Plant–Insect interactions from Middle Triassic (late Ladinian) of Monte Agnello (Dolomites, N-Italy) – Initial pattern and response to abiotic environmental pertubations

Torsten Wappler, Evelyn Kustatscher, Elio Dellantonio

The Paleozoic–Mesozoic transition is characterized by the most massive Phanerozoic mass extinction at the end of the Permian. Nevertheless, an impressive adaptive radiation of herbivorous insects occurred on gymnosperm-dominated floras not earlier than during the Middle to Late Triassic, penecontemporaneous with similar events worldwide, all which exhibit parallel expansions of generalized and mostly specialized insect herbivory on plants, expressed as insect damage on a various plant organs and tissues. The flora from Monte Agnello is markedly distinct, as deposited in subaerially pyroclastic layers with exceptionally preserved details. Thus, the para-autochthonous assemblage give insights into environmental disturbances, caused by volcanic activity, profoundly impact the structure and composition of herbivory patterns. These diverse Middle Triassic biota supplying extensive evidence for insect herbivore colonization, resulting in specific and complex herbivory patterns involving the frequency and diversity of 20 distinctive damage types (DTs). These DT patterns show that external foliage feeders, piercer-and-suckers, leaf miners, gallers, and oviposition culprits were intricately using almost all tissue types from the dominant host plants of voltzialean conifers (e.g., *Voltzia*), horsetails, ferns (e.g., *Neuropteridium*, *Phlebopteris*, *Cladophlebis* and *Thaumatopteris*) seed ferns (e.g., *Scytophyllum*), and cycadophytes (e.g., *Bjuvia and Nilssonia*).

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5   **Italy) – Initial pattern and response to abiotic environmental pertubations**

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20   INTRODUCTION

21   Since nearly 400 million years continental arthropods and vascular plants are major elements in

22   terrestrial ecosystems worldwide and their varied ectophytic and endophytic associations can provide a

23   unique and direct record of the plant-insect interactions in the past (e.g., Labandeira & Currano 2013).

24   In 2006, Labandeira proposed four pulses of herbivore expansion, where the observed Palaeozoic

25   arthropod herbivory patterns – covering the first two phases – are mainly expressed by damage patterns

26 caused by mites and apterygote and/or basal pterygote herbivores on pteridophyte and basal

27 gymnospermous plant hosts and are profoundly different from those that originated after the end-

28 Permian mass extinction (Labandeira 2006a; Labandeira 2006b). Preliminary work on plant-insect

29 interactions from early to late Permian floras of the Southern Alps indicates a moderately diverse

30 pattern of damage occurring in a variety of habitats prior to the P-Tr crisis (pers. observation T.

31 Wappler, 2013), penecontemporaneous with similar events in U.S. Southwest (e.g., Schachat et al.

32 2014), Gondwana (Adami-Rodrigues et al. 2004a; Adami-Rodrigues et al. 2004b; Cariglino &

33 Gutiérrez 2011; Gallego et al. 2014; Iannuzzi & Labandeira 2008; Prevec et al. 2009; Slater et al.

34 2012), or Cathaysia (e.g., Glasspool et al. 2003). Nevertheless, herbivory expansion 2 was profoundly

35 disrupted by environmental perturbations at the P-Tr boundary. The Early Triassic has been

36 traditionally viewed as an unusual time marked by suppressed origination rates and low diversity (e.g.,

37 Benton & Emerson 2007) generally attributed to the effects of extreme environmental conditions

38 inflicted on Early Triassic ecosystems (e.g., Looy et al. 1999; Grauvogel-Stamm & Ash 2005;

39 Roopnarine et al. 2007; Tong et al. 2007) but taphonomical biases cannot be excluded at least for

40 European floras (Kustatscher et al. 2014b). In general, records of Early Triassic insects or of insect

41 damage on plants are scant worldwide (comp. Table 1), so little is known about the mechanics and

42 timing of diversification of this ecologically important group following the end-Permian mass-

43 extinction event (Kustatscher et al. 2014b; Labandeira and Currano, 2013). Shcherbakov (2008a) even

44 concluded that the entire class of insects was strongly reduced in diversity at the P-Tr boundary but

45 following the end-Permian biotic crisis insect faunas already contained many elements common to

46 modern insects (e.g., Aristov et al. 2013; Béthoux et al. 2005; Shcherbakov 2008b; Lukashevich et al.

47 2010; Żyła et al. 2014; Haig et al. 2015) building the nucleus for the onset of the third pulse of

48 herbivore expansion, coupled with an impressive adaptive radiation of herbivorous insects. Their

49 associations with plants became significantly diverse being major elements for keystone communities

50 in terrestrial ecosystems worldwide (e.g., Ash 2014; Grauvogel-Stamm & Kelber 1996; Kustatscher et

51 al. 2014b; Labandeira 2006a; Labandeira 2006b; Labandeira & Currano 2013; McLoughlin 2011;

52 Moisan et al. 2012; Pott et al. 2008; Scott et al. 2004). Simultaneously, a major three-phased floral

53 change has been proposed for Europe and probably worldwide (e.g., Grauvogel-Stamm & Ash 2005).

54 The first stage lasted from the Induan to early Anisian, which in Europe is characterized by a

55 "survival" interval dominated by the lycopsid *Pleuromeia* Corda ex Giebel 1853 and conifers coupled

56 with relatively low levels of plant-insect interactional diversity (Kustatscher et al. 2014b); this is

57 followed by a "recovery" interval characterized by the resurgence of lycophytes, sphenophytes, ferns,

58 cycadophytes, conifers, ginkgophytes and seed ferns. The second stage occurred from the late Anisian

59 to the Carnian. The third covers the Norian and Rhaetian stages, which is pivotal to understanding the

60 evolution of trophically modern ecosystems (e.g., Benton 2010; Labandeira 2006b; Labandeira &

61 Currano 2013).

62 Thus, the late Middle Triassic (Ladinian) floras of the Dolomite Region in the Southern Alps of

63 northeastern Italy provide an intriguing window into the early evidences for Herbivore Expansion 3.

64 Ladinian floras from the Dolomites have been extensively studied in recent years (e.g., Kustatscher et

65 al. 2014a; Kustatscher & Van Konijnenburg-van Cittert 2005 and references therein), evidencing a

66 dominance of conifers (*Voltzia*, *Pelourdea*), while cycadophytes, seed ferns, ferns, horsetails, and

67 lycophytes are much rarer. Nevertheless, the flora from Monte Agnello is markedly distinct from other

68 Ladinian floras of the Dolomites by its higher diversity and abundance in cycadophytes, seed ferns and

69 ferns. It is currently the best documented and most diverse late Middle Triassic biota in the Alps

70 documenting a rich vascular plant record, including moderate levels of external foliage feeding,

71 piercing-and-sucking, galling, and ovipositional damage.

72 Of particular importance, from a taphonomic viewpoint, the Dolomites were subject to significant

73 volcanic activity, beginning in the late Ladinian. Consequently, conditions for exceptional preservation

74 were high. Although most of the volcanic complexes were submarine, locally, such as in the area of

75 Predazzo, subaerial eruptive centers existed (Hoernes 1912; Leonardi 1967), which alter the natural

76 environment to variable extents and initiate very different effects of community composition, structure,

77 function, and successional turnover on local and regional scales (e.g., Walker & Wardle 2014). This

78 makes the Monte Agnello ideal for examining the response that such environmental perturbation had

79 on community structures and offers the possibility to study the ecological expansion of interactional

80 diversity recorded from the varied habitats.

81

82 **Geological and paleontological setting**

83 Monte Agnello (Fig. 1) represents an area that was marginally influenced by the Ladinian volcanic

84 activity of the Predazzo volcano and is characterized by a well-preserved stratigraphic succession (e.g.,

85 Kustatscher et al. 2014a). The 250 meters thick volcanic succession is composed of "explosion

86 breccia" at the base, followed by lava breccia, and alternations of lava flows and tuffs (Calanchi et al.

87 1977; Calanchi et al. 1978; Lucchini et al. 1982). The "explosion breccia" comprises lithic fragments

88 (calcareous, volcanic and metamorphic fragments, clastic rocks, isolated crystals), related to the

89 Permo-Triassic volcano-sedimentary succession and the metamorphic basement (Vardabasso 1930).

90 The lithic fragments of the breccia are bound by carbonate and/or chlorite-serpentine cement (Calanchi

91 et al. 1977). The thickness of this "explosion breccia" varies between 25 meters at Monte Agnello and

92 10 meters at Censi. The volcanic succession accumulated mostly in a subaerial environment, and is

93 related to explosive phreatic activity (e.g., bomb sags, antidunes, accretionary lapilli; Calanchi et al.

94 1977; Lucchini et al. 1982).

95 The flora is preserved in the tuff lenses at the base of the "explosion breccia" of the volcanic

96 succession at Predazzo (Kustatscher et al. 2014a), that hinder an appropriate stratigraphic correlation

97 between the diffrerent sites. Considering that they are related to one or perhaps a few phreatomagmatic

98   events within the timley restricted late Ladinian volcanism the possible time difference between the

99   single localities is however very reduced. The flora is composed by a large number of fronds, stems

100 and reproductive organs of sphenophytes, ferns, seed ferns, cycadophytes and conifers. Due to the

101 preservation in tuff layers, the organic material is missing, sometimes the remains are preserved only as

102 impressions. Several stem fragments belong to the sphenophytes. The ferns are represented by

103 Osmundaceae (*Neuropteridium elegans* (Brongniart) Schimper in Schimper and Schenk, 1879),

104 Matoniaceae (*Phlebopteris fiemmensis* Kustatscher et al., 2014a) and Dipteridaceae (*Thaumatopteris*

105 sp.). For the latter two families it is the so far oldest fossil record for the Northern Hemisphere.

106 Additional ferns of unknown botanical affinity are *Cladophlebis ladinica* Kustatscher et al., 2014a,

107 *Cladophlebis* sp. (Osmundaceae and/or the Dicksoniaceae) and *Chiropteris monteagnellii* Kustatscher

108 et al., 2014a (Dipteridaceae?). The seed ferns are represented by leaf fragments of *Scytophyllum*

109 *bergeri* Bornemann, 1856. The cycadophyte leaf fragments probably belong to the genera *Bjuvia*

110 Florin, 1933, *Taeniopteris* Brongniart, 1828 and/or *Macrotaeniopteris* Schimper, 1869 as well as

111 *Nilssonia* Brongniart, 1828 and *Apoldia* Wesley, 1958. The conifers are represented by shoots of

112 *Voltzia* Brongniart, 1828 and *Pelourdea* Seward, 1917 leaves. These plants grew probably during a

113 humid spell, recently proposed for the late Ladinian of the Dolomites (Preto et al. 2010 and references

114 therein).

115

116 MATERIAL AND METHODS

117 *Data collection*

118 Fossil plant assemblages were quantitatively censused from multiple sites at the base of the „explosive

119 breccia", that crops out on the northwestern slope of Monte Agnello – Censi, overlying a carbonate

120 platform of late Anisian to Ladinian age (Sciliar Dolomite). About 684 specimens have been collected

121 from eight distinctive sites denoted by the prefixes MA 1 – MA 8 (Fig. 1; Table 2). Sample size ranges

122 from 2 to 244 plant remains, depending primarily on the quality and accessibility of the fossils. For the

123 quantitative study, each identifiable plant fossil was counted. Of the plant fossil specimens collected at

124 Monte Agnello, all that were adequately preserved and exceeded a minimum size of 0.5 cm^2 were

125 examined for insect damage. Parts and counterparts were matched whenever possible to avoid

126 duplication. When possible, all specimens were assigned to a known species or plant morphotype. All

127 analyzed specimens are housed at the Museo Geologico delle Dolomiti, Predazzo. Specimens

128 occurring on the same rock slab are identified by different letters following the catalogue number while

129 capital letters indicate parts and counterparts of the same specimen.

130 The most recent approach toward understanding the patterns of herbivory in the fossil record involves

131 quantification of both the richness and intensity of insect damage (Wilf & Labandeira 1999;

132 Labandeira et al. 2002, 2007; Kustatscher et al. 2014b). The richness of herbivory is determined first

133 by establishing a classification system of distinctive, diagnosable damage types, or DTs, that can be

134 used generally in studies of herbivore damage to plants.. DTs then are grouped into functional feeding

135 groups (FFG). Seven functional feeding groups are present in the Monte Agnello flora [(i) external

136 foliage feeding, subdivided into hole, margin, surface feeding and skeleotization; (ii) piercing and

137 sucking; (iii) oviposition, though not truly feeding interaction but rather egg-laying that leaves a

138 significant record of plant damage; (iv) mining and (v) galling]. To date, over 290 fossil DTs have been

139 identified (pers. comm. C.C. Labandeira). Finally the DTs are ranked by their host specificity (HS),

140 ranging from 1 for generalists to 3 for high host-plant specialization, which then allows non-

141 generalized DTs (e.g., those with HS of 2 and 3) to be analyzed separately.

142 Each foliar element was photographed using a Canon EOS 30D camera with a Canon EF-S 60 mm

143 f/2.8 macro lens or a Nikon Coolpix E4500. All photographs were optimized using Abobe Photoshop

144 CS6 and Adobe Lightroom 5.

145

146 *Institutional abbreviations*

147 MGP, Museo Geologico delle Dolomiti, Predazzo. Specimens occurring on the same rock slab are

148 identified by different capital letters following the catalogue number.

149

150 *Quantitative analysis*

151 Quantitative analyses of insect damage were done using R version 3.1.0 (www.r-project.org). For

152 damage diversity analyses, sample size was standardized by selecting random subsets of foliar

153 elements without replacement and calculating the damage diversity for the subsample. Subsets of the

154 data were subjected to rarefaction using an analytic method detailed below, which extends the solution

155 found by Wappler et al. (2012) to cases where individuals may belong to multiple classes and allows

156 the explicit reconstruction of probability distributions for the rarefied sample (Heck et al. 1975). This

157 process was repeated 5000 times, and the results were averaged to obtain the standardized damage

158 diversity for the bulk flora and four single sub-localities (MA1, MA5, MA7, MA8). The remaining

159 sub-localities were removed from the census because the target sample size of at least 40 specimens

160 was not reached. The standard deviations (SD) for the resamples were calculated to provide sample

161 error bars. The same procedure was used to standardize damage diversity sub-sampled to 40 foliar

162 elements of which sufficient material was available.

163

164 RESULTS

165 *Damage on the bulk Monte Agnello flora*

166 Of the 684 plant remains examined from the Monte Agnello flora, 83, or 12.13 %, exhibit some sort of

167 damage represented by 20 different damage types. The taxa or morphotypes examined were

168 represented by foliage, axes, stem fragments, fructifications, and dispersed seeds (Table 2). A total of

169 95 damage type occurrences were observed throughout the bulk flora: 45 on cycadophytes

170   (representing 36.5% of all specimens), 37 on seed ferns (8.0%), ten on conifers (44.3%), and three on

171   ferns (7.6%) (Table 3), suggesting that selective feeding by insect herbivores preferentially targeted

172   particular seed plants. This pattern of selectivity was also recognized within the early late Permian

173   (Wuchiapingian) of the Gröden/Val Gardena Sandstone from the Bletterbach Gorge of the Dolomites

174   (Northern Italy) (pers. observation T. Wappler, 2013). Thus, herbivory recorded for the Monte Agnello

175   sites represent nearly all of the fundamental modes of herbivory, excluding fungal infection, which was

176   not observed (see Gunkel & Wappler 2015). Multiple DTs or functional feeding groups were only

177   recorded in 1.6 % of the plant remains whereas the majority were only damaged in one way (~11 %).

178   Seven distinctive functional feeding groups have been detected on the foliar elements from Monte

179   Agnello, most of which occur on particular plant hosts. Types of the external foliage feeding constitute

180   78.9 % of all DT occurrences and preferentially occurred on the seed fern *S. bergeri* and consists of the

181   exophytic consumption of live plant tissues, subdivided into skeletonization and margin-, hole- and

182   surface feeding; this is the most common ensemble of Triassic damage types (Labandeira & Prevec

183   2014; pers. observation T. Wappler, 2013) (Fig. 2). Those of the galling FFG provided 11.5 % of all

184   DT occurrences and are more or less evenly distributed among conifers, ferns and seed ferns (Figs. 3C-

185   D, G). It represents the most biologically complex of all major interactions, and represents arthropod-

186   induced abnormal cell proliferation that can occur on all major plant organs (e.g., Kustatscher et al.

187   2014b; Scott et al. 2004); examples are widely known (e.g., Stone & Schönrogge 2003). Oviposition,

188   though not a feeding interaction, was present in 5.2 % of all DT occurrences; examples are common

189   (Ghosh et al. 2015; McLoughlin 2011) (Figs. 3E-F, I). Minor levels of insect damage were present for

190   the piercing-and-sucking (Fig. 3J) and mining FFGs (Fig. 3H), responsible for 3.1 % of all DT

191   occurrences. Leafminers construct distinct leaf mines, most of which are quite conspicuous and

192   represent a form of endophagous herbivory

193 in which a herbivore targets and feeds on fluid tissues such as phloem, mesophyll or epidermal cell

194 protoplasts (Sinclair & Hughes 2010); examples are uncommon and the possible mining structure on

195 the pteridosperm *Scytophyllum bergeri* (Fig. 3H) indicates that the origin and diversification of the

196 leaf-mining habit occurred about 92 million years before the first appearance of fossil angiosperms

197 (Ash 1997; Gnaedinger et al. 2014; Kustatscher et al. 2014b; McLoughlin 2011; Moisan et al. 2012;

198 Pott et al. 2008).

199

200 *Damage on individual species*

201 Among the 28 taxa represented at Monte Agnello less than half indicate some kind of damage,

202 whereas, three – *Scytophyllum bergeri*, *Bjuvia* cf. *dolomitica* and *Nilssonia* sp. – are the most

203 herbivorized taxa (71,6 % of all DT occurrences) but only representing one-third of the flora (Table 2).

204 The most abundant plant species are the conifers *Voltzia* sp. (Fig. 3C) and *Voltzia* sp. 2, which have the

205 lowest damage frequency (2.44–2.94 %) of the common Monte Agnello taxa. Ferns are nearly equally

206 as diverse as the seed ferns but damage frequency is at least ten times less abundant than among the

207 seed ferns (Table 3; Fig. 3D). Sphenophytes displayed so far no signs of insect-mediated herbivory but

208 the small number of sampled specimens probably did not cover the complete set of herbivory structures

209 yet.

210

211 *Damage at distinct sub-localities*

212 Plant material is generally preserved at the base of the "explosion breccia" at an angle to the bedding

213 rather than compacted into a single horizon. Transport, therefore, must have been short, and the fossil

214 leaf assemblages must be considered as para-autochthonous (e.g., Hanley et al. 2007). Minimal

215 transport allows us to track considerable changes in species composition and insect folivory over short

216 distances and recognize possible heterogeneity in the structure and composition of the source plant

217   communities and their associated herbivores. Large-scale disturbances, in contrast, may profoundly

218   alter the composition and structure of plant communities and are rarely uniform in their influence on

219   vegetation (Kustatscher et al. 2014a). Variations of floral composition and insect herbivore damage at

220   four sub-localities (MA1, MA5, MA7, MA8) censused are shown in Fig. 4 and Table 4. MA1 has the

221   highest floral diversity (22 ssp.), followed by MA5 (16 ssp.) and MA7 (15 ssp.). MA8 is an extremely

222   low-diversity flora (7 ssp.). Interestingly, all sites are strongly dominated by a single plant group

223   representing in all cases over half of the characteristic plant material known from each of the sub-

224   localities. The most abundant plant lineage at MA5–MA8 is conifers, whereas at MA1 57% of the

225   taphocoenosis is composed of cycadophytes. However, when analyzing herbivory on individual host

226   groups at the four sub-localities, total damage frequency and external foliage feeding is

227   overwhelmingly found on seed-fern hosts (Fig. 4), except MA7 where the preferred host-plants are

228   cycadophytes.

229

230   DISCUSSION

231   Volcanogenic deposits are valuable for the preservation of in situ sequential stages of biotic change

232   that are not commonly represented in the fossil record therefore plant-insect assemblages recognized in

233   this study appear compositionally and ecologically unique (Currano et al. 2011; Dale et al. 2005).

234   Thus, the para-autochthonous early late Ladinian flora of the Monte Agnello (Dolomites, N-Italy)

235   offers insights into the patterns of arthropod herbivory during the beginning of the third pulse of

236   herbivore expansion (*sensu* Labandeira 2006a; Labandeira 2006b; Labandeira & Currano 2013: fig. 1)

237   and the way herbivores responded to environmental perturbation and the reorganization of community

238   structure. Even though our data are preliminary the palaeoecological and temporal setting of the early

239   late Ladinian flora of the Monte Agnello in the Dolomites supports three major conclusions that

240   parallel those drawn from data known from intensively studied Gondwanan sites.

241   (1) *Dominance of seed plant herbivory*. The dominance of seed plant herbivory by local arthropod

242   herbivores particularly that known since the Permian across western Euamerica (e.g., Schachat

243   et al. 2014), Europe (Geyer & Kelber 1987; Bernardi et al. in prep.), Cathaysia (Glasspool et al.

244   2003), and extensive glossopterid-dominated floras across Gondwana (e.g., Cariglino &

245   Gutiérrez 2011; McLoughlin 2011; Prevec et al. 2009) is also a conspicuous component of the

246   late Anisian to Ladinian environments. This documents the persistence of the preferential

247   targeting selected groups of seed plants, like cycadopytes and seed ferns in Monte Agnello,

248   particularly by external foliage feeders, supporting Feeny's apparency hypothesis (Feeny 1976),

249   as seed plants were more abundant and conspicuous, and therefore would be more apparent to

250   herbivore consumption. However, for the Monte Agnello data, a more likely explanation favors

251   increased herbivory based on the leaf anatomy, suggesting that particular physiological traits,

252   like the scleromorphic structures of conifer taxa reduce the palatability and digestibility of such

253   plant material or act as a deterrent when more palatable plants are available (Labandeira &

254   Anderson 2005).

255   (2) *Increase of interactional diversity and rise of the leaf-mining habit*. There is an increase in

256   plant-insect interactional diversity during the Early to Late Triassic in eastern Euamerica and

257   Gondwana regions (e.g., Kustatscher et al. 2014b; Scott et al. 2004), coupled with an increase

258   in the diversity of FFGs, DTs, and associated herbivore behaviors observed at Monte Agnello,

259   compared to insect damage from earlier known floras (e.g., Kustatscher et al. 2014b). Of

260   particular importance is the presence of the leaf-mining habit in which holometabolous insect

261   larvae consume inside the parenchymal, epidermal, vascular, or other tissues of a plant, leaving

262   the outer wall of the epidermis undamaged (Hering 1951). The earliest documented leaf-mining

263   fossil records have been reported from Kyrgyzstan, Austria, Australia and South Africa in

264   deposits of Middle to Late Triassic age (comp. Table 1).

265   (3) *Volcanic activity and site-specific habitat differences*. The data presented here show that

266   volcanogenic deposits are valuable for the creation and preservation of in situ sequential stages

267   of biotic change not commonly represented in the fossil record. These episodic volcanic

268   activities directly influenced the evolution of the environment, plant community and their

269   associated herbivores, resulting in vegetational heterogeneity can impact both the likelihood

270   and strength of interactions between plants and insect herbivores (e.g., Agrawal et al. 2006;

271   Currano et al. 2011). Therefore the heterogeneity among the sub-localities indicates that

272   ecosystems undergo compositional and structural changes during their occupancy of a site,

273   which explain variations in plant physiognomy, plant and insect herbivore composition, or their

274   paleoecology (Table 4). This conclusion is supported by (1) the percentage of herbivorized

275   plant host specimens, (2) the elevated number of DTs on each host plant, and (3) difference in

276   evenness and the relative abundance distributions of damage within the single sub-localities.

277

278 These conclusions warrant further verification from investigations of additional new sites to clarify

279 patterns of arthropod herbivory during this crucial period of time where terrestrial ecosystems start to

280 become modern.

281

282 ACKNOWLEDGEMENTS

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536 The authors declare there are no competing interests.

Author Contributions

538 • Torsten Wappler analyzed the data, wrote the paper, prepared figures, and reviewed drafts of the

539 paper.

540 • Evelyn Kustatscher wrote the paper, prepared figures, and reviewed drafts of the paper.

541 • Elio Dellantonio contributed on the geology, reviewed drafts of the paper, and contributed with

542 iconography.

Table 1(on next page)

Arthropod damage on Triassic plants

List of published records of arthropod damage on Triassic plants.

2   Table 1. List of published records of arthropod damage on Triassic plants.

Study	Age	Formation and locality	Damage type
Nathorst (1876); Nathorst (1878)	Rhaetian (Late Triassic)	Pålsjö, Scania, Sweden	• possible oviposition scars on *Podozamites*
Ghosh et al. (2015)	Norian / Rhaetian (Late Triassic)	Parsora Formation (Dhaurai Hill beds); South Rewa Gondwana Basin, central India	• disc-like galls on *Dicroidium hughesii*
Walker (1938); Ash (1997); Ash (1999); Ash (2000); Ash (2001); Ash (2005); Ash & Savidge (2004); Ash (2014); Creber & Ash (2004)	Norian (Late Triassic)	Chinle Formation, Petrified Forest National Park, Arizona, USA	• marginal and non-marginal feeding traces on *Cynepteria*, *Marcouia*, *Zamites*, *Sphenopteris*, *Macrotaeniopteris*, *Dechellyia*, *Nilssoniopteris* • possible oviposition scars and insect eggs on *Dechellyia*, *?Equisetites* • coprolite-bearing borings in *Itopsidema*, *Araucarioxylon*, *Schilderia*
Adami-Rodrigues et al. (2008)	Norian (Late Triassic)	El Tranquilo Group, Laguna Colorada Formation; Santa Cruz, Argentinia	• specific and complex herbivory patterns of several FFG's
Feng et al. (2014); Hsü et al. (1974)	Keuper (Late Triassic)	District Yungjen, Yunnan, China	• crescent-shape bite marks on *Mixopteris* • intense skeletonization *Dictyophyllum nathorstii*
Gallego et al. (2003); Gallego et al. (2004); Gnaedinger et al. (2007); Gnaedinger et al. (2008); Gnaedinger et al. (2014)	Carnian-Norian (Late Triassic	La Ternera Fm. (Quebrada La Cachivarita locality; La Ternera hill area, Copiapó Province, and the Las Breas Fm. (Punta del Viento locality, Vicuña, Elqui Province), Chile	• oviposition scars on *Heidiphyllum*, *Pseudoctenis*, *Taeniopteris*
Strullu-Derrien et al. (2012)	Carnian (Late Triassic)	De Geerdalen Formation; Hopen Island, Svalbard Archipelago	• aggregations of pellets or coprolites within bennettitalean roots • gall-like structures within the cortical or pith tissues of the larger (probable bennettitalean) axes
Rozefelds & Sobbe (1987); Tillyard (1922); Webb (1982)	Carnian (Late Triassic)	Blackstone Formation, Ipswich Coal Measures Group; Sydney Basin, New South Wales, Australia	• possible oviposition scars and insect eggs on *Nilssoniopteris* • possible galls or eggs on *Dictyophyllum* • mining structures on

			Heidiphyllum, Ginkgoites
Meller et al. (2011); Pott et al. (2008); Aschauer & Wappler unpubl. Data	Carnian (Late Triassic)	Lunz Formation; Lunz am See, eastern Northern Calcerous Alps, Austria	• possible oviposition scars and insect eggs on *Nilssoniopteris* • possible mining structures on *Nilssonia* • marginal and non-marginal feeding traces on *Nilssoniopteris*, and other bennettitalean leaves
Moisan et al. (2012)	Carnian (Late Triassic)	Madygen Formation; Turkestan Mountains, southwestern Kyrgyzstan, Central Asia	• oviposition scars on *Isoetites*
Anderson & Anderson (1983); Anderson & Anderson (1985); Anderson & Anderson (2003); Labandeira & Anderson (2005); Scott et al. (2004)	Carnian (Late Triassic)	Molteno Formation; Karoo Basin, KwaZulu- Natal, Eastern Cape and Northern Cape, South Africa	• specific and complex herbivory patterns involving the frequency and diversity of 79 distinctive damage types (DTs) on about 220 whole-plant species (liverworts, lycopods, horsetails, ferns, cycads, peltasperms, corystosperms, hamshawvialeans, ginkgoaleans, voltzialean conifers, bennettitaleans, gnetophytes)
Linck (1949); Roselt (1954)	Carnian/Ladinian (Upper/Middle Triassic)	Bedheim, Germany	• borings in *Dadoxylon* • possible oviposition scars on *Equisetites*
Geyer & Kelber (1987); Kelber & Geyer (1989)	Upper Ladinian (Middle Triassic)	Lettenkohle of Alsace, France; Lower Keuper of Franconia, Germany	• crescent-shape bite marks on *Schizoneura*, *Taeniopteris* • possible oviposition scars and insect eggs on *Equisetites*
Heer (1877)	Ladinian (late Middle Triassic)	Neuewelt, Lettenkohle, Switzerland	• possible oviposition scars on *Equisetites*
Minello (1994)	Ladinian (Middle Triassic)	Xinigua, Rio Grande do Sul, Santa Maria Formation (Rosario do Sul Group), Brazil	• coprolite-bearing borings in *Araucarioxylon*
Grauvogel-Stamm & Kelber (1996)	Early Anisian (Early Middle Triassic)	Grès à Voltzia Formation; Grès-à-Voltzia, northern Vosges Mountains, France	• crescent-shape bite marks on *Neuropteridium* • possible eggs entangled in plant debris
McLoughlin (2011)	Anisian – Ladinian (Middle	Wivenhoe Hill, Esk Trough,	• oviposition scars on

	Triassic)	Esk Formation; Queensland, Australia	*Taeniopteris*
McLoughlin (2011)	Olenekian – Anisian (late Early to early Middle Triassic)	Turrimetta Head, Sydney Basin; New South Wales, Australia	• gall on *Dicroidium*
Kustatscher et al. (2014b)	Olenekian (Lower Triassic)	Solling Formation; Bremke and Fürstenberg, Germany	• specific herbivory patterns involving the frequency and diversity of 8 distinctive damage types (DTs) • external feeding damage on *Tongchuanophyllum. Neuropteridium*, *Pelourdea* • mid-vein gall on *Tongchuanophyllum* • linear series of lenticular or ovoidal oviposition scars on *Tongchuanophyllum*

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Table 2(on next page)

Floral and insect damage composition late Ladinian flora from Monte Agnello, Dolomites, Italy.

Table 2. Floral and insect damage composition late Ladinian flora from Monte Agnello, Dolomites, Italy. DMG, percentage of damage; Spec. Spezialized damage; PS, Piercing and sucking; Ovi, Oviposition; FFG, Functional Feeding groups; DTO, Damage type occurrence.

2   Table 2. Floral and insect damage composition late Ladinian flora from Monte Agnello, Dolomites, Italy. DMG, percentage of damage;

3   Spec. Spezialized damage; PS, Piercing and sucking; Ovi, Oviposition; FFG, Functional Feeding groups; DTO, Damage type occurrence.

Species	# leaves	% DMG	% Spec	% Gall	% Mine	% External	% PS	% Ovi	DTs	#FFGs	DTO All	DTO Spec	DTO External	DTnumbers
Bjuvia cf. *dolomitica*	113	15.93	0.89	0.89		14.16		0.89	9	5	21	1	18	1;2;3;12;14;17;29;80;100
Chiropteris montagnellii	12													
Cladophlebis ladinica	24	4.17						4.17	1		1			101
Cladophlebis sp.	4													
Cone indet.	3													
Elatocladus sp.	1													
Equisetoid stem fragment	1													
Indet.	5													
Neuropteridium elegans	3													
Nilssonia cf. *neuberi*	40	10.00				10.00			1	1	4		4	12
Nilssonia sp.	34	23.53	2.91			20.59	2.94		6	3	10	1	9	1;2;7;12;13;128
Pelourdea sp.	4	25.00				25.00			1	1	1		1	12
Phlebopteris fiemmensis	6	33.33	16.67	16.67		16.67			2	2	2	1	1	2;80
?Podozamites sp.	17	17.65						17.65	2		3			72;100
Pterophyllum sp.	1													
Radicites sp.	1													
Schizoneura paradoxa	6													

Scytophyllum bergeri	55	54.55	7.27	3.64	1.82	49.09			8	4	37	4	34	3;5;12;13;14;40;63;80
Seed	2													
Sphenozamites sp.	37	13.51	2.70			13.51			3	2	5	1	5	2;8;12
Stem indet.	6													
Taeniopteris sp.	8	25.00				25.00			2	1	2		2	12;14
Thaumatopteris sp.	3													
Voltzia sp. 1	84	3.57	1.19	2.38			1.19		2	2	3	1		48;121
Voltzia sp. 2	41	2.44		2.44					1	1	1			121
Voltzia sp. indet.	170	2.94		2.35		0.59			2	2	5		1	12;121
Wood	3													
Total	**684**	**12.14**	**1.32**	**1.61**	**0.15**	**9.36**	**0.29**	**0.73**	**20**	**7**	**95**	**9**	**75**	**1;2;3;5;7;8;12;13;14;17;29;40;48;63;72;80;100;101;121;128**

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Table 3(on next page)

Floral and insect damage composition of the late Ladinian flora from Monte Agnello, Dolomites, Italy on higher classification level.

Floral and insect damage composition of the late Ladinian flora from Monte Agnello, Dolomites, Italy on higher classification level. DMG, percentage of damage; Spec. Spezialized damage; PS, Piercing and sucking; Ovi, Oviposition; FFG, Functional Feeding groups; DTO, Damage type occurrence.

2 Table 3. Floral and insect damage composition of the late Ladinian flora from Monte Agnello, Dolomites, Italy on higher classification

3 level. DMG, percentage of damage; Spec. Spezialized damage; PS, Piercing and sucking; Ovi, Oviposition; FFG, Functional Feeding

4 groups; DTO, Damage type occurrence.

Plant groups	# leaves	% DMG	% Spec	% Gall	% Mine	% External	% PS	% Ovi	DTs	#FFGs	DTO All	DTO Spec	DTO External	DTnumbers
Conifer	303	1.00	0.33	2.31		0.66	0.33		3	3	10	1	2	12;48;121
Cycadophytes	250	16.00	1.20	0.40		13.60	0.40	1.60	14	6	45	3	38	1;2;3;7;8;12;13;14;17;29;72;80; 100;128
Indet.	16													
Ferns	52	5.77	1.92	1.92		1.92		1.92	3	2	3	1	1	2;80;101
Seed ferns	55	54.55	7.27	3.64	1.82	49.09			8	4	37	4	34	3;5;12;13;14;40;63;80
Sphenophytes	8													
Total	**684**	**12.13**	**1.32**	**1.61**	**0.15**	**9.36**	**0.29**	**0.73**	**20**	**7**	**95**	**9**	**75**	**1;2;3;5;7;8;12;13;14;17;29;40; 48;63;72;80;100;101;121; 128**

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Table 4(on next page)

Floral diversity and evenness

Floral diversity and evenness

2   Table 4. Floral diversity and evenness.

Flora	N	S	Rarefied species diversity at 40 leaves	Rarefied external damage diversity at 40 leaves	Rarefied specialized damage diversity at 40 leaves	Pielou`s J	Simpson D
MA1	244	22	12.89±1.52	2.30±1.13	0.63±0.69	0.89	1.89
MA5	236	16	9.03±1.41	3.19±1.08	0.68±0.75	0.73	1.83
MA7	125	15	9.38±1.47	1.29±0.49	na	0.63	1.70
MA8	44	7	6.85±0.36	0.93±0.25	na	0.75	1.71

3

1

Simplified geological map of the Monte Agnello area (Dolomites, N-Italy)

Figure 1. Simplified geological map of the Monte Agnello area (Dolomites, N-Italy), modified from Vardabasso (1930). MA1–MA8, fossil sites.
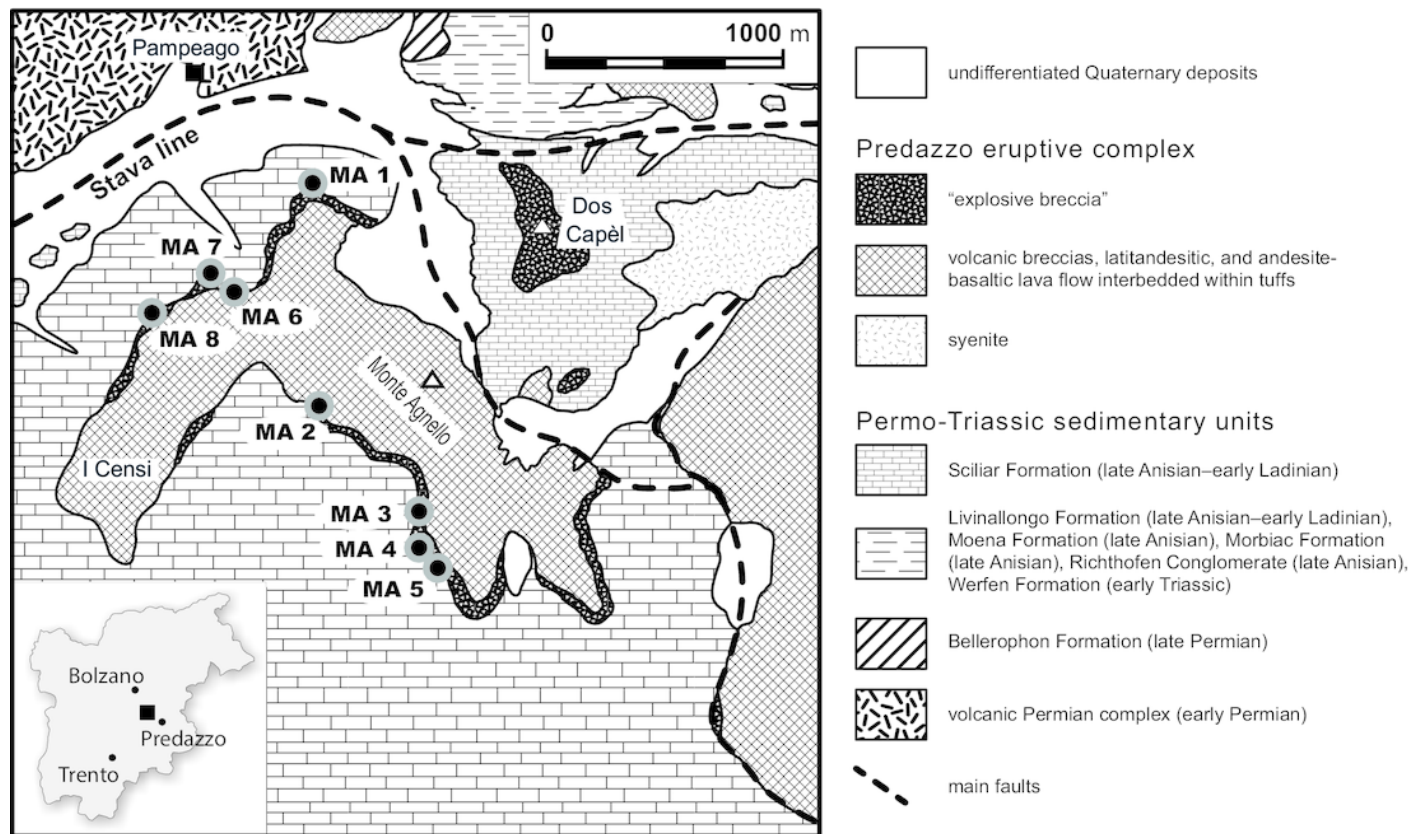
2

Examples of external foliage feeding at Monte Agnello (Dolomites, N-Italy).

Examples of external foliage feeding at Monte Agnello (Dolomites, N-Italy). A, *Scytophyllum bergeri* Bornemann, 1856 with intensively consumed leaf margins (DT12, 14) (MGP63/97). B, Hole feeding indicated by leaf removal on both sides of the primary veins (DT63) on *S. bergeri* Bornemann, 1856 (MGP196/39A-B). C–D, Hole feeding on a Sphenophyte (DT8) (MGP194/106), enlarged in D. E, Marginal feeding on the cycadophyte *Nilssonia* cf. *neuberi* Stur ex Pott et al. 2007 (DT12) (MGP191/6A). F, Excision of leaf to primary vein (DT14) on *Bjuvia* cf. *dolomitica* Wachtler & van Konijnenburg-van Cittert, 2000 (MGP181/11A). G, Removal or abrasion of surface tissues with a weak reaction rim (DT29) indicated by the dotted lines on *B.* cf. *dolomitica* Wachtler & van Konijnenburg-van Cittert, 2000 (MGP196/43). H, Cuspate excision (DT81) on *S. bergeri* Bornemann, 1856 (MGP171/28), enlarged in I. J–L, External foliage feeding on *B.* cf. *dolomitica* Wachtler & van Konijnenburg-van Cittert, 2000 (MGP195/69A), deep excision of leaf margin enlarged in K (DT12) and interveinal tissue removed in L (DT17). Scale bars: striped, 10 mm; solid, 5 mm; dotted, 1 mm.
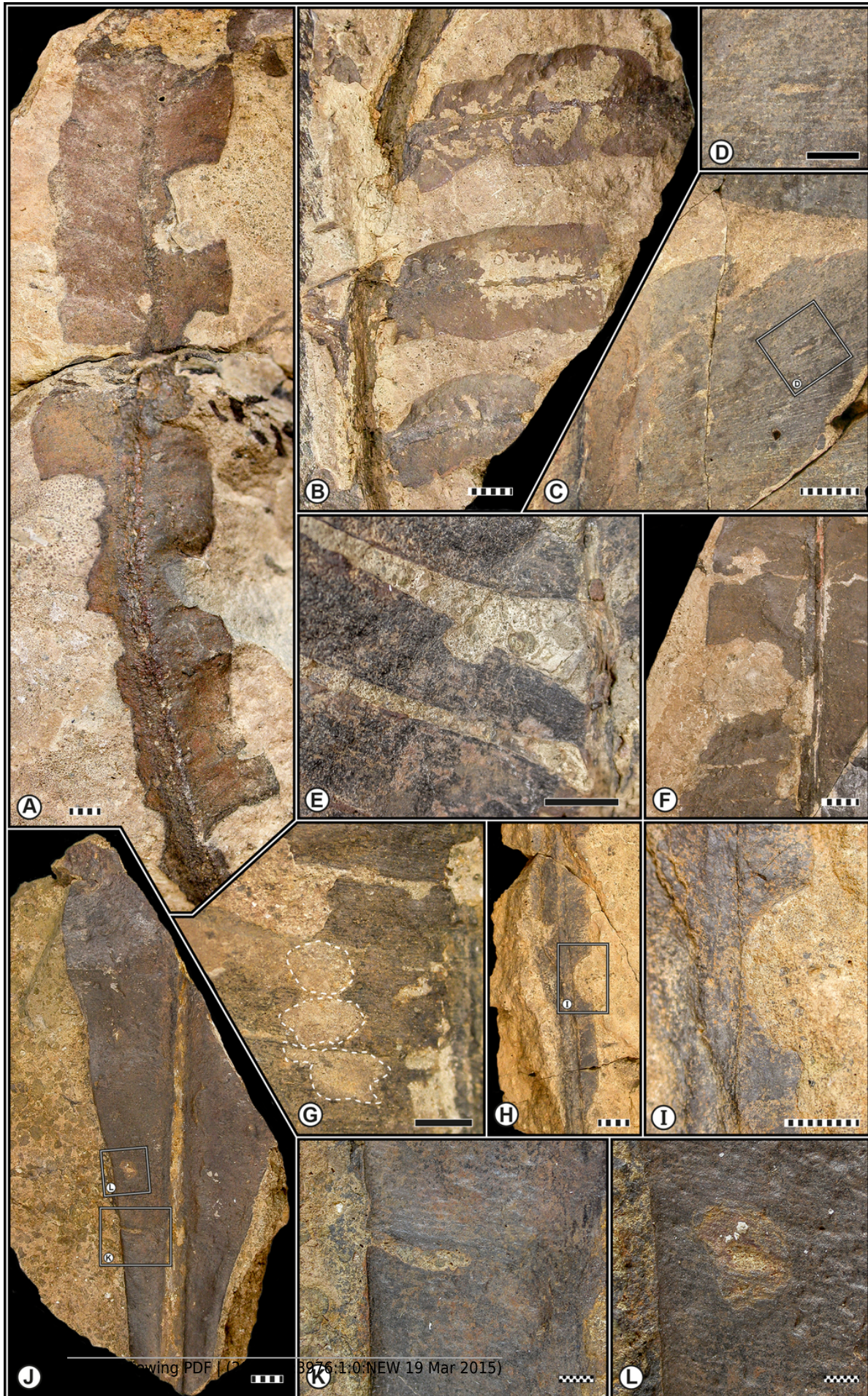
3

Examples of internal foliage consumption at Monte Agnello (Dolomites, N-Italy).

Examples of internal foliage consumption at Monte Agnello (Dolomites, N-Italy).
A–B, Elliptical piercing and sucking punctures on the conifer *Voltzia* sp. 1 (MGP196/35), enlarged in B (DT48). C, Ellipsoidal, sessile bud gall from branchlet (DT121) on the unaffiliated *Voltzia* sp. 1 (MGP171/81). D, Small, hemispherical, thoroughly carbonized structures (DT80) on *Phlebopteris fiemmensis* Kustatscher et al., 2014 (MGP181/57C), indicated by arrows. E, Fern *Speirocarpus* sp. (MGP197/69B) showing lenticular-ovoidal foliar oviopsition scars (DT101), indicated by arrows. F and I, Lenticular-ovoidal foliar oviopsition scars (DT100) on the unaffiliated cycadophytes (MGP196/6; MGP196/7A). G, Undifferentiated galling structures (DT80) on a seed-fern (MGP63/94), indicated by arrows. H, Semilinear, frass-laden, mining structure with a smooth and rimmed margin (DT40) on *Scytophyllum bergeri* Bornemann, 1856 (MGP63/98A), asterisk indicates initial place of oviposition. J, Ellipsoidal scale impressions with roughened surface (DT128) on the cycadophyte *Nilssonia* cf. *neuberi* Stur ex Pott et al. 2007 (DT128) (MGP194/72A). Scale bars: striped, 10 mm; solid, 5 mm; dotted, 1 mm.

4
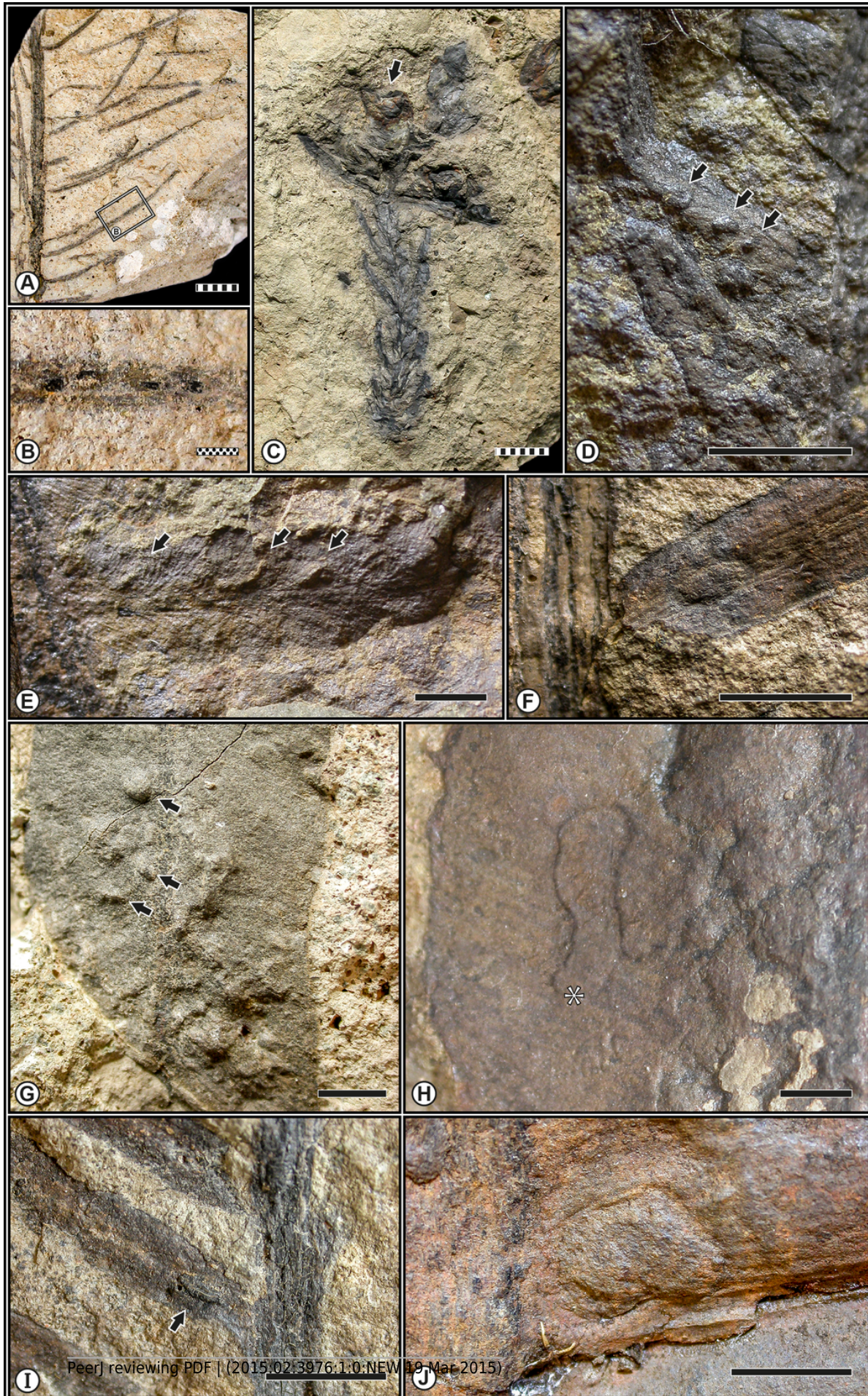
Plant and damage composition within the single sub-localities

Figure 4. Plant and damage composition within the single sub-localities. Pie charts showing the frequency specimen data by A. Host plant abundance (pooled in higher taxonomic ranks). B–D. Damage composition. MA1, MA5, MA7, MA8, fossil sites.