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ORIGINAL PAPER

Evolution of a complex behavior: the origin and initial diversification of foliar galling by Permian insects

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Abstract A central notion of the early evolution of insect galling is that this unique behavior was uncommon to rare before the diversification of angiosperms 135 to 125 m.yr. ago. However, evidence accumulated during recent years shows that foliar galls were diverse and locally abundant as early as the Permian Period, 299 to 252 m.yr. ago. In particular, a diversity of leaf galling during the Early Permian has recently been documented by the plant-damage record of foliar galls and, now, our interpretation of the body-fossil record of culprit insect gallers. Small size is a prerequisite for gallers. Wing-length measurements of Permian insects indicate that several small-bodied hemipteroid lineages originated early during the Permian, some descendant lineages of which gall the leaves of seed plants to the present day. The earliest foliar gallers likely were Protopsyllidiidae (Hemiptera) and Lophioneuridae (Thripida). Much of the Early Permian was a xeric interval, and modern galls are most common in dry, extra-tropical habitats such as scrubland and deserts. Plant-damage, insect body fossils, and the paleoclimate record collectively support the ecological expansion of foliar galling during the Early Permian and its continued expansion through the Late Permian.

Keywords Body mass · Diet · Hemiptera · Late Paleozoic · Leaves · Lophioneuridae · Paleoecology · Protopsyllidiidae · Wing length

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Introduction

Modern leaf galls occur primarily on angiosperm leaves, occasionally on conifers, and rarely on non-angiospermous broadleaf taxa such as ferns, cycads, *Ginkgo*, and gnetaleans (Raman 2012). This distribution has led to the widespread belief that leaf galling evolved during the diversification of angiosperms (Roskam 1992; Scott et al. 1994; Raman et al. 2005; Schaefer et al. 2005). However, fossil leaf galls on seed plants occur during the preangiospermous Mesozoic (Labandeira 2014) and throughout the Permian (Labandeira 2013), the latter buttressed by recent reports from additional Permian localities, habitats, and plant hosts (Table 1). The observed prevalence of galling during the Permian is consistent with the relevant paleoclimate record—the earlier part of this interval characterized by overall aridity (Montañez and Poulsen 2013)—and with the elevated incidence of modern galling in xeric habitats (Fernandes and Price 1992).

Permian leaf galls could have been induced by mites, insects, or both. The Eriophyoidea, an ancient lineage of plant-associated mites that includes many modern gall-inducers (Boczek and Shevchenko 1996), might have been responsible for some gall occurrences found in Permian broadleaved gymnosperms, particularly as an eriophyoid body fossil, a specialized galler, recently was reported from the Middle Triassic of

Table 1 Documented leaf galls from the Early Permian. The occurrences marked with an asterisk (*) are possible galls; all others are probable or definitive. References are listed in the supplemental information

Host plant	Affiliation	Locality and occurrence	Age	References
Vjaznikipteris rigida	Peltaspermales	Vyazniki, Russia	Upper Permian (Changhsingian)	Krassilov and Karasev (2009)
Glossopteris browniana	Glossopteridales	Mohuda Formation, Jharia Coalfield, India	Upper Permian (Wuchiapingian)	Banerjee and Bera (1998)
Glossopteris bucklandensis	Glossopteridales	Black Alley Shale, Bowen Basin, Australia	Upper Permian (Wuchiapingian)	McLoughlin (2011)
Glossopteris xiphophylla	Glossopteridales	Black Alley Shale, Bowen Basin, Australia	Upper Permian (Wuchiapingian)	McLoughlin (2011)
Glossopteris sp.	Glossopteridales	Clouston Farm, Karoo Basin, South Africa	Upper Permian (Wuchiapingian)	Prevec et al. (2009)
*Glossopteris parallela**	Glossopteridales	Cooyal, New South Wales, Australia	Upper Permian (Wuchiapingian)	Holmes (1995)
Glossopteris acutifolia	Glossopteridales	Illawarra Coal Measures, Sydney Basin, Australia	Upper Permian (Wuchiapingian)	McLoughlin (2011)
Auritifolia waggoneri	Peltaspermales	Colwell Creek Pond, Texas, USA	Lower Permian (Kungurian)	Schachat et al. (2014)
Evolsonia texana	Gigantopteridales	Colwell Creek Pond, Texas, USA	Lower Permian (Kungurian)	Schachat et al. (2014)
Sandrewia texana	Peltaspermales	Colwell Creek Pond, Texas, USA	Lower Permian (Kungurian)	Schachat et al. (2014)
Supaia thinnfeloiodes	?Peltaspermales	Colwell Creek Pond, Texas, USA	Lower Permian (Kungurian)	Schachat et al. (2014)
Taeniopteris spp.	?Cycadophyta	Colwell Creek Pond, Texas, USA	Lower Permian (Kungurian)	Schachat et al. (2014)
Glossopteris sp.*	Glossopteridales	Raniganj Coalfield, India	Lower Permian (Kungurian)	Srivastava (1987, 1994)
Glossopteris taeniopteroides	Glossopteridales	Liddar Valley, Mamal Nala Section, Kashmir Himalaya	Lower Permian (Artinskian)	Pant and Srivastava (1995)
Palaeovittaria kurtzii	Filicales	Vryheid Formation, Karoo Basin, South Africa	Lower Permian (Artinskian)	McLoughlin (2011)
Gangamopteris obovata	Glossopteridales	Morro do Papaléo Mine, Paraná Basin, Brazil	Lower Permian (Sakmarian-Artinskian)	Adami-Rodrigues et al. (2004); de Souza Pinheiro et al. (2012)
Autunia cf. *conferta*	Peltaspermales	Coprolite Bone Bed, Texas, USA	Lower Permian (Sakmarian)	Labandeira and Allen (2007)
Odontopteris readi	Medullosales	Archer City Formation, Texas, USA	Lower Permian (Asselian)	Stull et al. (2013)
Odontopteris sp.	Medullosales	Rotliegende, Southern Germany	Lower Permian (Asselian)	Potonié (1893); Conway Morris (1981)

Austria (Schmidt et al. 2012). Although the Paleozoic mite body-fossil record extends deep into the Paleozoic (Norton et al. 1988), such occurrences are attributed to detritivorous lineages not known to induce galls. By contrast, insects have a more complete fossil record from the late Paleozoic and appear to have engaged in a wide range of phytophagous behaviors (Labandeira 2013).

No single morphological feature can be used exclusively to distinguish hexapodan gallers from their non-gall-inducing relatives. Insects of different lineages induce leaf galls through varied developmental control of their plant host (Raman 2012). Three features appear to be typical of gall-inducing insects: (1) a long-term specialized association with a particular plant lineage; (2) fleshy bodies with soft cuticles; and (3) small body size (Ananthakrishnan and Raman 1989; Schaefer et al. 2005). In a few lineages, gallers are larger than their non-galling relatives; however, their broader encompassing clades exhibit small body sizes overall. For example, gallers within the Margarodidae (giant scale insects) are considerably larger than non-galling members of the same family and are also larger than other related families within the Coccoidea (scale insects) (Gullan et al. 2005). However, galling insects are typically smaller than free-living species within the same clade, such as thrips gallers of the Terebrantia (Ananthakrishnan and Raman 1989), or the Cynipoidea, of which the non-galling macrocynipoid clades (4.0–15.0 mm long) are significantly larger on average than the galling microcynipoid clades (1.0–10.0 mm long) (Csóka et al. 2005).

The prevailing small size of galling insects is attributable to nymphs, larvae, and occasionally adults that must complete the gall-inhabiting stage of their development within one growing season. The gall itself must not be so large as to significantly reduce plant-host fitness (Schaefer et al. 2005). In addition, smaller herbivores are generally more specialized (Novotny and Basset 1999; Brändle et al. 2000), and specialized associations between the plant host and its herbivore favor the origination of galling (Schaefer et al. 2005). A hardened integument, such as rigid cuticle, would be unwieldy within the close quarters of an insect gall (Schaefer et al. 2005), favoring fleshy insects. Of these three features, the only evidence available for Paleozoic insects is body size. Direct measurements of body length are lacking because intact body fossils are rare. Nevertheless, wings are almost always the most frequently preserved insect body parts, and wing length serves as a reasonable proxy for insect body size (Dudley 2000; Clapham and Karr 2012).

Table 2 Families represented by two or more specimens within the small wing-length (<5.85 mm) cluster

Order	Family	Min	Med	Mean	Max	First appearance	*p* value
Lophioneurida	Lophioneuridae	1.50	2.60	2.73	5.70	Permian	0.0000
Hemiptera	Protopsyllidiidae	1.40	3.15	3.36	5.00	Permian	0.0000
Coleoptera	Permosynidae	1.82	3.00	2.90	5.40	Permian	0.0000
Coleoptera	Schizocoleidae	1.80	3.50	3.59	7.20	Permian	0.0003
Coleoptera	Taldycupedidae	1.90	2.83	3.01	4.50	Permian	0.0004
Coleoptera	Rhombocoleidae	1.75	3.68	4.13	7.60	Permian	0.0831
Psocodea	Psocidiidae	2.80	4.60	5.33	10.00	Permian	0.0868
Neoptera incertae	Apheloneuridae	2.70	3.00	3.47	4.80	Permian	0.0879
Mecoptera	Nedubroviidae	2.95	3.75	3.82	5.00	Permian	0.1047
Hemiptera	Archescytinidae	2.05	7.00	7.28	18.00	Carboniferous	0.1120
Psocodea	Permopsocidae	3.20	4.35	4.13	5.00	Permian	0.1441
Coleoptera	Curculiopsidae	2.30	3.90	3.92	4.85	Permian	0.1661
Hypoperlida	Permembiidae	1.80	5.50	6.04	12.40	Permian	0.4864
Mecoptera	Permopanorpidae	4.00	4.25	4.25	4.50	Permian	0.4938
Hemiptera	Prosbolidae	3.75	10.40	12.32	31.89	Carboniferous	0.5766
Diaphanopterodea	Asthenohymenidae	3.90	7.00	6.39	10.00	Carboniferous	0.6161
Mecoptera	Nannochoristidae	3.50	4.50	4.63	6.00	Permian	0.7312
Notoptera	Tshekardominidae	3.30	10.00	10.73	18.50	Permian	0.8288
Mecoptera	Permotanyderidae	4.00	4.50	4.50	5.00	Permian	0.8521
Mecoptera	Permotipulidae	4.40	4.70	4.70	5.00	Permian	0.8521
Cnemidolestodea	Tillyardembiidae	4.00	10.00	9.39	14.00	Permian	0.8521
Permotrichoptera	Microptysmatidae	3.60	5.00	5.31	8.30	Permian	0.9022
Mecoptera	Permochoristidae	3.50	7.50	7.56	24.00	Permian	0.9462
Miomoptera	Palaeomanteidae	2.50	5.70	6.28	42.00	Carboniferous	0.9566
Notoptera	Lemmatophoridae	4.30	8.90	9.57	22.00	Permian	0.9602
Eoblattida	Soyanopteridae	4.50	5.50	6.20	9.00	Permian	0.9700
Hemiptera	Surijokocixiidae	4.30	4.90	4.90	5.50	Permian	0.9800
Protelytroptera	Archelytridae	4.00	4.90	5.00	6.00	Permian	0.9822
Coleoptera	Permocupedidae	3.00	4.70	4.74	8.00	Permian	0.9828
Hemiptera	Ipsviciidae	4.00	6.20	6.34	9.00	Permian	0.9852
Coleoptera	Tshekardocoleidae	4.20	10.00	10.11	15.00	Permian	0.9887
Psocodea	Archipsyllidae	5.20	5.45	5.45	5.70	Permian	0.9980
Glosselytrodea	Jurinidae	4.75	6.60	6.74	10.00	Permian	1.0000
Mecoptera	Kaltanidae	4.50	7.10	8.13	19.00	Permian	1.0000
Mecoptera	Mesopsychidae	4.25	5.60	5.75	10.00	Permian	1.0000
Protelytroptera	Protelytridae	5.00	6.75	7.31	11.60	Permian	1.0000
Mecoptera	Protomeropidae	4.80	7.00	7.29	12.00	Carboniferous	1.0000
Hemiptera	Scytinopteridae	3.70	6.00	6.39	10.50	Permian	1.0000

All measurements are in millimeters. *p* values are for a one-sided Kolmogorov-Smirnov test

min minimum wing length during the Paleozoic, *max* maximum wing length during the Paleozoic, *mean* mean wing length during the Paleozoic, *med* median wing length during the Paleozoic

In this contribution, wing-length measurements are provided for Paleozoic insects. These wing-length data provide estimates of body mass (Clapham and Karr 2012) that were compared between lineages and then compared to the Paleozoic fossil record of leaf galls. This comparison is used to identify the insect lineages that evolved a smaller body size during the Permian and may have been responsible for the fossil record of leaf galling from this interval.

Materials and methods

Paleobiology Database (PBDB) wing measurement data were downloaded on 17 September 2013, accessed through the "Measurements of Specimens" option in the "Download" menu, using the group name "insect." Following the procedure established by Clapham and Karr (2012), comprehensive measurements of insect forewings included taxa with membranous and hardened morphologies, the latter consisting of tegmina, elytra, and hemelytra. All analyses were performed in R (Development Core Team 2014). Cluster analysis of all insect wing lengths from the Paleozoic was carried out with the densityMclust function in the mclust package (Fraley et al. 2012). The smallest wing-length cluster was examined in further analyses. The 26 families represented by only one specimen were removed from the dataset, and the natural log of each wing length was used for all further statistical analyses. Levene's test was used to test variance homogeneity and the Shapiro-Wilks test was used to test for normality. The Kruskal-Wallis test was performed, followed by one-sided Kolmogorov-Smirnov tests in which each family was compared to all others to identify specific lineages with significantly small wing lengths.

Minimum insect wing length through the entirety of the Phanerozoic was estimated with the rq function in the quantreg package (Koenker 2013), which calculated the 0.01 quantile of insect wing length (tau=0.01), based on a polynomial regression, for each geologic stage for which 30 or more wing measurements were available. Because radiometric age dates are not associated with any fossils in this study, the date assigned to each specimen was the midpoint (to the nearest 500 thousand years) of the geologic stage to which it belongs. Stage midpoint assignments were based on the latest available geochronology (Gradstein et al. 2012). The Pennsylvanian–Permian relationship between estimated minimum wing length and paleocontinental glaciation, a paleoclimate proxy, was estimated using the base-R function cor. To determine the rate of change in estimated minimum wing length, the first derivative of the polynomial regression was hand-coded in R and calculated for the midpoint of each stage of the Pennsylvanian and Permian.

Table 3 Body length ranges, in millimeters, for extant insect lineages that include many gall-inducers on leaves (Borror and White 1970; Borror et al. 1989). The body length/wing length ratio is around 1 in many other insect lineages that span Paleoptera, Hemimetabola, and Holometabola (Malmqvist 2000; Kristensen 2003). References are listed in the supplemental information

Taxon	Length (mm)
Thysanoptera	0.5–5
Psyllidae	2–5
Cecidomyiidae	1–5
Cynipinae	2–8

Results

A cluster analysis shows that Paleozoic wing lengths are distributed multimodally into four clusters. The smallest cluster consists of insect wings less than 5.85 mm in length and contains 38 families represented by multiple specimens. Families in this cluster show significant variance heterogeneity of log wing length (Levene's test: $p<0.0001$), and these values are not normally distributed (Shapiro-Wilks test: $p<0.0001$), necessitating the use of nonparametric tests. A Kruskal-Wallis test confirms that the families in this cluster have significantly different wing lengths ($p<0.0001$). The Kolmogorov-Smirnov test, implemented to identify specific families with

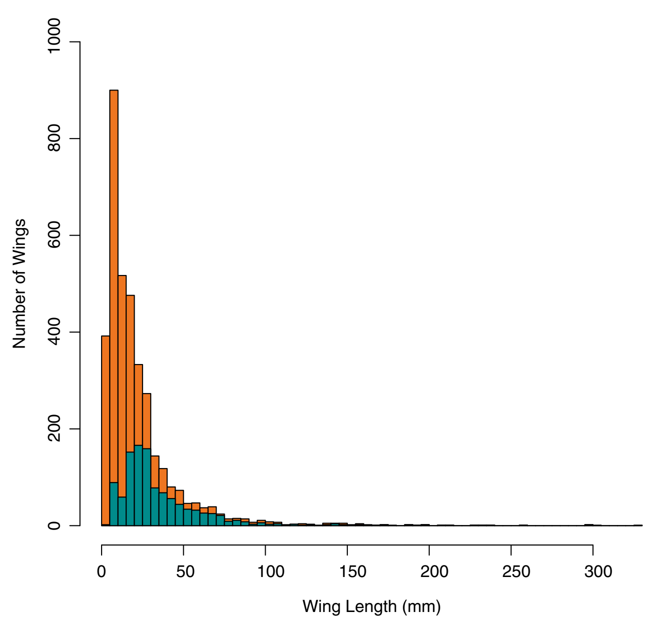

Fig. 1 Frequency distribution of insect wing lengths during the Paleozoic, based on data from the Paleobiology Database. Wing lengths from the Late Carboniferous (=Pennsylvanian) are represented in *blue*; wing lengths from the Permian, in *orange*

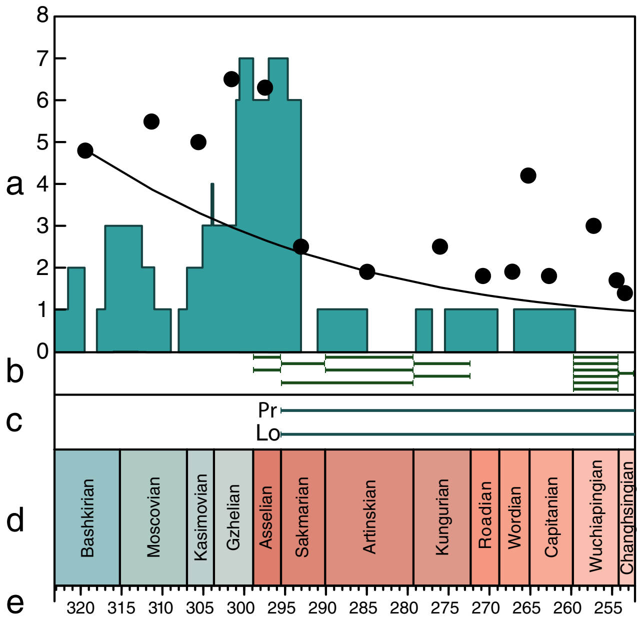

Fig. 2 Data pertaining to paleoenvironment, insect morphology, and temporal distribution of leaf galls. **a** Minimum insect wing lengths in millimeters (*dots*); estimated minimum insect wing length through time (*solid line*); and the number of paleocontinents on which grounded ice was present (*bars*), used here as a proxy for cool climates (Montañez and Poulsen 2013). **b** The stratigraphic ranges of documented incidences of leaf galls—each *line* represents one flora from which leaf galls have been found (Table 1). **c** The documented stratigraphic ranges of insect lineages that may have galled leaves during the Paleozoic: *Pr* = Protopsyllidiidae; *Lo* = Lophioneuridae. **d** Geologic stages used for midpoint calculations in **a** above (Gradstein et al. 2012). **e** Age, in millions of years before the present (Gradstein et al. 2012)

significantly small wing lengths, shows that 33 families within the cluster had non-significantly small wing lengths ($p>0.05$); the remaining 5 families had extremely significantly small wing lengths ($p<0.0005$). These families are, in effect, the very smallest of the small-winged taxa (Table 2): Permosynidae, Schizocoleidae, and Taldycupedidae (Coleoptera); Protopsyllidiidae (Hemiptera); and Lophioneuridae (closely related to Thysanoptera). The first three families belong to the Archostemata, the basalmost extant clade of Coleoptera (Beutel et al. 2008). In modern ecosystems, this clade is intricately associated with wood, cambium, and bark tissues (Hamilton 1978). This life-habit also is documented for closely related Permian archostematan ancestors (Beutel et al. 2008), which also are linked to borings in Middle Permian conifer wood (Naugolnykh and Ponomarenko 2010). There is no evidence that modern Archostemata or their Permian ancestors have ever been associated trophically with foliage (Beutel et al. 2008). Unlike the three beetle lineages, which are highly unlikely culprits for Paleozoic leaf galling, the Protopsyllidiidae and Lophioneuridae—major Permian lineages of the Hemipteroidea—are viable candidates for early leaf gallers on foliage. Documentation from the Paleobiology Database indicates that these two families first appeared during the Early Permian, as did foliar galls (Stull et al. 2013). The body sizes of Permian representatives of these two families are similar to the body sizes of extant lineages that include leaf gallers (Table 3).

The Paleozoic insects with the very smallest wing lengths occur almost exclusively from the Permian (Fig. 1). The wing lengths of the smallest insects decreased as glaciers receded ($r=0.7485$), with estimated wing length decreasing most sharply during the Pennsylvanian (0.13–0.08 mm/m.yr.), and then more slowly during the Permian (0.07–0.01 mm/m.yr.) (Figs. 2 and 3). As the rate of wing length decrease began to level off, leaf galls first appeared. The earliest documented leaf galls are from the Asselian stage of the Permian (Stull et al. 2013; Table 1), an interval in which grounded ice covered much of the earth's land surface, as had been the case earlier during the Pennsylvanian. As continental glaciers receded during the Permian, evident in both Euramerica and Gondwana, a warmer, dryer habitat became available and the prevalence of leaf galling appears to have increased (Fig. 2).

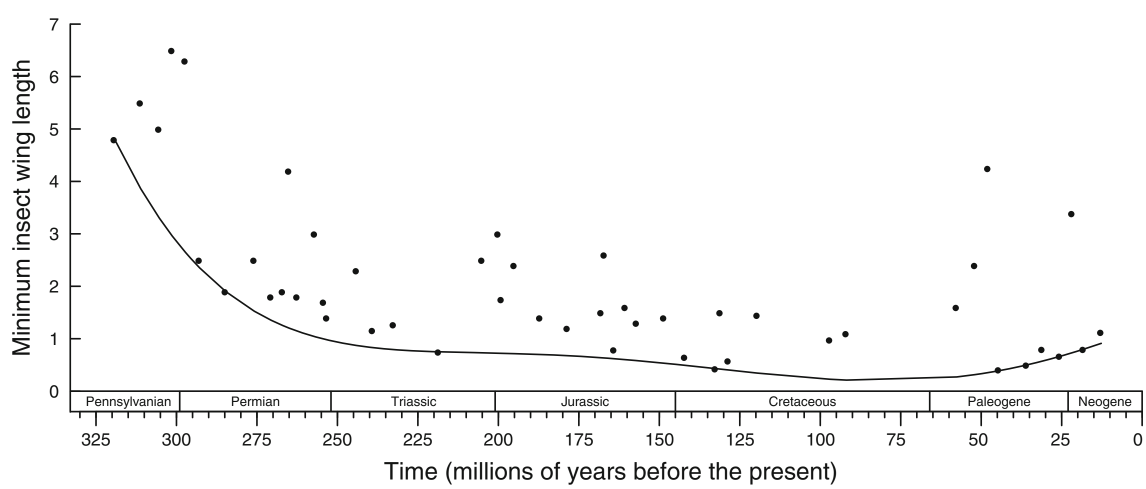

Fig. 3 Minimum insect wing length throughout the Phanerozoic, in millimeters: minimum observed wing lengths (*dots*); estimated minimum wing length through time (*solid line*)

Discussion

Modern hemipteroid insects—psocodeans, hemipterans, and thysanopterans—often gall leaves. Among Permian Hemiptera, the family Protopsyllidiidae accounts for the highest proportion (42.22 %) of Paleozoic wing lengths under 5.85 mm. This sternorrhynchan family first appeared during the Sakmarian Stage of the Early Permian, diversifying with initial, suborder-level divergences in the Kungurian Stage at the end of the epoch (Shcherbakov 2000). The earliest known fossil sternorrhynchan clade, the Archescytinidae, a sister-group to the Protopsyllidiidae, also has its earliest occurrence during the Sakmarian Stage and similarly had body sizes of less than 5 mm (Shcherbakov 2000). Although the plant-host associations and reproductive strategies of Permian Hemiptera are still not entirely understood, certain archescytinids are believed to have laid their eggs in gymnosperm reproductive organs (Becker-Migdisova 1985). Becker-Migdisova's (1985) morphological evidence of ovipositor structure is an example of earlier studies that complement our current knowledge of the eight types of hemipteroid damage on plants: principally piercing-and-sucking lesions, but also scale cover damage on epidermal tissues (Prevec et al. 2009; Schachat et al. 2014). The major modern lineages of Sternorrhyncha also included gall-inducers that target gymnospermous and angiospermous foliage (Schaefer et al. 2005).

The family Lophioneuridae also has an earliest occurrence during the Sakmarian Stage of the Early Permian and represents either a paraphyletic stem-group leading to (Beckemeyer 2004) or the sister-group of (Grimaldi and Engel 2005) the Thysanoptera. Gall-induction has arisen multiple times within both extant thysanopteran suborders, the Terebrantia and Tubulifera (Mound and Morris 2005). The presence of the Lophioneuridae among gymnosperm-dominated floras, and the mid-Cretaceous extinction of the Lophioneuridae (Grimaldi and Engel 2005), concurrent with the diversification of angiosperms and the consequent decline of gymnosperms (Lupia et al. 1999), suggests that the Lophioneuridae were specialized gymnosperm herbivores.

All extant hemipteroid gallers induce a gall response from the host plant by either ovipositional or feeding activity (Raman 2012), rather than by specific secretions associated with lesions during oviposition, as is the case with other insect gallers (Meyer 1987). This mechanism of gall-induction likely extends back to the Permian, as two hemipteroid families identified in our analysis, the Protopsyllidiidae and Lophioneuridae, occur during the Permian (Shcherbakov and Popov 2002) and were likely gall-inducers. The Protopsyllididae, such as *Tchecardaella tchecardaensis*, bore relatively long, laterally flattened ovipositors (Becker-Migdisova 1948) that penetrated shallow plant tissues for insertion of eggs. The Lophioneuridae, in contrast, possessed shorter, rasp-like ovipositors (*Tschekardus*, Vishniakova 1981) that likely punctured very shallow epidermis. Two additional hemipteran families also may have been gallers, as indicated by the variety of ovipositors designed for endophytic penetration of plant tissues. These ranged from abdominally coiled, watchspring ovipositors for placement of eggs deep into parenchymatic and vascular tissues in the Archescytinidae (*Archescytina*, Becker-Migdisova 1961), to the shorter, stout, punching ovipositors of the Prosobolopseidae (*Prosobolopsis*, Becker-Migdisova 1960).

In 1991, A.C. Scott wrote, "Most gall-producing arthropods are insects whose families have their origins in the Mesozoic or Tertiary. They include the Hemiptera (bugs), Hymenoptera, Coleoptera, Lepidoptera, and Diptera. It is not surprising, therefore, that only one Permian example of a gall has been recorded. Galls become more common, and occur often on angiosperm leaves, in the mid to Late Cretaceous and become much more common in the Tertiary" (p. 60). The recent increase in documentation of Permian leaf galls (Table 1) contradicts this notion, long shared by paleontologists and neontologists alike (Raman et al. 2005). Though modern insect families that include gallers do not extend back to the Paleozoic, the ancestors and relatives of some of these families appear to have also galled Permian leaves.

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