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

ROMULO CENCI
Programa de Pós-Graduação em Geologia, UNISINOS. Av. Unisinos, 950, 93022-750, São Leopoldo, Rio Grande do Sul, Brazil. romulocenci@hotmail.com

KAREN ADAMI-RODRIGUES
Núcleo de Estudos em Paleontologia e Estratigrafia, Centro das Engenharias, Universidade Federal de Pelotas. Rua Xavier Ferreira, 02, 96010-440, Pelotas, RS, Brazil. karen.adami@gmail.com

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 (25º to 38º S or N).

Key words: insect-plant interaction, galling-insects, Dicroidium Flora, 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 fertile 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; Vasilienko, 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 Xylopterus sp., Baileya, 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 Coryystospermales, and by a lower expression on Equisetales and Incertae sedis (Figure 3).

The gall density on Coryystospermales 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 (Incertae sedis) is lower; however, Equisetales is represented by stems rather than leaves, differing from the other paleobotanical groups. Galls found on Taeinipterus sp. leaves are less represented than on Ginkgoales and Coryystospermales.

In the paleofloristic analysis, the galls were most present on the taxon Coryystospermales, followed by Equisetales and Ginkgoales, and finally Incertae 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 Coryystospermales over other groups is commonly found in other Dicroidium floras worldwide (Anderson & Anderson,
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 inducers 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 inducers 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 paleocological 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

**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.

<table>
<thead>
<tr>
<th>Galling insects species</th>
<th>Plant organ galled</th>
<th>Habitat</th>
<th>Galls per leaves and stems (n)</th>
<th>Plants (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pachypsylla venusta</em> (Homoptera: Psylidae)</td>
<td>Leaves</td>
<td>Xeric</td>
<td>0.364</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesic</td>
<td>0.064</td>
<td>20</td>
</tr>
<tr>
<td><em>Andricus tecturnarum</em> (Hymenoptera: Cynipidae)</td>
<td>Leaves</td>
<td>Xeric</td>
<td>14.490</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesic</td>
<td>0.244</td>
<td>5</td>
</tr>
<tr>
<td><em>Neuroterus lamellae</em> (Hymenoptera: Cynipidae)</td>
<td>Leaves</td>
<td>Xeric</td>
<td>0.396</td>
<td>20</td>
</tr>
<tr>
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<td></td>
<td>Mesic</td>
<td>0.080</td>
<td>11</td>
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<tr>
<td><em>Cantarinia</em> sp. (Diptera: Cecydomyiidae)</td>
<td>Leaves</td>
<td>Xeric</td>
<td>0.711</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesic</td>
<td>0.194</td>
<td>10</td>
</tr>
<tr>
<td><em>Incertae sedis</em> (Diptera: Cecydomyiidae)</td>
<td>Leaves</td>
<td>Xeric</td>
<td>0.541</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesic</td>
<td>0.182</td>
<td>17</td>
</tr>
<tr>
<td><em>Aciurina trixa</em> (Diptera: Tephritidae)</td>
<td>Buds</td>
<td>Xeric</td>
<td>0.600</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesic</td>
<td>0.433</td>
<td>20</td>
</tr>
<tr>
<td><em>Asphondilia garryae</em> (Diptera: Cecydomyiidae)</td>
<td>Buds</td>
<td>Xeric</td>
<td>95.070</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mesic</td>
<td>98.000</td>
<td>8</td>
</tr>
<tr>
<td><em>Rhopalomyia chrysothamni</em> (Diptera: Cecydomyiidae)</td>
<td>Stems</td>
<td>Xeric</td>
<td>0.728</td>
<td>10</td>
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<td></td>
<td></td>
<td>Mesic</td>
<td>0.435</td>
<td>10</td>
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<td>Stems</td>
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<td>Leaves</td>
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* 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 paleecological 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 galls 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 (25º to 38º 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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