Plant-insect interactions of the Passo das Tropas outcrop, Santa Maria Formation, southern Brazil (Late Ladinian)

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Abstract:

This work focuses on traces produced in vegetative organs of the Triassic *Dicroidium* Flora, demonstrating a high rate of the damage types in corystosperm plants. The data correspond to *Dicroidium* Flora strata Lagerstätten from the Ladinian (Passo das Tropas outcrop = PTO), Santa Maria Formation, Paraná Basin. We use a qualitative and quantitative approach for morphological characterization of the traces, together with ontogenetic aspects of the plant-hosts for interpretation. The insect traces on Ladinian plants are composed principally of an infestation of scales (324 units). Furthermore, 16 mine traces and 76 traces interpreted as scars of oviposition are also registered. The different damage types were grouped in 17 damage types (DT), six of which are new. The correlation two-tailed test was applied for the pinna-pinnule height ($p = 0.07$) and width ($p = 0.37$) of corystosperms. The maximum scale diameter (new DT C) is not significantly correlated to the limb measures of the corystosperms, suggesting that a significant relation between the scale and the leaf size does not exist. The leaves of the corystosperms with scales appear significantly larger in width (Mann-Whitney, $U = 11639$, $p < 0.0001$), suggesting that herbivore organisms selected larger leaves. The external feeding indexes (11,45%), DT diversity and choice of host plants exhibit patterns that are similar to those found in Carnian sites from the Molteno Formation (Middle-Upper Triassic) of southern Africa.

Keywords: *Dicroidium* Flora, endophytic habit, scale insect, Santa Maria Formation, lagerstätten

The Triassic strata studied here is located in the City of Santa Maria, southern Brazil (29°44´37, 85´´S and 53°47´31, 12´´W), along the BR 392 highway. The phytofossils were extracted from 2.20 m of laminated mudstone. This mudstone alternates with massive, planar, and trough cross-bedded sandstones and conglomerates, the latter containing gravels and boulders of mud.

The material consists of 550 plant samples of the *Dicroidium* Flora, being composed of partial and entire corystosperm, ginkgoalean, cycadophyte, and voltzialean leaves, and stems of sphenophytes (Equisetaceae). The *Dicroidium* Flora assemblage comprises the following corystosperm genera that were determined based on the presence of their diagnostic features: *Xylopteris* (Frenguelli) Stipanicic & Bonetti 1996, Zuberia Frenguelli 1946 and *Dicroidium* Gothan 1912. Ginkgoalean taxa were previously identified by Barboni & Dutra (2015) and Barboni et al. (2016).

The record of damage types by order of diversity is the following: oviposition (6 DTs), surface feeding (3 DTs), piercing and sucking (4 DTs), mines (2 DTs), margin feeding (1 DTs), hole feeding (1 DT) (Fig. 1). The *Dicroidium* flora of the PTO shows an abundance of scales (piercing-and-sucking) in corystosperms (82%), its distribution being related to the wide of the foliar organ of the host plants.

Corystosperms have different leaf morphotypes, where the congeneric *Dicroidium* related forms are the most used as host (42.2%), followed by congeneric *Zuberia* forms (27.4%) and the congeneric *Xylopteris* forms (10.2%). Ginkgo congeneric hosts have similar rates of trace proportion compared with *Zuberia* forms (*Baiera*/24.1%, *Sphenobaiera*/33.3%). In addition, the Ginkgoaceae forms are the second most abundant host and have a lower rate of herbivorized proportion (25.5%) compared with corystosperms. However, Ginkgoaceae have the highest rate of interacted hosts when the ovipositions are summed (57.5%). The *Baiera* (51.7%) and *Sphenobaiera* (75%) morphotypes present the highest rates of interacted leaf proportions, but with a low number of specimens (47 leaves) compared with the corystosperms (424 leaves).

The Molteno Formation (Middle to Late Triassic) are examples compatible with trace patterns from PTO. At least 14 locations from the Molteno Formation have DT diversity (106 localities studied) that are comparable to PTO. Furthermore, damage types that occurred in PTO showed a diversity of ovipositions of 6 DTs similar to the maximum indexes of diversity of the Triassic from the Molteno Formation (see Labandeira et al., 2013). Labandeira et al. (2013) also register one of the localities of Ladinian age with a lower diversity of 11 DTs from PTO (16 DTs). The DT diversity recorded from PTO has similar indices to the localities of Carnian sites from Africa. Lara et al. (2016) record the DT12 and oviposition on a stem of a sphenophyte from the Potrerillos Formation (Carnian) of the Cuyana Basin, Mendoza, Argentina; both traces are registered in the PTO, and, as well, in the same plant groups.

African strata document the largest variety of damage types in Mesozoic strata so far, mainly the Aasvoëlberg 411 site. The similarity in DTs from the Aasvoëlberg 411 site and from PTO is demonstrated by the occurrence of 6 equal DTs, which are hosted by the same groups of plants (*Heidiphyllum*, *Dicroidium*, ginkgoalean leaves) (Labandeira et al. 2013).

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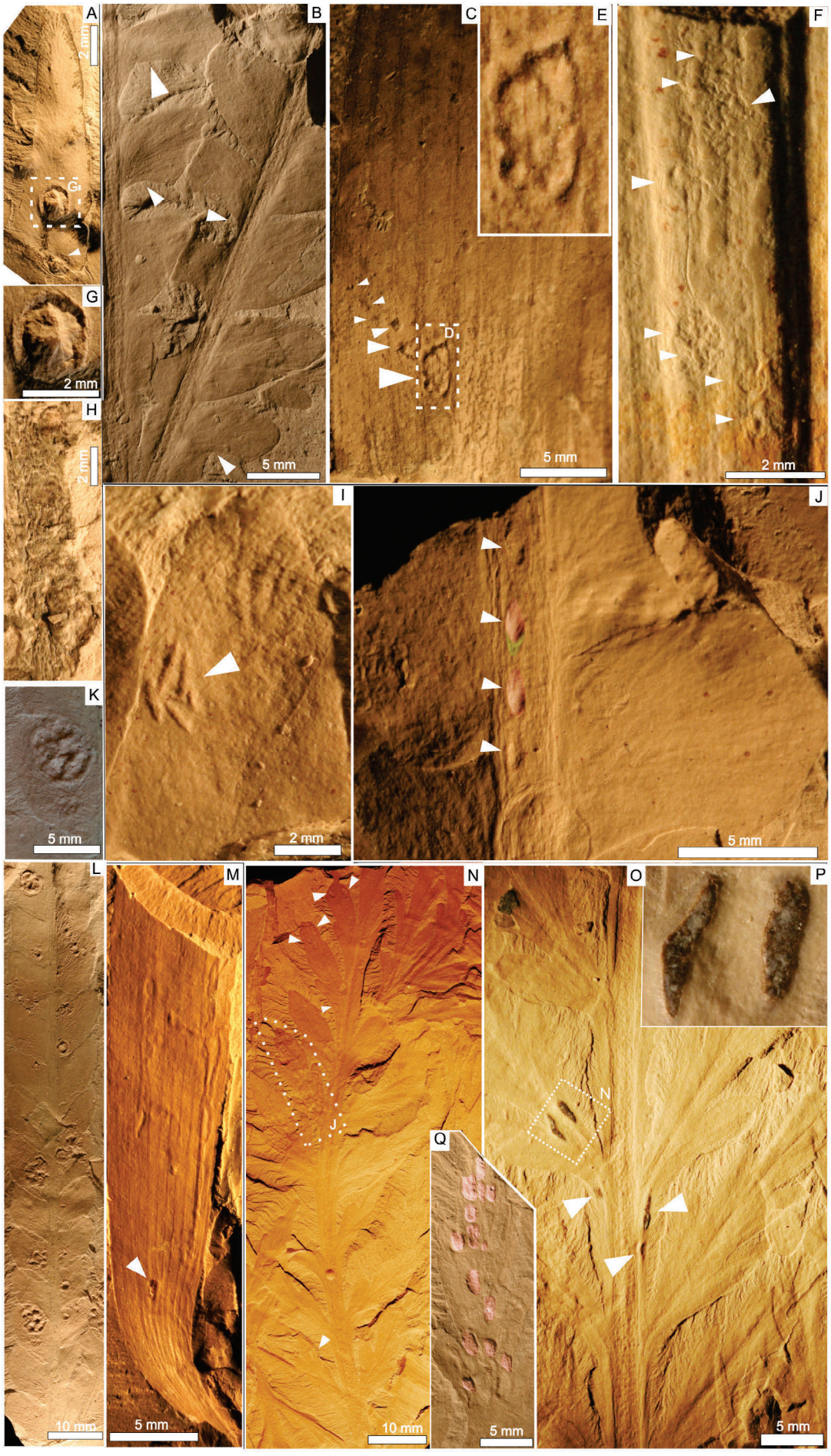

Fig. 1. Damage type representatives of the PTO. Scales and mines in the left side area: A, G: Large scale (pinna) and juvenile scales on *Dicroidium longifolium* (ULVG11137/new DT C). H: Scale distributed on *Zuberia* sp.; the region with scales were enlarged (ULVG11028/new DT C). K, L: Scales in the most infested specimen distributed in the entire leaf area on *Dicroidium odontopteroides* (ULVG9353/new DT C). M: Mine in *Heidiphyllum* sp.; oviposition site (arrow) (ULVG9297/DT71). External feeding traces in the upper right area: B: Three margin feeding in different pinnae of *Dicroidium odontopteroides* (ULVG11070/DT12). C, D: Surface feeding in five spots on *Heidiphyllum* sp., see detail in figure D (ULVG11124/new DT A). F: Wrinkled marginal tissue reacted by the insect puncturing in the lamina on *Sphenobaiera sulcata* (ULVG-9763/new DT B). Oviposition in the lower right area: I: Oviposition overlapping egg scars without reaction tissue on *Dicroidium odontopteroides* (ULVG11194/new DT D). J: Egg scars in one oviposition action on *Dicroidium odontopteroides;* egg scars (pinkish areas) and the tissue reaction below (yelowish area) (ULVG9163b/new DT E). N, Q: Oviposition on *Xylopteris* sp., the egg scar is in pinkish color (ULVG11389/DT102). O, P: Egg scars on *Xylopteris rigida* (ULVG11397/DT76).