. II, fig. 5.	Gzhelian-Asselian	Itarare Sub-Group, base of Tubarão Group	Core number 2-I.G.G, São Paulo State, Paraná Basin, Brazil	<i>Narkemina</i> sp. 'A'	As above	
Pinto & De Ornellas, 1978a, pl. I, fig. 8, pl. II, fig. 6.	Gzhelian-Asselian	Itarare Sub-Group, base of Tubarão Group	Core number 2-I.G.G, São Paulo State, Paraná Basin, Brazil	<i>Narkemina</i> sp. 'B'	As above	
Pinto & De Ornellas, 1978a, pl. I, fig. 9, pl. II, fig. 7.	Gzhelian-Asselian	Itarare Sub-Group, base of Tubarão Group	Core number 2-I.G.G, São Paulo State, Paraná Basin, Brazil	<i>Narkemina</i> sp. 'C'	As above	
Pinto <i>et al.</i> , 2000, fig. 7.	Permian	Mangrullo Member of Melo Formation	El Baron Ranch, Uruguay	<i>Perlapsocus formosoi</i>	Order Plecoptera (Perlaria), Family Perlapsocidae (Stoneflies)	
Pinto, 1996, fig. 1	Gzhelian-Asselian	Pallero Member, Bajo de Veliz Formation	Argentina	<i>Rigattoptera ornellae</i>	Order Protorthoptera (Extinct Order, stem-Orthoptera), Family Rigattopteridae (Paraphyletic basal Neoptera)	Extant Orthoptera are major plant herbivores, and possess mandibulate mouthparts adapted for biting and chewing leaf matter. Orthopterans or stem-orthopterans may have been responsible for many of the signs of leaf-margin feeding on fossil leaves from the Permian.
Pinto & De Ornellas, 1978a, pl. I, fig. 1, pl. II, fig. 1.	Gzhelian-Asselian	Itarare Sub-Group, base of Tubarão Group	Core number 2-I.G.G, São Paulo State, Paraná Basin, Brazil	<i>Proedischia mezzalirai</i>	Order Protorthoptera, Family Proedischiidae, (Paraphyletic basal Neoptera)	

fossils. These include > 60 hemipteran (true bug) taxa and substantial numbers of Mecoptera (scorpionflies and hangingflies), members of the extinct order Protelytroptera and, interestingly, Thysanoptera (thrips), which are unknown from other Permian Gondwanan sites (Table 3). Other orders found among these deposits include Coleoptera (beetles), the extinct Glosselytrodea, Neuroptera (lacewings and their relatives), Odonata (dragonflies and their kin), Plecoptera (=Perlaria), Psocoptera (booklice or barkflies) and Trichoptera (caddisflies) (Table 3).

In Antarctica, reports of insect body fossils are understandably scarce in comparison to other regions of Gondwana, and mostly lack precise age constraints. Nevertheless, there are two known Permian hemipterans, and a single plecopteran (perlarian), along with numerous acid-macerated arthropod mesofossils and microcoprolites extracted from permineralized *Glossopteris*-bearing deposits (Table 3).

Reports of Permian terrestrial arthropod body fossils from India are primarily concentrated in the Cisuralian (e.g., Mamal Formation, Talchir Formation), in addition to some reports from the mid-Permian Barakar Formation from the Raniganj Coalfield. To date, these are dominated by Blattodea, supplemented by several taxa of Coleoptera, Hemiptera and Mecoptera (Table 3). Further, two specimens of acid-extracted oribatid mites (*Acarus indicus*) have been described from the Cisuralian Manjir Formation of Himachal Pradesh (Kumar *et al.*, 2011).

From Africa, the vast majority of Permian terrestrial arthropod body fossils come from Lopingian deposits of the Beaufort Group, and Cisuralian strata of the Ecca Group (South Africa), although there are scattered reports of insect body fossils from other deposits (e.g., in the Congo [DRC], Madagascar, and Zimbabwe; see Table 3). Current African records are dominated by hemipterans, grylloblattids and mecopterans (Table 3). Indeed, 'grylloblattids' appear to be particularly abundant and diverse in Gondwanan Permian deposits in comparison to assemblages from the Northern Hemisphere where they comprise a lesser component of the entomofauna (Aristov & Mostovski, 2013; Pretorius *et al.*, 2021). Also present are Blattodea, Coleoptera, Miomoptera, Neuroptera, Protorthoptera, Palaeodictyopteroidea, Paoliida and Paraplecoptera (Table 3). Strata of the Ecca Group have also produced the only non-insect hexapod known from the Permian of Gondwana, the collembolan *Permobrya mirabilis* (Riek, 1976c).

From the major Permian insect-bearing deposits of South America, a large proportion of the body fossils come from the lowermost Permian (Asselian) Itararé Group of the Paraná Basin (Brazil), the Bajo de Véliz Formation of Argentina, and other units around the Carboniferous-Permian boundary (Table 3). Although these insect fossils co-occur with *Glossopteris* plant remains, they include elements more typical of Carboniferous insect faunas. Some younger Permian

insects have been reported from ?Kungurian strata of the Irati Formation, Brazil, and from Lopingian strata of the Falkland Islands (Table 3). South American records have a relatively high proportion of Blattodea (cockroaches and their relatives), Grylloblattida (icebugs), Paraplecoptera, Palaeodictyoptera (extinct 'six-winged insects') and Hemiptera. Also preserved are Coleoptera, Mecoptera, Neuroptera, Odonata, Plecoptera and the extinct Protorthoptera (Table 3).

Of the arthropod groups found as body fossils among the glossopterid biome, several stand out as candidates for the various styles of plant-damage found in palaeobotanical remains. Orthopteran-like insects (including 'protorthopterans'), which possessed generalized chewing mouthparts likely played an important role in active herbivory, and may have been the producers of some of the signs of leaf-margin feeding and other phytophagy on Permian plants (Adami-Rodríguez *et al.*, 2004a). The relatively large number of hemipterans known from several of the Gondwanan sites points to an important role for this group in Permian glossopterid-dominated forests. The specialized piercing-and-sucking mouthparts of hemipterans may be the generators of various pustules and small scars on fossil plant tissues targeting the xylem, phloem and mesophyll of the host plants—although a similar role could also have been fulfilled by the extinct Palaeodictyoptera, which also possessed distinctive elongate piercing-and-sucking mouthparts (Labandeira & Phillips, 1996). Coleoptera appear to have first arisen in the Permian (Zhang *et al.*, 2018), and certainly included phytophagous forms, likely responsible for various signs of herbivory and wood-boring.

Outside the Insecta, oribatid mites were likely an important Permian group of arthropod herbivores (especially wood-borers) and detritivores as they are in modern forest soil ecosystems. Mites are an ancient group of arachnids that are a major pest on modern crop plants, causing foliar symptoms, such as stippling, leaf bronzing, necrosis, inrolling of leaf margins, galling and distortion of tissues. These arachnids are probably responsible for many of the densely packed agglomerations of microcoprolites found among permineralized remains of Permian plant tissues (e.g., Kellogg & Taylor 2004; Slater *et al.*, 2012). Body fossils of myriapods—an important arthropod group of plant detritivores, but also some herbivores—are lacking in Permian Gondwana, although trackways attributable to myriapods (e.g., *Diplichnites gouldi*) are not uncommon (e.g., Briggs *et al.*, 2010).

Non-arthropod damage

Non-arthropod damage to living leaves, prior to fossilization, can be separated into abiotic and biotic damage. These damage types are difficult to distinguish (Fig. 4D), and many of them resemble forms commonly attributed to arthropods. Diseases and damage types on plants caused by non-arthropod biotic agents were reviewed by Labandeira &

Prevec (2014). When diagnosing plant diseases or determining the cause of damage to well-studied, modern crop plants, plant pathologists make detailed field observations, and may employ an array of laboratory tests, to identify the pests and pathogens that cause them. Typically these studies comprise an assessment of the local environment and growing conditions, farming practices, distribution and intensity of symptoms on the plants, and very importantly, the characteristic signs of the disease, or in the case of insect pests, the presence of herbivores themselves. Plant pathologists rely on the presence of both symptoms and signs to conclusively identify the causative agents of biotic damage to plants. Symptoms refer to the modified appearance of the plant tissue, including features such as chlorosis, necrosis, galling, tissue distortion, and excision of leaf tissue. Signs of insect pests include coprolites, webbing, live insects and exuviae, and in the case of pathogens, fungal hyphae, leaf mould, reproductive structures and spores. In the fossil record, such signs are extremely rarely preserved, particularly since most studies utilize adpression fossils for data collection.

Palaeontologists focussing on plant herbivory face a daunting task in distinguishing abiotic from biotic damage, and insect-mediated damage from plant disease. Ultimately, proposing a causal agent for plant damage on the detached organs of long extinct plants is highly subjective, and errors in damage classification can inflate estimates of insect diversity in studies that rely on damage type and host specificity data as proxies. Below, we highlight several of the non-arthropod groups that may have played a role in generating damage to plant parts in the Permian *Glossopteris* flora.

Nematodes are significant invertebrate pests of modern plants. These microscopic roundworms can cause significant damage to plant foliage, stems and roots. On foliage they may form patchy chlorosis and necrosis of tissues partially restricted by veins, and resulting in angular, wedge-shaped lesions, and larger lesions towards the base of the leaf. Nematodes can cause knotting or galling of roots, and may cause secondary symptoms of water stress by impeding water uptake. Despite being ubiquitous in modern environments, and among the most numerous of all animals, fossil nematodes are exceptionally rare and confined to Konservat Lagerstätten (e.g., Poinar *et al.*, 2008). Thus far, we are unable to ascribe any of the observed Permian damage types definitively to nematodes, but they were potential producers of some of the vein-bounded lesions on leaves of glossopterids and associated plants. Similarly, we can not yet ascribe specific damage types to pulmonate gastropods (but see the comments on hole feeding above).

An obscure form of foliar infection that could be mistaken in the fossil record for galls, oviposition scars or surface feeding by arthropods, are lesions caused by parasitic green alga of the genus *Cephaleuros*. In extant floras, these fairly rare parasites cause fluffy to crusty, circular spots with filamentous margins, on coriaceous leaves, such as those of

magnolia, guava, coffee and avocado (Joubert & Rijkenberg, 1971). Spots tend to occur over primary veins, another similarity shared with leaf galls, and may be arranged in regular linear patterns that could be mistaken in the fossil record as indicative of arthropod behaviour. Damage types 52 and 34 of Labandeira *et al.* (2007) show remarkable similarities to these pathogenic features.

Viral diseases in extant plants can produce various symptoms depending on the pathogen and the part of the plant affected. Viruses may be transmitted by arthropods, particularly hemipterans, and therefore, are worth considering as agents of disease associated with insect damage. Viruses typically cause symptoms such as distortion, puckering, stunting and irregular growth of plant organs, vein clearing (chlorosis of tissues immediately adjacent to veins), and diffuse mottling, mosaic or ringed patterns of chlorosis consistent with DTs 23, 79, 112 (Labandeira *et al.*, 2007; Labandeira & Prevec, 2014). These patterns of chlorosis are difficult to confirm in fossil plants because the diffuse nature of the discolouration may not preserve in adpressions.

Fungal and bacterial diseases as agents of plant damage are probably greatly under-diagnosed in studies focussing on plant-insect interactions. Many plant pathogens cause lesions that, in the fossil record, would be very similar to arthropod surface-feeding traces, oviposition scars, or in cases where the necrotic centre of the lesion is lost or partially detached from the living tissues, hole-feeding traces (e.g., Labandeira *et al.*, 2007; DT01 and DT10). Bacterial diseases can manifest as chlorotic, water-soaked lesions that may become necrotic as the disease develops, and can range in size and shape from small, discrete circular lesions, to large, irregularly shaped marginal lesions that may be partially confined by the leaf venation, or may coalesce to form scorching symptoms similar to those typical of severe water stress (DT114). Both fungi and bacteria can cause galls and cankers on stems and leaves. Non-pathogenic epiphyllous fungi on *Glossopteris* leaves can also produce surface stainings or thickenings reminiscent of arthropod damage (Bajpai & Maheshwari, 1987). Harper *et al.* (2016, 2017) and Slater *et al.* (2013) have summarized some of the fungal and oomycete interactions associated with permineralized Permian Gondwanan plants. As yet, little work has been carried out on bacterial damage to austral Permian plants, although bacteria are known to have produced microscopic degradation features on fossil lycopsid megaspores (Bajpai & Maheshwari, 1986).

Plant defences

Apart from various cases of mimicry, camouflage, indirect defences (e.g., mutualistic associations with defender organisms), and ecological strategies (e.g., regular leaf shedding), modern plants employ primarily simple physical (e.g., spines, hairs and waxy cuticles) or chemical (e.g. glands or sap with alkaloids, resins, cyanogenic glycosides, and

phenolic compounds) to protect themselves from arthropod attack (Schardl & Chen, 2010). Plant defences can be categorized as ‘constitutive’ (features always represented in the plant), or ‘induced’ (features produced in response to damage or stress generated by herbivores). Here, we primarily consider constitutive physical defences, since these have the greatest potential to be preserved in the fossil record.

Given the broad extent of herbivory recorded in fossil plants across Gondwana, there are surprisingly few examples of obvious physical defensive features on the plants. Some potential examples of defensive adaptations are evident in conifers. For example, *Ferrugliocladus riojanum* has acute-tipped and thickened apices to both its ovuliferous cone scales and microsporophylls (Archangelsky & Cúneo, 1987, pl. 3, fig. 4, pl. 4, fig. 1; pl. 6, fig. 4; pl. 8, figs 1, 2) that suggest possible defensive adaptations against seed-feeding or palynophagous arthropods. Similarly, the spinose tips of sporophylls in the equisetalean *Cruciatheca genoensis* Cúneo & Escapa (2006, fig. 4C, D, fig. 5B) might represent defences against insects feeding on spores in the strobilus. *Walkomiella indica* from India (Surange & Singh, 1953) and unidentified leaves from the Permian of Antarctica (McLoughlin *et al.*, 1997, fig. 3G; Slater *et al.*, 2015, fig. 6H) possessed spinose projections along the lamina margin that might have been a deterrent to margin-feeding insects. *Ginkgophyllum diazii* from the uppermost Carboniferous or lowermost Permian of Argentina (Archangelsky & Leguizamón, 1980) also has prominent cuticular hairs along the margins of lamina segments that may have acted to disrupt systematic feeding or movement along the leaf edge. *Noeggerathiopsis brasiliensis* (Guerra–Sommer, 1989, pl. 4, fig. 3; Degani–Schmidt & Guerra–Sommer, 2019, fig. 3C–H) from the Permian of Brazil, and similar forms attributed to *Noeggerathiopsis* from Antarctica (McLoughlin & Drinnan, 1996), have relatively prominent conical papillae over the leaf surface and margins. These might have impeded insect movement on the lamina, although these features tend to be more elongate and denser in the abaxial stomatiferous grooves suggesting a more important role in the regulation of transpiration. A few *Glossopteris* species also bear prominent papillae, especially on the abaxial surface (Guerra–Sommer, 1992, pl. 4, fig. D) but these are also most pronounced around stomata suggesting that they played a greater role in the regulation of gases within the leaf. The concentration of papillae along the veins in *Glossopteris papillosa* Guerra–Sommer (1992, pl. 5, fig. A) might be indicative of protection of the vascular supply from mucivorous herbivores. Degani–Schmidt & Guerra–Sommer (2016) identified a mix of scattered unicellular and stellate trichomes on the abaxial cuticle of *Glossopteris pubescens*, and the concentration of these hairs over the veins could conceivably have provided defence against piercing-and-sucking insects. We find no evidence that glossopterids bore defensive spines (contra McCoy *et al.* 2021).

Other, less certain defences might include the enrollment of the polysperm in *Homevaleia gouldii* (Gould & Delevoryas, 1977; Nishida *et al.*, 2007) to protect the enclosed developing ovules from herbivores. Since many broad-leafed seed plants in the Gondwanan Permian were deciduous (although see Gulbranson *et al.* 2012 for arguments related to an evergreen habit in some glossopterids), it is possible that these plants simply adopted a strategy of producing a large number of leaves in a season, many of which could be sacrificed to herbivory without significant resource loss. On this basis, the plants may have avoided investing resources in the production of elaborate or energetically costly physical or chemical defences. At least some Permian Gondwanan plants are known to have produced glandular bodies in their leaves. For example, Fanton *et al.* (2006) recorded resiniferous glands in the leaves of *Krauselcladus canoinhensis* that might have played a role in defence against herbivory.

Carter (1999) reported dispersed putative glossopterid phytoliths from the Guadalupian or Lopingian Weller Coal Measures of Antarctica that might have provided a deterrent to foliar herbivores. However, the identity of these structures as phytoliths and their source from glossopterids remain equivocal. If they do represent phytoliths, then an origin from sphenophytes is just as likely, since extant taxa of that group are known to precipitate large quantities of silica spicules in stem and leaf tissues (Kaufman *et al.*, 1971), and anatomical studies of glossopterid leaves are yet to identify any phytolith-like structures (Pigg & McLoughlin, 1997).

IMPLICATIONS

Our compilation of published records (Tables 1, 2), shows that arthropod damage is widespread on Permian plants across Gondwana (Fig. 2) but that the intensity and diversity of damage varies greatly according to the number and type of palaeobotanical studies carried out in particular regions and whether or not studies have particularly targeted the representation of herbivory features. For example, records from South America are heavily skewed towards Cisuralian and Guadalupian reports owing to the scarcity of studies on Lopingian floras from that region. This contrasts with Australia, where most studies have focused on Lopingian floras (Fig. 6). The Antarctic record of herbivory is heavily biased towards examples of boring, palynophagy and detritivory owing to the large number of anatomical studies of permineralized wood, roots, leaves and coprolites carried out from that region.

Owing to the patchiness of available data, and the scarcity of studies that have employed a quantitative approach to palaeoherbivory, it is difficult to draw strong conclusions concerning variations in the temporal or geographic distributions of herbivory styles in the Permian of Gondwana. Nevertheless, most functional feeding groups are represented throughout the Permian fossil record if Gondwana is

considered as a whole (Fig. 6). Leaf mining is the only major category of herbivory for which evidence remains equivocal in the Gondwanan Permian. Published examples of seed herbivory are essentially restricted to a single assemblage from the Cisuralian of South America (Dos Santos *et al.*, 2020), although there are possible additional cases from the early Permian of India (Srivastava, 1995; Chandra & Singh, 1996) and South Africa (Anderson & Anderson, 1985). Given that seeds were potentially a rich food source, it is surprising that few polysperms (ovuliferous organs) of glossopterids show evidence of herbivory. The only damage to ovuliferous fructifications we noted are examples of equivocal margin-feeding damage causing curvature of the polysperm apex illustrated by Benecke (1976). Margin feeding, apex feeding and hole feeding on leaves are consistently well represented throughout the Permian (Fig. 6). Surface feeding is moderately well represented but the examples of this damage category tend to be less securely identified than other forms of herbivory. Examples of skeletonization are relatively sparse and also subject to alternative interpretations of fungal/bacterial damage, physical attrition or diagenetic alteration of the leaf. Although never the dominant form of herbivory, galling is consistently represented in low to moderate abundance throughout the Permian (Fig. 6). Oviposition scarring is prominent in several assemblages (Fig. 6). Oviposition damage is particularly rich on glossopterid leaves (e.g., Fig. 5J, L–T) and this is largely responsible for the apparent global peak reported for the Permian by Romero–Lebrón *et al.* (in press) for egg-laying damage through the Phanerozoic. We suspect that this apparent peak might be a consequence of more intense collecting and surveying of the literature for this interval, and we recommend detailed investigations of Mesozoic assemblages to better gauge the diversity of this arthropod behaviour through time.

Glossopterids are the dominant plant group showing signs of herbivory in all Gondwanan floras. This order of plants hosts all of the major functional-feeding-group/subgroups recognized in the survey. Within Glossopteridales, damage is represented predominantly on *Glossopteris*, but is also evident on various less common leaf taxa in the order (e.g., *Velizia*, *Rubidgea*, *Euryphyllum*, *Palaeovittaria*, *Ilexoidephyllum*, *Belemnopteris*, *Rhabdotaenia?*, *Gangamopteris*), and on vegetative or fertile bracts (Tables 1, 2). Foliar damage is most widely reported, but all parts of the glossopterid plant were under herbivory pressure as evidenced by extensive trunk- and root-wood boring and pollen-bearing coprolites (Slater *et al.* 2012). Indeed, wood boring and detritivory may have been an especially favoured strategies at high palaeolatitudes where living foliage of the major broad-leafed plant groups was unavailable during the dark winter season owing to widespread deciduousness in the vegetation.

Other gymnosperms host fewer examples of arthropod damage, but this is generally consistent with their lesser representation in the Permian vegetation. Of these plant

groups, cordaitaleans (*Noeggerathiopsis*) and ginkgoaleans (*Ginkgoites*, *Rhipidopsis*) are the most widely reported to host damage, and this is generally in the form of margin/apical feeding or hole feeding. *Botrychiopsis*, which was common in earliest Permian floras but declined markedly thereafter, bears a moderate representation of mostly external foliage-feeding damage and rare galls. Rare gymnosperms (e.g., *Eremopteris*, *Saportaea*, *Dunedoonia*, and various conifers) bear either equivocal examples of apex feeding and oviposition scars or lack evidence of herbivory altogether. Some needle-shaped leaf segments of *Ginkgophyllum cricumensis* and *G. diazii* illustrated by Archangelsky & Arrondo (1974, figs 1–8) or *Rhodea cricumana* (Dolianiti, 1953c, fig. 1; Rigby, 1969, fig. 15) are abruptly truncated, but it is unclear whether these represent arthropod herbivory, some other form of physical attrition or preparatory damage.

Given their abundance in the fossil flora, sphenophytes host relatively few clear examples of arthropod damage. Of those few cases, most examples are recorded on the foliage of sphenophylls (*Sphenophyllum*, *Trizygia*) as relatively simple forms of margin-, hole- and surface-feeding damage. Clusters of oviposition scars are notably represented on some sphenophyte axes (Beattie 2007). Likewise, obvious damage to fern foliage (mostly external foliage feeding and oviposition scarring) is less represented in illustrated examples than would be expected given the relative prominence of this understory group in the palaeovegetation. At least some specialized herbivory in the form of galling is evident on fern foliage (Pant & Misra, 1977, pl. 3, fig. 1; Cariglino, 2018). Extant ferns are known to host various chemical and microanatomical physical defences against arthropod herbivores (Farias *et al.*, 2020). In the absence of chemical (biomarker) signatures from the fossils, and few cuticular studies of pteridophyte fossils from Gondwana, we can not determine whether the Permian ferns employed similar degrees of herbivore defence.

We found very little evidence of arthropod damage to lycopsid remains (Prevec *et al.*, 2009; Cariglino, 2018), although fungal damage is not uncommon (McLoughlin *et al.*, 2015). This is somewhat surprising given that arborescent representatives of this group constitute a significant component of some South American Permian floras (Cúneo & Andreis, 1983; Souza de Faria *et al.*, 2009; Cariglino *et al.*, 2012). We suspect that there may be biases against illustration of damaged free-sporing plant foliage and difficulties in recognition of damage to the needle-like foliage and sporophylls of many lycopsids and sphenopsids. This is reinforced by the recognition of specialized palynophagy in permineralized fern sporangia (Slater *et al.* 2012) that has not yet been recognized in compression floras. The very poor record of non-vascular plants from Permian strata of the Southern Hemisphere precludes identification of arthropod interactions with the presumably extensive bryophyte-grade ground-stratum vegetation.

Although quantitative data from Gondwana is sparse, the general representation of feeding strategies in the *Glossopteris* biome is broadly consistent with that of Permian floras from the palaeoequatorial belt of Euramerica and Cathaysia. The Cisuralian Mitchell Creek Flats flora of Texas in the western Euramerican floral province (Schachat *et al.*, 2015) hosts a wide representation of feeding styles with the broadest range of occurrences on the dominant gymnosperm group (*Taeniopteris*). This flora differs from coeval Gondwanan assemblages by its high incidence and diversity of galls, suggestive of an arid setting. The upper Sakmarian “Copolite Bone–Bed” assemblage from Texas is atypical in having very low levels of herbivory, the vast majority of which occurs on the two dominant peltaspermales (*Autunia*) and medullosan (*Odontopteris*) plants (Labandeira & Allen, 2007). The Artinskian floras of Baylor County, Texas (Beck & Labandeira, 1998) have higher levels of feeding intensity and diversity but the interactions are again most pronounced on the dominant broad–leafed gigantopterid plants in the assemblages. The Kungurian Colwell Creek Pond flora of Texas hosts a broad spectrum of damage types with damage again concentrated on peltaspermalean and taeniopterid gymnosperms, and with notable specialization of feeding strategies on specific plant taxa and organs (Schachat *et al.*, 2014).

In Italy (eastern Euramerican floral province), both the Kungurian Tregiovo and Wuchiapingian Bletterbach floras are consistent with the typical signal from Permian Gondwanan floras in hosting modest but varied arthropod damage with a much higher proportion of generalized than specialized herbivory compared to more equable ratios evident in the Triassic (Labandeira *et al.*, 2016). Margin and hole feeding dominate the damage spectrum in the Italian Permian assemblages, and are predominantly evident on broad–leafed taeniopterid cycadophytes and pteridosperms. The Italian floras differ primarily in having damage expressed on a broader range of plant groups than is typical in any one Gondwanan assemblage (Labandeira *et al.*, 2016).

Early Permian wetland floras of China also show a broad spectrum of damage features (five functional feeding groups) with a dominance of apex–, margin– and hole–feeding (Feng *et al.*, 2020), but this is expressed more equally on fern and cycadophyte (*Taeniopteris*– and *Pterophyllum*–like) leaves in contrast to humid high–palaeolatitude and arid palaeoequatorial settings where arthropod interactions with pteridophytes are relatively sparse. By the Lopingian, herbivory in the wet–tropical vegetation of South China (preserved in the Kayitou Formation) was most concentrated and diverse on the dominant broad–leafed gymnosperms: gigantopterids and pecopterids (Medullosales?) (Liu *et al.*, 2020). The Kayitou Formation assemblage records at least six functional feeding groups, excluding skeletonization, seed herbivory, and leaf mining. Hole and margin feeding remain overwhelmingly the dominant styles of damage.

Clearly, there are similar aspects to herbivory patterns in the different floral provinces of the Permian, especially the focusing of damage on the dominant broad–leafed seed–plant groups. However, these initial surveys also highlight potential regional differences, with notably higher proportions of specialist herbivory in some dryland settings and greater targeting of pteridophytes in the tropical humid floras.

FUTURE WORK

Since most previous studies of herbivory from the Gondwanan Permian are of incidental observations on specific plant fossils or investigations of special styles of preservation (e.g., permineralizations), the challenge for future research in this field will be to employ standardized sampling and quantitative analysis of damage features to provide more rigorous measures of interactions through time and across palaeolatitudes. Fortunately, several recent studies have provided protocols for sampling with respect to palaeoherbivory and have utilized a battery of statistical techniques that offer more precise approaches to assessing the temporal and geographic distributions of damage types (Labandeira & Currano, 2013; Schachat *et al.*, 2018; 2020; Currano *et al.*, in press). Such approaches will be especially important for assessing the impact on plant–arthropod associations during the transition between the icehouse climates of the earliest Permian to the extreme hothouse climates of the earliest Triassic. The critical thermal threshold near the end of this transition that marked the end–Permian extinction witnessed the collapse of the *Glossopteris* biome and was perhaps the only event in the entire evolutionary history of Insecta that saw an abrupt turnover in insect orders (Labandeira, 2005, 2006). The results of Gondwana–wide quantitative investigations of herbivory and arthropod representation through the Permian will have particular importance to the modern world in which greenhouse–gas–induced warming is expected to raise global temperatures significantly over the next 80 years (IPCC, 2013).

The immediate impact on insect faunas in the wake of the end–Permian extinction of glossopterids is not known with any certainty since Early Triassic insect faunas are rare (Shcherbakov, 2008a). The few body fossil assemblages available seem to indicate that Early Triassic insects were mostly represented by ‘survivor’ taxa, i.e., groups that were present in the latest Permian but persisted with lesser diversity (Shcherbakov, 2008b). Clearly, plant and insect communities had rebounded in diversity and complexity by the Middle to Late Triassic (Anderson *et al.*, 1999; Labandeira, 2006), but the lack of rich Early Triassic insect assemblages makes it difficult to directly gauge the diversity and feeding guilds of insects in the immediate aftermath of the end–Permian crisis. In the absence of body fossils, arthropod damage on fossil leaves offers the best opportunity to assess the role of insect herbivores in the post–extinction recovery biotas. Current

work by the lead author on fossil plant assemblages from the Sydney Basin in eastern Australia, one of the few areas containing a well-preserved succession of Early Triassic floras, globally, aims to clarify the patterns of herbivory through the immediate recovery phase following the end-Permian crisis.

Taphonomic influences affect the representation of arthropod–plant interactions available in the fossil record. Nevertheless, special styles or environments of preservation offer opportunities to examine specific feeding strategies. Wood boring is more–or–less detectable only in permineralized plant remains, which are generally rare and dependent largely on the availability of large quantities of free silica or calcium carbonate in groundwaters during early diagenesis. Since large quantities of Permian permineralized wood and peat are available from several regions of Gondwana, serial sectioning of these remains offers the potential for unravelling the three-dimensional architecture of boring styles, which might improve identifications of the excavator organisms.

Improvements in imaging also offer opportunities for better categorization and discrimination of plant damage types. X-ray and neutron-beam tomographic reconstructions of fossil plant parts are now providing resolution of anatomical features below the level of cells and organelles (Bomfleur *et al.*, 2014; Mays *et al.*, 2017) and are likely to be increasingly applied to the identification of coprolites, entombed organisms and chamber architecture of borings within permineralized woods and other plant organs. Fluorescence microscopy and confocal laser scanning microscopy offer additional tools for improved discrimination, identification and characterization of microinvertebrate and fungal herbivores and parasites in permineralized and mummified plant remains (Strullu-Derrien *et al.*, 2017; McLoughlin *et al.*, in press). Further, in the absence of high-resolution optical microscopy or scanning electron microscopy, small (<1 mm diameter) dish-shaped perithecia of epiphyllous fungi on leaves and stems of Permian plant compressions (Lutz *et al.*, 1992) could readily be confused for piercing–and–sucking damage. These high-resolution imaging techniques will be crucial for advancing the accuracy of damage–type identification into the future.

As pointed out by Labandeira (1998a), detritivory and herbivory involve distinctly different modes of feeding, the demarcation of which is critical for resolving the origin and macroevolutionary pattern of the dominant insect feeding styles. Much of the focus of our investigation and previous studies from Gondwana has been placed on the role of herbivores in the palaeocommunity. The Permian forests probably also hosted a broad array of arthropod detritivores for which we have relatively little information from either the plant or animal body fossil records. Preliminary studies of coprolite morphology and contents, suggest that arthropod detritivores were diverse in the Permian (Slater *et al.* 2012, 2015). Careful bulk acid–maceration of Gondwanan plant-bearing sediments and recovery of organic residues is likely

to yield considerable information, based on coprolites and mouthpart or other exoskeletal remains, on detritivores that occupied the much-neglected leaf litter communities of Permian high-latitude forests.

We have not attempted to review the role of vertebrates in this study. Indeed few previous investigations have provided convincing evidence of the diet of Permian Gondwanan vertebrate herbivores. Assumptions about the plant foods of choice for austral Permian vertebrates derive largely from dentition, animal stature, and the types of plants co-preserved with the animals. For example, Rayner (1992) inferred sphenophytes to have been the primary fodder for the dominant stocky dicynodont herbivores of the Lopingian in the Karoo Basin, South Africa, but there is little direct supporting evidence. Mature glossopterid trees would appear to have been out of reach of most Permian vertebrates, but juvenile plants and shed reproductive organs were potential food sources for browsing animals. Zavada & Mentis (1992) suggested that a decline in the average size of glossopterid leaves (microphyllly) and increased undigestible carbon (lignin) content towards the end of the Permian was a direct response of glossopterids to herbivory pressure from a diversifying contingent of vertebrate herbivores. However, there is again little direct evidence to support herbivory of glossopterids by vertebrates, and the reduction in leaf size is more likely to have been a response to warmer and drier continental–interior climates towards the end of the Permian (Prevec *et al.*, 2010; Frank *et al.*, 2021). A way forward in this field is to analyze the contents of herbivore coprolites. Thus far, most coprolites from the Karoo Basin derive from carnivorous vertebrates (Smith & Botha-Brink 2011)—a taphonomic megabias that applies to vertebrate coprolites in general (Bradley, 1946; Hunt & Lucas, 2012; Qvarnström *et al.*, 2016). However, a concerted search effort might be fruitful for obtaining a representative selection of herbivore fossil excrement, since such remains can yield extensive information on vertebrate diets and associated micro-organisms.

CONCLUSIONS

Glossopterids were at the centre of a complex component community that involved herbivory, parasitism and detritivory on essentially all parts of the host plant. More broadly, the high-latitude Permian forests also supported a moderate range of invertebrate and vertebrate carnivore guilds. Our survey indicates over 500 discrete damage–plant–stratigraphic occurrences spread over the entire geographic range of the *Glossopteris* biome and extending from the earliest Permian to the end-Permian mass extinction. All major functional feeding groups are confidently represented in the fossil herbivory record except leaf mining, for which only equivocal evidence exists. Within these feeding guilds, a diverse array of more specific damage types is evident. In the absence of detailed quantitative analyses, and owing to some stratigraphic

and geographic gaps, temporal and spatial patterns in the representation of particular damage types are difficult to resolve. In general, the major functional feeding groups appear to be represented in similar proportions throughout the Permian, although some specialized herbivory strategies (e.g., galling) might have become more diverse towards the end of the period. The body fossil record of insects is patchy and derived mostly from a few well-studied lagerstätten but it provides evidence of a broad spectrum of arthropod families occupying glossopterid forests throughout the Permian. Our survey of plant–arthropod interactions provides baseline data for future quantitative analyses of Gondwanan Permian herbivory. Given the extensive leaf assemblages available from near polar to equatorial settings in the Permian of Pangea, there is considerable potential for future work to track the quantitative variation in herbivory across all latitudes and through time as an expression of changes to terrestrial ecosystems during a shift from an icehouse to a hothouse world.

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