RECORD OF GALL ABUNDANCE AS A POSSIBLE EPISODE OF RADIATION AND SPECIATION OF GALLING INSECTS, TRIASSIC, SOUTHERN BRAZIL

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ABSTRACT – A possible episode of coevolution between galling insects and plants is reported. It was identified by a high infestation (density) of fossil gall found on the compressed *Dicroidium* Flora from the Triassic (Ladinian–Carnian) Passo das Tropas Member, Santa Maria Formation, Paraná Basin. The galls were found on phytofossils in 2.2 m thick mudstones with horizontal lamination, intercalated between coarse and medium-grained sandstones with clasts and cross-lamination at the base and top of the section. The associations were identified with a stereomicroscope, after which they were quantified within each botanical group, along with their type, in order to calculate the average number of galls per leaf (density). The overall density found was 4.018. *Corystospermales* was the predominant botanical group (87.81%), with a gall density of 4.281, followed by Ginkgoales, Equisetales, and *Incertae sedis*. Current ecological studies indicate that a xerophytic paleoenvironment correlates with high infestations of galling insects. However, many taphonomic, biological, and ecological factors may be involved, resulting in different hypotheses from the same data. On the other hand, they support the interpretations of this record in other aspects discussed. Furthermore, the identified gall density can be interpreted from a paleobiogeographical perspective, showing dispersion at low altitudes and intermediate subtropical latitudes (25° to 38° S or N).

Key words: insect-plant interaction, galling-insects, *Dicroidium* Flora, Gondwana.

RESUMO – Um possível episódio coevolutivo de insetos galhadores é registrado. Esta ocorrência foi verificada devido à alta infestação (densidade) de galhas fósseis encontrada nas impressões/compressões da Flora *Dicroidium* para o Triássico (Ladiniano–Carniano), Membro Passo das Tropas, Formação Santa Maria, Bacia do Paraná. As galhas estão registradas em fitofósseis em argilitos laminados com 2,2 m de espessura, intercalados a camadas de arenitos de grãos médios a grossos, com grânulos e laminação cruzada na base e no topo. As interações foram identificadas com estereomicroscópio, quantificadas e qualificadas em cada grupo botânico para as análises estatísticas, nas quais foi aplicada a média de galhas por folhas (densidade). A densidade geral encontrada foi 4,018. *Corystospermales* foi o grupo predominante (87,81%) com 4,281 de densidade, seguido por outros grupos em menores taxas: Ginkgoales, Equisetales e *Incertae sedis*. A hipótese gerada pela composição das densidades nas paleofloras foram comparadas com padrões ecológicos atuais, os quais indicam um paleoambiente xerofítico para altas infestações de galhadores. Além disso, outros fatores tafonômicos, biológicos e ecológicos podem estar envolvidos, resultando em diferentes hipóteses para esses dados, por outro lado, suportam o registro em outros fatores discutidos. Do mesmo modo, a densidade de galhas verificada pode ser interpretada utilizando uma abordagem paleobiogeográfica, demonstrando a dispersão em baixas altitudes e latitudes subtropicais intermediárias (25° a 38° S ou N).

Palavras-chave: interação inseto-plantas, insetos galhadores, Flora *Dicroidium*, Gondwana.

INTRODUCTION

Plant-insect interactions are the consequence of coevolution, which began with a need by insects to obtain food resources. When the insects met the defenses and strategies that the plants employed against those attacks over a long period during their evolutionary history (Mello & Silva-Filho, 2002), both groups evolved diversifying into a large number of species (Bernays & Chapman, 1994). In this way, insects and plants reproduce a fascinating and complex ecological relationship around the world (Adami-Rodrigues, 2003; Bernays & Chapman, 1994; Del-Claro & Torenzan-Silingardi, 2012).

Among these interactions, gall formation is one of the relationships that have been described from the fossil record. Their induction is caused by insects from a diverse group of clades, namely, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera (Price, 2005), with Diptera and Hymenoptera being the groups most represented. Galls are viewed as excellent tools for ecological studies, because they are abundant, diverse, and sessile, occurring in all biogeographically regions around the world (Fernandes & Price, 1988, 1991; Fernandes *et al.*, 2001). They have been used in observational and experimental studies, and also to test ecological evolutionary hypotheses (Fernandes & Price, 1988; Price *et al.*, 2004). In addition, quantitative

analyses of galls in the fossil record have been used to demonstrate paleoenvironmental changes (Wilf, 2008), since galling insects obtain benefits from their endophytic habitat, such as protection against desiccation, possible predators, and are useful as a weatherproof structure (Santos *et al.*, 2012). Furthermore, galling insects are abundant mainly in xeric habitats, and also show a preference for low altitudes and intermediate subtropical latitudes (Price *et al.*, 1998). They have also been reported in association with infertile soils (Blanche & Westoby, 1995). These factors imply many ecological hypotheses for the study of galling insects, which have been used by a few paleobiologists as tools to show changes in the climate and geographical distribution (Sarzetti, 2011; Wilf, 2008), and to a lesser extent applied to ecological–evolutionary hypotheses of the fossil record.

Galling insects currently show a preference for infecting leaves (Labandeira, 1998), and in the fossil record, impressions/compressions of leaves are the most abundant when compared with other plant remains that have been collected from outcrops around the world, recorded in the databases of museums and collections, and registered on the Paleobiology Database (Wilf, 2008).

Looking at the fossil record, the oldest gall reported appears in the Upper Pennsylvanian (Labandeira & Phillips, 1996), and galls continue appearing until the Permian, a period with a high number of examples reported in the Northern Hemisphere (Labandeira & Allen, 2007; Schachat *et al.*, 2014; Schachat *et al.*, 2015; Potonié, 1893; Van Ameron, 1973; Vasilenko, 2007; Weiss, 1904) and in Southern Gondwana, where they have been reported in association with different paleofloras (Adami-Rodrigues *et al.*, 2004; Banerjee & Bera, 1998; Pant & Srivastava, 1995). In the Mesozoic galls are registered from the Middle Triassic, in Australia (McLoughlin, 2011), with a higher occurrence found in the Molteno Formation, which shows an expression of exophytic herbivory and leaf-mining, dated to the Carnian (Upper Triassic) (Scott *et al.*, 2004). However, the records are sparse, and the previous studies do not take advantage of the potential of these traces (Adami-Rodrigues, 2003).

After the discovery of the new Passo das Tropas outcrop, where Cenci (2013) described the presence of insect activity on *Dicroidium* Flora leaves, a quantitative analysis was needed. Then, the aim of this paper is to discuss the following topics: (i) can the density of galls be used as a tool to confirm the probable episode of radiation and speciation of galling insects in the Middle Triassic? (ii) what factors may control the gall presence in that past environment, and (iii) the conclusion that gall density can be used in a possible paleoclimate reconstruction, and to infer the paleogeographical position of the locality.

MATERIAL AND METHODS

Geological setting

The fossils come from an exposure of the Passo das Tropas Member type section, located in Santa Maria County, at coordinates 29°44'37.85"S and 53°47'36.12"W (Figure 1).

The phytofossils are preserved in a 2.2 m thick mudstone with horizontal lamination, intercalated between coarse and medium-grained sandstones with cross-lamination at the base and top of the section.

The studied outcrop was previously correlated with the type section of the Passo das Tropas Member (Guerra-Sommer *et al.*, 1999), due to its proximity, the sedimentary facies, and the composition of the *Dicroidium* Flora previously published (Barboni & Dutra, 2015; Barboni *et al.*, 2016). The paleoflora registered were *Xylopteris* sp., *Baiera*, *Sphenobaiera*, and *Ginkgo*-related fertile forms, which extended the Passo das Tropas Member to the Carnian, being assigned to the Ladinian–Carnian boundary, Passo das Tropas Member, Santa Maria Formation, of the Paraná Basin (Barboni & Dutra, 2015; Barboni *et al.*, 2016).

Statistical analysis

The analysis included impressions/compressions of the paleoflora from six field assemblages (N=414). The samples were prepared using, as a basis, a special methodology for laminated mudstone (Barboni *et al.*, 2008). The samples are deposited in the Life and Earth History Laboratory, Unisinos University. Using a stereomicroscope, the structures attributed to gall induction were identified, and were subsequently imaged and quantified. For comparison the average (*m*) was calculated for each group of paleoflora.

RESULTS

The exceptional preservation of these galls is unprecedented in the Middle/Upper Triassic (Ladinian–Carnian) of South America. A number of 659 galls on *Dicroidium* Flora leaves in 164 impression/compression samples were identified (Figure 2). The average values show the greatest density of galls on Ginkgoales, closely followed by Corystospermales, and by a lower expression on Equisetales and *Incertain sedis* (Figure 3).

The gall density on Corystospermales is the second-highest value in comparison with the other paleobotanical groups, but they are the most represented leaves in the assemblage, followed by Ginkgoales (Figure 3). The amount of material related to Equisetales and groups of uncertain affinity (*Incertain sedis*) is lower; however, Equisetales is represented by stems rather than leaves, differing from the other paleobotanical groups. Galls found on *Taeniopteris* sp. leaves are less represented than on Ginkgoales and Corystospermales.

In the paleofloristic analysis, the galls were most present on the taxon Corystospermales, followed by Equisetales and Ginkgoales, and finally *Incertain sedis* (Figure 3).

DISCUSSION

The observation that galling insects prefer leaf organs is currently recognized (Santos *et al.*, 2012), and is reflected in the fossil record of galls, 80% of which are found on leaves (Labandeira, 2002). Besides, the higher abundance of Corystospermales over other groups is commonly found in other *Dicroidium* floras worldwide (Anderson & Anderson,

Figure 1. Site of the Passo das Tropas outcrop (arrow) in its correlated geological and geographical setting (modified from Barboni & Dutra, 2013, first assembled by Faccini, 2000).

1989, 1995; Artabe *et al.*, 2007; Retallack, 1977), which is also similarly demonstrated by its abundance in another outcrop belonging to the Passo das Tropas Member (Da Rosa *et al.*, 2009).

Can the density be used as a tool to confirm the probable episode of radiation and speciation of galling insects in the Middle Triassic?

The abundance of galls reported in this paper is due to the high density of galls per fossil leaf, exceeding the results found by Fernandes & Price (1992) for current galling insects, such as *Andricus tecturnarum* (Hymenoptera: Cynipidae), which establishes galls on *Quercus turbinella* (Fagaceae). This comparison of ratios is the only one that shows superior values when compared to other densities of gall fossils, having the other four current gall lower densities (Table 1). The taphonomic bias makes comparisons with these current

densities difficult, and there are no calibration studies on the influence of the types of plant-hosts and gall inductors in similar depositional environments. This taphonomic bias influences the preservation and rate of leaf debris in the paleoenvironment, due to the particularities of the relationship between the plants and galling-insects (Abrahamson & Weis, 1997). Moreover, the polyphyletic origin of galling-insects is still in discussion, which makes impossible to identify the inductors that may have characterized the ecological–evolutionary phenomenon.

Factors that may have influenced gall presence in past environments

In modern environments, the examination of a known number of plants with the leaf organs removed directly from the plant host, as in Fernandes & Price (1992), is an advantage in comparative studies. Conversely, in paleoenvironments,

Figure 2. Photographs of figured gall fossils on leaves of each functional feeding group from the Upper Triassic Passo das Tropas outcrop. **A**, seed gall on *Umkomasia* type attributed to *Corystospermales* single-seed. **B**, *Neocalamites* sp. stem with galls changing the vein arrangement, **C**, circular galls on fern of *Dicroidium* sp. **D**, different sizes of ovoid galls distributed on leaf of *Dicroidium odontopteris*. **E**, *Sphenobaiera* sp. infested with galls. **F**, gall on *Dicroidium odontopteris* leaf enlarged. **G**, Gall on mid-vein of *Taeniopteris* sp. **H**, tridimensional gall and disrupted gall on *Dicroidium odontopteris*. Scale bars: A–E, H = 10 mm; F = 5 mm.

the taphonomic factors may control the preservation of fossil leaves that did not suffer abscission from their original plants. Thus, the rates presented herein are not from an exact number of individual plants, but from leaf debris dropped without known origin.

The density results can also be related to the action of modern insects (Fernandes & Price, 1992) (Table 1). For instance, the number of leaves that have their impressions/compressions preserved may be lower than the number of fronds originally connected to the host plant. Modern galls could easily be counted more than fossil galls, owing to the greater amount of data available for interpretation. On the other hand, the plant hosts could have induced leaf abscission as a mechanism to protect against the attack of the gall inducer (Santos *et al.*, 2012), which could have increased the number of leaves with galls in this paleolake setting preserved in the Passo das Tropas outcrop; in this way, the action of the galling insects would have strengthened the density of galls preserved in this paleoenvironment.

It is noteworthy that the morphological aspects of corystosperm leaves, although they were not examined in the final averages analysis, stand as forked fronds rather than a unique leaf area. Variations in their leaf limb areas, which are small but numerous (Guerra-Sommer & Pires, 2011), could be factors requiring further research on how this particularity bias the data.

The paleoecological conditions, such as the seasonal climate reported for Gondwana in continental basins worldwide (Artabe *et al.*, 2007; Cantrill *et al.*, 1995;

Elliot, 1975), could be factors related to the building of communities of deciduous and xerophytic paleoflora (Barboni *et al.*, 2016), which may increase leaf abscission rate in that paleoenvironment in a specific season. This means that the presence of galling insects may have some association with the *Dicroidietum zuberi xylopterosum* (xerophytic woodland) proposed by Retallack (1977) for Australasia. In addition, the latter author reported that the composition of that xerophytic woodland was influenced by soil infertility and a high water

Figure 3. Graph showing rate comparison of galls and leaf numbers in each paleobotanical group.

Table 1. Rates of Fernandes & Price (1992) of current leaves and galls on each botanical group joined to rates of palaeogalls on each palaeobotanical group.

Galling insects species	Plant organ galled	Habitat	Galls per leaves and stems (<i>m</i>)	Plants (<i>n</i>)
Present insect data				
<i>Pachypsylla venusta</i> (Homoptera: Psyllidae)	Leaves	Xeric	0.364	25
		Mesic	0.064	20
<i>Andricus tecturnarum</i> (Hymenoptera: Cynipidae)	Leaves	Xeric	14.490	10
		Mesic	0.244	5
<i>Neuroterus lamellae</i> (Hymenoptera: Cynipidae)	Leaves	Xeric	0.396	20
		Mesic	0.080	11
<i>Cantarinia</i> sp. (Diptera: Cecydomyiidae)	Leaves	Xeric	0.711	14
		Mesic	0.194	10
<i>Incertae sedis</i> (Diptera: Cecydomyiidae)	Leaves	Xeric	0.541	14
		Mesic	0.182	17
<i>Aciurina trixa</i> (Diptera: Tephritidae)	Buds	Xeric	0.600	25
		Mesic	0.433	20
<i>Asphondilia garryae</i> (Diptera: Cecydomyiidae)	Buds	Xeric	95.070	14
		Mesic	98.000	8
<i>Rhopalomyia chrysothamni</i> (Diptera: Cecydomyiidae)	Stems	Xeric	0.728	10
		Mesic	0.435	10
Fossil data				
??	Leaves	Xeric	4.455	??*
??	Leaves	Xeric	4.281	??*
??	Stems	Xeric	2.750	??*
??	Leaves	Xeric	1.000	??*

* Fossil galls do not show evidence of galling insect inductors.

** Number of plants is not recorded on fossils; only the number of leaves is recorded.

stress, which may be a disadvantage to the paleoflora, while giving support to galling insects as described by Blanche and Westoby (1995) for modern insects. These factors strengthen the findings of this paper.

In yet another point, as wildfires are found to be frequent in the Triassic worldwide (Abu Hamad *et al.*, 2013; Nabbenfeld *et al.*, 2010; Petersen & Lindstrom, 2012; Shen *et al.*, 2011). Studies examining these phenomena may shed more light on the question of paleoecological control on galling insects, since wildfires are discussed nowadays as acting as a factor in the speciation and radiation of galling insects (Mendonça, 2001), concomitantly stimulating the formation of new sites for oviposition, which may control those communities (Bush, 1975, 1994; Nyman & Julkunen-Titto, 2000).

In relation to current factors, a vast knowledge about galling insects is linked to (i) the association of galling insects and xerophytic plant groups with their strategies to prolong leaf connection to the plant and their lower rates of abscission, production of secondary compounds and nutrient deficiency (Santos *et al.*, 2012); (ii) on the other hand, galling insects act as drains, mobilizing nutrients from other plant sources (Nyman & Julkunen-Titto, 2000). Galling insects become able to overcome the chemical defenses of plants, so these insects prefer the xeric vegetation in stressed habitats due to the low concentration of available nutrients in the environment and excess secondary compounds (Fernandes, 1990; Fernandes & Price, 1988, 1992); (iii) in addition, the concomitant production of meristems is related to new oviposition sites for galling insects. These factors may be associated with these new controllers of burned sites (Mendonça, 2001). This production of synchronized sprouts increases the chance of errors and oviposition replacement hosts, resulting in the process of sympatric speciation as it is best known in the case of herbivorous insects and galling insects (Bush, 1975, 1994; Nyman & Julkunen-Titto, 2000); (iv) xeric environments hinder the progression of fungi and natural predators, diminishing the mortality of the galling insects' larvae, resulting in a greater abundance in xeric than in mesic habitats (Fernandes & Price, 1992). Thus, the series of factors above is considered as potentially responsible for the speciation and radiation of galling insects in environments with water shortages (Fernandes, 1990). Our results could possibly be showing an episode of this coevolutionary stage and the galling insects' fitness in the fossil record. Krassilov & Rasnitsyn (2008) similarly discovered high gall diversity in a Cretaceous mangrove paleohabitat in Israel. Thus, the significant presence of galls may be indicating an adaptive success of these insects, representing the fitness of these endophytic herbivores, which may have taken advantage of ecological conditions that resulted in their abundance.

Can the gall density be used to deduce a possible micropaleoclimate and for paleogeographical inferences to the paleoenvironment?

Qualitative and quantitative studies of plant–insect interactions and the recognition of their proportions can be used as an indicator of paleoenvironmental conditions and paleoclimate (Wilf, 2008), but can also be used for the analysis

of the evolution of insect behavior (Adami-Rodrigues, 2003). As already discussed, the studies made on the composition of galling insects in xeric and mesic environments in current plant–insect interactions (Fernandes & Price, 1991, 1992), along with reports of these associations in the fossil record, make these insect traces on plants indicators of dry climates (Sarzetti, 2011).

In this way, paleoenvironmental information deduced from other Triassic outcrops indicates seasonality variations in climate, as was verified by reports from Argentina (Artabe *et al.*, 2007; Spalletti *et al.*, 2005; Gastaldo *et al.*, 2005) and Africa (Price *et al.*, 1998). The presence of galling insects, which has been associated with stressed habitats in the Triassic, and linked to soil infertility (Blanche & Westoby, 1995), suggests a possible xeric microclimate for these strata from the Passo das Tropas outcrop.

The patterns of distribution and diversity of current galling insects do not show a latitudinal model, although they have a greater richness in intermediate subtropical latitudes (25° to 38° S or N) (Price *et al.*, 1998). These intermediate latitudes correspond to the position of Rio Grande do Sul State in the Triassic (Anderson, 2001). An altitudinal pattern is also recognized; galling insects present a higher species richness and abundance at low altitudes on a regional scale (Fernandes & Price, 1988, 1991, 1992; Price *et al.*, 1991), what can be the situation of the studied association. Thus, the use of the presence and abundance of galls based on the current altitudinal pattern (Fernandes & Price, 1988) may allow inferences about the probable position of the paleoenvironment at low altitudes where the galls were reported.

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