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2 **Resin exudation and resinicolous communities on *Araucaria***
3 ***humboldtensis* in New Caledonia**

4 **Christina Beimforde¹ · Leyla J. Seyfullah¹ · Vincent Perrichot² ·**
5 **Kerstin Schmidt³ · Jouko Rikkinen^{4,5} · Alexander R. Schmidt¹**

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8 **Abstract** Conifers of the endemic species *Araucaria*
9 *humboldtensis* on Mont Humboldt in New Caledonia
10 exhibit extensive resin exudation. The resin flows of these
11 threatened trees are here shown to be induced by two beetle
12 species, which bore into branches and branchlets, leading
13 to abundant outpouring of resin, which gradually solidifies
14 into often drop-shaped resin bodies. The exudate is colo-
15 nized by a resinicolous and likely insect-vectored asco-
16 mycete, *Resinogalea humboldtensis*, which is only known
17 from Mont Humboldt. The fungus grows into fresh resin
18 and eventually develops ascomata on the surface of solid-
19 ifying resin. The solidified resin is also colonized by
20 another fungus, a dematiaceous hyphomycete. Based on
21 protein coding (CO1, CAD, ArgK) and ribosomal (LSU)
22 genes, the larger branch-boring beetle is a weevil of the
23 tribe Araucariini, which represents the sister group of all

other cossonine weevils. The smaller beetle species 24
belongs to the longhorn beetles (Cerambycidae). The 25
strong host specificity of the Araucariini, along with the 26
occurrence of two unique fungi, suggests that the resin- 27
associated community is native and has evolved on the 28
endemic conifer host. The formation of large amber 29
deposits indicates massive resin production in the past, but 30
the environmental triggers of exudation in Mesozoic and 31
Cenozoic ecosystems remain unclear. Our observations 32
from Mont Humboldt support the notion that the occur- 33
rences of small drop-shaped amber pieces in Triassic to 34
Miocene amber deposits were linked to ancient insect 35
infestations. 36

Keywords Amber · *Araucaria humboldtensis* · 38
Araucariini · Coleoptera · Resinicolous fungi · 39
Resinogalea · Weevils 40

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Introduction 41

Some conifers and angiosperms produce large amounts of 42
resin from wounds in the wood in order to seal injuries and 43
to prevent microbial infections and infestations by arthro- 44
pods (Farrell et al. 1991; Gershenson and Dudareva 2007; 45
Howe and Schaller 2008). Due to its compounds (ter- 46
penoids or phenolics), resin not only provides a mechanical 47
barrier but also protects plants through its toxic properties 48
(Bednarek and Osbourn 2009; Rautio et al. 2011; Sipponen 49
and Laitinen 2011). 50

Fossilized plant resins (ambers) date back to the Car- 51
boniferous 320 million years ago (Bray and Anderson 52
2009), but are found only in trace quantities until the Early 53
Cretaceous (Schmidt et al. 2012). In contrast, massive 54
amber deposits have been preserved in Cretaceous 55

- 56 (Barremian-Campanian) and in Eocene to Miocene sedi- 109
 57 ments (Penney 2010). Worldwide, accumulation of this 110
 58 amber occurred in widespread Cretaceous and Cenozoic 111
 59 forests with resinous tree species. However, it remains 112
 60 uncertain why the trees produced so much resin at these 113
 61 particular times. Climate changes, the advent of wood-in- 114
 62 festing insects and microorganisms, and/or even the 115
 63 appearance of certain conifer or angiosperm species might 116
 64 have triggered the massive resin outpourings (Schmidt 117
 65 et al. 2012; Labandeira 2014; Dal Corso et al. 2015). 118
- 66 Mesozoic resin-producing tree species typically include 119
 67 conifers of the Araucariaceae and the extinct family 120
 68 Cheirolepidiaceae (Langenheim 1995, 2003; Roghi et al. 121
 69 2006a, b; Nohra et al. 2015). Later, probably since the Late 122
 70 Cretaceous and early Cenozoic, angiosperms such as 123
 71 Dipterocarpaceae (Rust et al. 2010) and Fabaceae (Lang- 124
 72 enheim 1995, 2003) started to contribute significantly to 125
 73 the amber fossil record. Among today's gymnosperms, 126
 74 many Pinaceae and Araucariaceae produce large quantities 127
 75 of resin (Langenheim 1995, 2003). While species of the 128
 76 former family are widespread in the Northern Hemisphere, 129
 77 extant Araucariaceae are predominantly found in mid- and 130
 78 southern latitudes (Borneo, Philippines, Chile, Argentina, 131
 79 southern Brazil, New Caledonia, New Zealand, Norfolk 132
 80 Island, Australia and New Guinea) with a major diversity 133
 81 centre in New Caledonia (Eckenwalder 2009). The disjunct 134
 82 extant distribution and the fossil record of the latter family 135
 83 suggest that araucarian conifers were more widespread in 136
 84 the past and probably represented a major component of 137
 85 Mesozoic forest ecosystems in both hemispheres (e.g. Lele 138
 86 1956; Miller 1977; Stockey 1982; Hill 1995; Kunzmann 139
 87 2007). 140
- 88 Presently the island of Grande Terre in New Caledonia 141
 89 has 19 Araucariaceae species of which 13 are endemic 142
 90 (Jaffré 1995; Gaudeul et al. 2012), and it has often been 143
 91 termed a Gondwanan refuge (Holloway 1979; Morat 144
 92 1993a, b). However, recent studies suggest that the species 145
 93 richness of New Caledonia's araucarians is rather a result of 146
 94 adaptive radiation in the post-Eocene era, mainly forced by 147
 95 unusual edaphic conditions, i.e. the widespread occurrence 148
 96 of ultramafic soils (Setoguchi et al. 1998; Gaudeul et al. 149
 97 2012; Escapa and Catalano 2013; Kranitz et al. 2014; 150
 98 Grandcolas et al. 2015). Nevertheless, with an evolutionary 151
 99 history of more than 200 million years, Araucariaceae are 152
 100 among the oldest extant conifers (Kunzmann 2007). In this 153
 101 respect, the conifer forests of New Caledonia offer an opti- 154
 102 mal site for the study of plant–environment interactions that 155
 103 are responsible for triggering resin production, past and 156
 104 present.
- 105 Here we show that the widespread and substantial resin 157
 106 exudation of *Araucaria humboldtensis* Buchholz 1949, an 158
 107 endangered (IUCN red list status) endemic New Caledonian 159
 108 mountain conifer, is induced by at least two species of beetles 160
 and that the exuded resin provides the habitat and nutrient 161
 source for at least two unique types of resinicolous fungi. 162
Araucaria humboldtensis occurs sporadically in the montane 163
 forests of Mont Mou, Mont Kouakoué and Montagne des 164
 Sources, but only close to the summit of Mont Humboldt is it 165
 the dominant timberline species (Fig. 1a). Our analysis of 166
 the plant–animal–fungal interactions at this unique location 167
 indicates that the wood-boring beetles are not recently 168
 introduced species, but native to New Caledonia and eco- 169
 logically important in providing continuous substrate for two 170
 endemic, potentially ancient fungi. Our overall observations 171
 also provide insights into possible means of resin production 172
 and amber formation in earth history: for example, the simi- 173
 larity between the Mont Humboldt resin droplets and those 174
 preserved as Triassic amber is striking. We propose that not 175
 all ancient resin productions should necessarily be inter- 176
 preted as anomalies caused by specific triggers such as high 177
 humidity (Dal Corso et al. 2015) or fire, but may have 178
 accumulated over time in humid forest environments. There 179
 is some indication also that the ancient resin surfaces may 180
 have supported specialized communities rather similar to 181
 that now described from Mont Humboldt (McKellar et al. 182
 2011; Tuovila et al. 2013). 183
- ## 184 Materials and methods 185
- ### 186 Field work 187
- 188 Resin flows of *Araucaria humboldtensis* on Mont Humboldt 189
 190 were examined and photographed in October 2005 and in 191
 192 November 2011. Samples of resin with fungi and wood- 193
 194 boring insects were taken on 9 November 2011 from trees 195
 196 close to the refuge (elevation 1345 m, coordinates 197
 198 21°52'57.52''S, 166°24'46.20''E), approximately 300 m 199
 200 north of the building (elevation 1320 m, coordinates 201
 202 21°52'46.79''S, 166°24'49.17''E), and along the summit trail 203
 204 approximately 300 m east of the shelter (elevation 1380 m, 205
 206 coordinates 21°52'54.89''S, 166°24'55.85''E). Fungi were 207
 208 stored dry in sealed containers, and insects were preserved in 209
 80% ethyl alcohol for storage and transport. 210
- ### 211 Repository 212
- 213 Specimens of *Resinogalea humboldtensis* are deposited in 214
 215 the herbaria at the MNHN Paris and in Helsinki (see Rikki- 216
 217 nen et al. 2016). Lumps of resin with the dematiaceous 218
 219 hyphomycete are housed in the Geoscientific Collections of 220
 221 the Georg August University Göttingen (GZG.BST.21894a– 222
 223 e). Beetle specimens are housed in the collection of the 224
 225 laboratory Géosciences Rennes (University Rennes I), col- 226
 227 lection numbers VP-NC-221 (Araucariini) and VP-NC-202 228
 229 (Cerambycidae). 230



Fig. 1 Resinous *Araucaria humboldtensis* on Mont Humboldt in New Caledonia. **a** Cloud forest of Mont Humboldt with *A. humboldtensis* as dominating tree species. **b** Tree with resin

outpourings on several branches. **c** Massive resin outpouring and death of distal branch end after infestation by weevil larvae of the Araucariini tribe

156 **Microscopy and imaging**

157 Samples were investigated under a Carl Zeiss Stereo Discovery
 158 V8 dissection microscope, and under a Carl Zeiss AxioScope
 159 A1 compound microscope, each equipped with a Canon EOS
 160 5D digital camera. In some instances, incident and transmitted
 161 light were used simultaneously. Figure 4a, c–e shows digitally
 162 stacked photomicrographic composites of up to 150 individual
 163 focal planes, obtained by using the software package Heli-
 164 conFocus 6.0 (HeliconSoft, <http://www.heliconsoft.com>) for
 165 an enhanced illustration of three-dimensional structures.

Cultivation of resinicolous fungi

For in vitro cultivation experiments, mycelia of the
 dematiaceous hyphomycete and spores from the mazaee-
 dum of *Resinogalea* were extracted and transferred to
 diverse sugar-based media: malt yeast extract agar (MYA,
 Ahmadjian 1967), malt extract agar (MEA, Blakeslee
 1915) and potato dextrose agar (PDA, Roth). Additionally,
 Canada balsam and/or small pieces of *Araucaria hum-
 boldtensis* resin were provided as potential nutrient sources
 for the fungi.

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176 DNA extraction and amplification

177 DNA was isolated using DNeasy Blood and Tissue Kit
 178 (Qiagen) by following the manufacturer's protocol for
 179 tissue samples. For the beetles, we amplified and
 180 sequenced fragments of the mitochondrial gene cyto-
 181 chrome oxidase 1 (COI), the D2–D3 segment of the nuclear
 182 large ribosomal subunit (28S), the nuclear protein arginine
 183 kinase (ArgK) and carbamoyl-phosphate synthase 2—as-
 184 partate transcarbamylase—dihydroorotase (CAD). The ITS
 185 region of the resinicolous fungi was amplified using primers
 186 ITS1F and ITS4. All primers used in this study are
 187 provided in supplementary information (Table S1). PCRs
 188 were performed in a 25- μ l volume containing final con-
 189 centrations of 0.5 μ M of each primer, 0.5 μ M of each
 190 dNTP, 1.25 units of GoTaq Hot Start DNA polymerase
 191 (Promega), Green PCR buffer with a final concentration of
 192 1.5 mM MgCl₂ and 1–2 μ l template DNA. A typical PCR
 193 cycle consisted of 2 min initial heating to activate the DNA
 194 polymerase and to ensure that the template DNA has
 195 denatured, 40 cycles of 94 °C for 45–60 s of denaturation,
 196 50–56 °C for 45–60 s of annealing, and 72 °C for 45–60 s
 197 of elongation and a final elongation step at 72 °C for
 198 10 min. PCR products were purified using Quick PCR
 199 Purification Kit from Qiagen. PCR products were
 200 sequenced in both directions with a MegaBACE 1000
 201 automated sequencing machine and DYEnamic ET Primer
 202 DNA Sequencing Reagent (Amersham Biosciences, Little
 203 Chalfont, UK). All sequences were assembled and edited
 204 using BioEdit version 5.0.9 (Hall 1999) and SeaView 4
 205 (Gouy et al. 2010).

206 Phylogenetic analysis of the beetles

207 Since no adults of the two beetle species were available for
 208 species identification, we substantiated morphological
 209 diagnostics with comprehensive molecular phylogenetic
 210 analysis. We combined our DNA sequence data obtained
 211 from four genes (COI, LSU, ArgK and CAD) of the large
 212 beetle species and from the COI gene for the small beetle
 213 species with data from the National Center for Biotech-
 214 nology Information (NCBI). All accession numbers are
 215 provided in supplementary notes (Table S2). Data sets for
 216 each gene were aligned separately using MAFFT version 6
 217 (Kato and Toh 2008) with subsequent manual adjustment
 218 to minimize the number of possible false homologies using
 219 BioEdit 5.0.9. (Hall 1999) and SeaView 4 (Gouy et al.
 220 2010). Unalignable regions and introns were excluded by
 221 using the mask function in BioEdit 5.0.9. All genes were
 222 subsequently combined in a super matrix using BioEdit
 223 5.0.9. Bayesian analyses were performed using Markov
 224 chain Monte Carlo (MCMC) in MrBayes 3.1.2 (Ronquist
 225 and Huelsenbeck 2003). Evolutionary models with six

substitution rates, gamma distributed rate variation and a
 proportion of invariable sites (GTR + I + G) were applied
 to each gene separately by allowing MrBayes to estimate
 specifications for the gamma shape parameter, proportion
 of invariance and rate matrix for each partition. Phyloge-
 netic analyses were performed using two parallel runs, each
 with four chains, for 10 million generations and sampling
 parameters every 1000 generations.

Most likely trees were sampled by using a burn-in of
 25%, and a 50% majority rule consensus tree was gener-
 ated. All analyses were performed on the freely available
 computational resource CIPRES (Miller et al. 2010).
 Assessing convergence and sufficient chain mixing (ef-
 fective sample sizes >200) was observed using Tracer 1.5
 (Rambaut and Drummond 2009). Resulting trees were
 visualized using FigTree (Rambaut 2006–2009, [http://tree.
 bio.ed.ac.uk/software/figtree/](http://tree.bio.ed.ac.uk/software/figtree/)).

Results and discussion

Field observations

A large proportion of *Araucaria humboldtensis* trees on
 Mont Humboldt exhibited conspicuous resin outpourings
 that were commonly associated with the death of branch-
 lets or sometimes even entire branches (Fig. 1b, c). There
 was no indication of damage caused by high winds or any
 other external mechanical impact. The *Araucaria hum-
 boldtensis* forest is located between approximately 1250
 and 1500 m elevation, a region with daily fog and rainfall
 ensuring constant high humidity year-round. Consequently,
 while wildfires are common on the lower slopes of Mont
 Humboldt, the timberline forest is not subjected to fire,
 which is another possible trigger of enhanced resin pro-
 duction (Scott 2000; Brasier et al. 2009; Najarro et al.
 2010). Instead, we observed that the resin outpourings
 consistently occurred on branches that had been infested by
 wood-boring beetles (Figs. 1, 2, 3).

Two differently sized species of wood-boring beetles
 were identified from the resin-exuding branches and
 branchlets. Larvae of both species caused substantial
 damage to the interior of the branch. Larvae of the smaller
 beetle species were predominantly found in the distal thin
 green branchlets (Figs. 2a–c, 3e), whereas larvae and
 pupae of the larger species occurred in the wider woody
 parts of mature branches (Figs. 1c, 3a–d). The boring
 activity of the smaller species induced the production of
 abundant resin drops of predominantly 3–4 mm size that
 solidified on the leaves and branchlet tips. Borings of the
 larger species often led to the death of distal branch ends or
 of entire branches (Fig. 1c). This is likely because the
 maximum width of the mature larvae is only slightly



Fig. 2 Drop-shaped resin pieces on *Araucaria humboldtensis* (a–c) and from Triassic and Eocene amber deposits (d, e). a Resin droplets on branchlets exuded after infestation by small beetles. b, c Small resin outpourings composed of several resin droplets.

d Amber droplets from the Triassic (Carnian) Heiligkreuz Formation in the Italian Dolomites. e Drop-shaped piece of Eocene Baltic amber. Scale bars 5 mm

275 smaller than mature branches of *Araucaria humboldtensis*
 276 so that both xylem and phloem are heavily damaged by the
 277 insect larvae (Fig. 3a, b).

278 Resin flows induced by the larger beetle species were
 279 drop-shaped to irregular, sometimes forming masses sur-
 280 rounding an entire branch (Fig. 1c). These larger resin
 281 outpourings commonly consist of several successive resin
 282 flows and obviously persist over many months, possibly
 283 even years (Figs. 1c, 4b).

284 **Wood-boring beetles**

285 The larger beetle species represents a weevil (family Cur-
 286 culionidae). According to our Bayesian analysis (Fig. 5), it
 287 belongs to the subfamily Cossoninae and likely represents
 288 a member of the Araucariini group, a tribe erected by
 289 Kuschel (1966) and presently accommodating the

neotropical genus *Araucarius* Kuschel 1966, and the four 290
 Oceanian genera *Coptocorynus* Marshall 1947, *Mastersi- 291*
nella Lea 1896, *Xenocnema* Wollaston 1973 and *Inosomus 292*
 Broun 1882 (Alonso-Zarazaga and Lyal 1999). The phy- 293
 logenetic analysis placed the smaller beetle species clearly 294
 outside the Curculionidae, and the morphological features 295
 of the larvae are characteristic for the family Cerambyci- 296
 dae. However, because of insufficient molecular data in 297
 public databases, we were not able to assign the smaller 298
 species to any group with any certainty. 299

The phylogenetic relationships of the Cossoninae 300
 (Fig. 5) revealed by our analysis are congruent with the 301
 results of Jordal et al. (2011). The monophyletic Arau- 302
 cariini tribe forms the sister group to the remaining Cos- 303
 soninae, and the Mont Humboldt weevil constitutes the 304
 first-order sister clade to the remaining Araucariini. 305
 Although only ambiguously supported (0.79 pp, Fig. 5), 306



Fig. 3 Beetle infestation in *Araucaria humboldtensis*. **a** Fragment of a branch with branchlets died off after erosion of the branch's interior by weevil larvae. **b** Weevil larva feeding the tissue of a branch. **c**,

d Larva (**c**) and pupa (**d**) of a weevil of the Araucariini tribe. **e** Small beetle larvae, a representative of the Cerambycidae, from the interior of the branchlet. Scale bars 1 cm (**a**), 5 mm (**b–d**) and 1 mm (**e**)

307 the affiliation of the weevil from Mont Humboldt to the
308 Araucariini group is conceivable because multiple inde-
309 pendent Bayesian analysis with different taxon samplings
310 for the Cossoninae all grouped the weevil from Mont
311 Humboldt to the Araucariini tribe (data not shown).

312 Jordal et al. (2011) recently confirmed that the sub-
313 family Cossoninae is monophyletic and includes the tribe
314 Araucariini. Within the Cossoninae, only members of the
315 monophyletic Araucariini are restricted to araucarian host
316 plants, while the remaining Cossoninae comprise lineages
317 feeding on angiosperms or Pinaceae. Both larvae and adults
318 of Araucariini live inside the bark and phloem of their
319 araucarian hosts (Mecke et al. 2005). Since mature bran-
320 ches of *Araucaria humboldtensis* were only slightly larger
321 in diameter than the larvae and pupae of the weevil spec-
322 imens within (Fig. 3a, b), it is difficult to deduce the pre-
323 ferred food of the larvae. However, phloem tissue was
324 certainly included in their diet.

325 New Caledonia's Araucariaceae are believed to have
326 diversified in post-Eocene times, mainly in response to the
327 highly unusual edaphic conditions on the island (Setoguchi
328 et al. 1998; Kranitz et al. 2014; Grandcolas et al. 2015).
329 Not surprisingly, Mecke et al. (2005) also showed that New
330 Caledonia harbours a wide variety of largely undescribed

weevil species that associate with different *Araucaria* 331
species. Due to their specialization on araucarian hosts and 332
basal position within the Cossoninae, the Araucariini are 333
suspected to represent an archaic lineage within the Cos- 334
soninae (Kuschel 1966, 2000; Sequeira and Farrell 2001; 335
Sequeira et al. 2000). The extreme host specificity may in 336
turn be related to the stable morphology and anatomy of its 337
araucarian hosts. Fossil data demonstrate that the phloem 338
anatomy of araucarians has not changed significantly since 339
Cretaceous times (Stockey 1994), and the trees are also 340
known to have produced resin by the mid-Cretaceous 341
(Nohra et al. 2015). Concurrently, resin flows of araucarian 342
conifers in humid forest ecosystems have existed for tens 343
of millions of years and potentially allowed the evolution 344
of highly specialized resinicolous organisms and associa- 345
tions (see Mecke et al. 2005). 346

Resiniculous fungi 347

The semi-solid resin of *Araucaria humboldtensis* on Mont 348
Humboldt provided suitable substrate for at least two 349
unique species of resinicolous fungi (Fig. 4). The first 350
fungus (Fig. 4a), a teleomorphic ascomycete, was recently 351
described as new and named *Resinogalea humboldtensis* 352

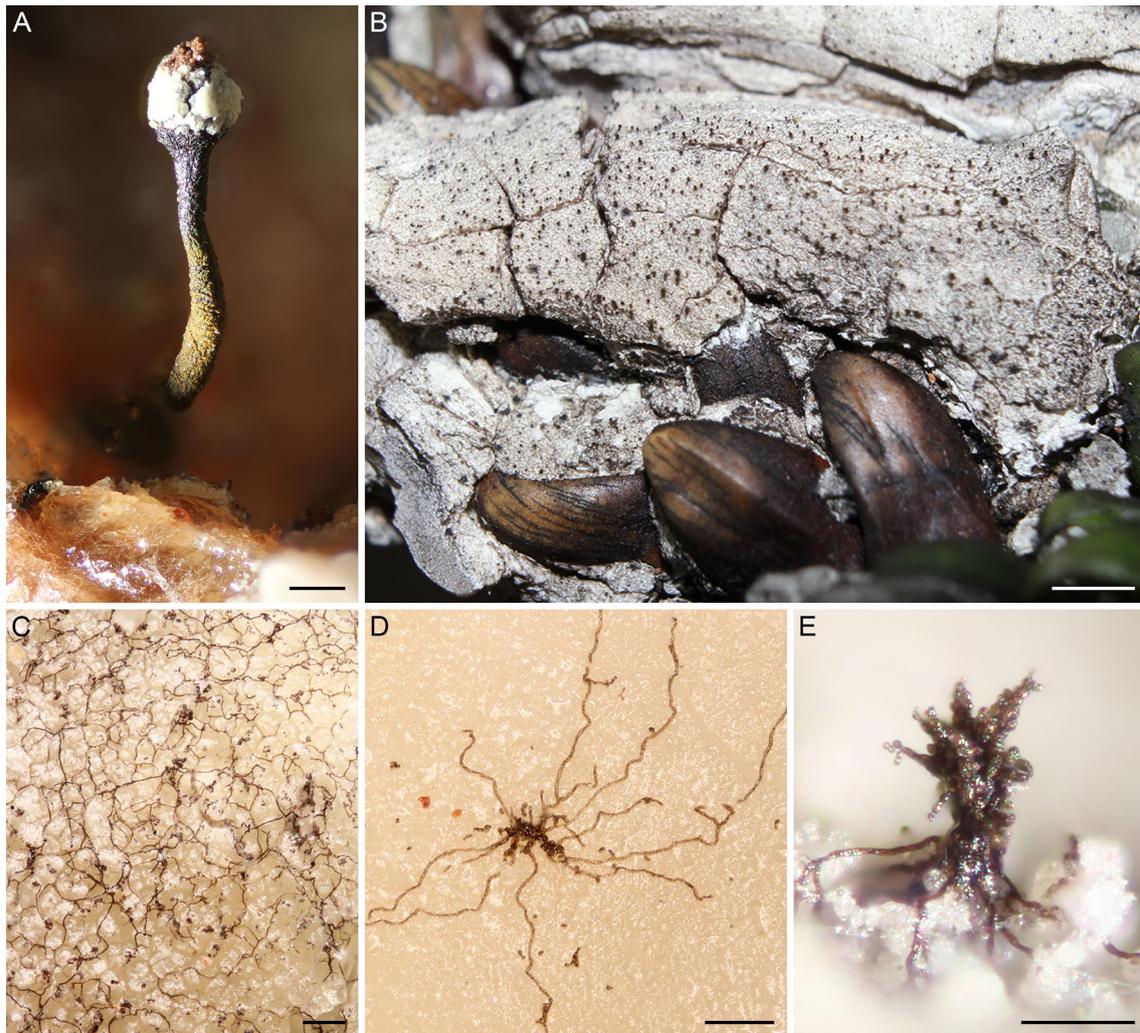


Fig. 4 Resiniculous fungi from *Araucaria humboldtensis*. **a** Ascoma of *Resinogalea humboldtensis* exposing ascospores on top. Hyphae inside the resin are visible in the lower left of the image. **b** Solidified resin densely overgrown by a dematiaceous hyphomycete. **c** Close-up of **(b)** showing the dark hyphae. **d** Growing young colony of the

dematiaceous hyphomycete with formation of conidia. **e** Conidiophores of the dematiaceous hyphomycete arising forming aggregated superficial hyphae and bearing simple acropetal chains of conidia. Scale bars 200 μm (**a**), 1 mm (**b**), 100 μm (**c**, **d**) and 50 μm (**e**)

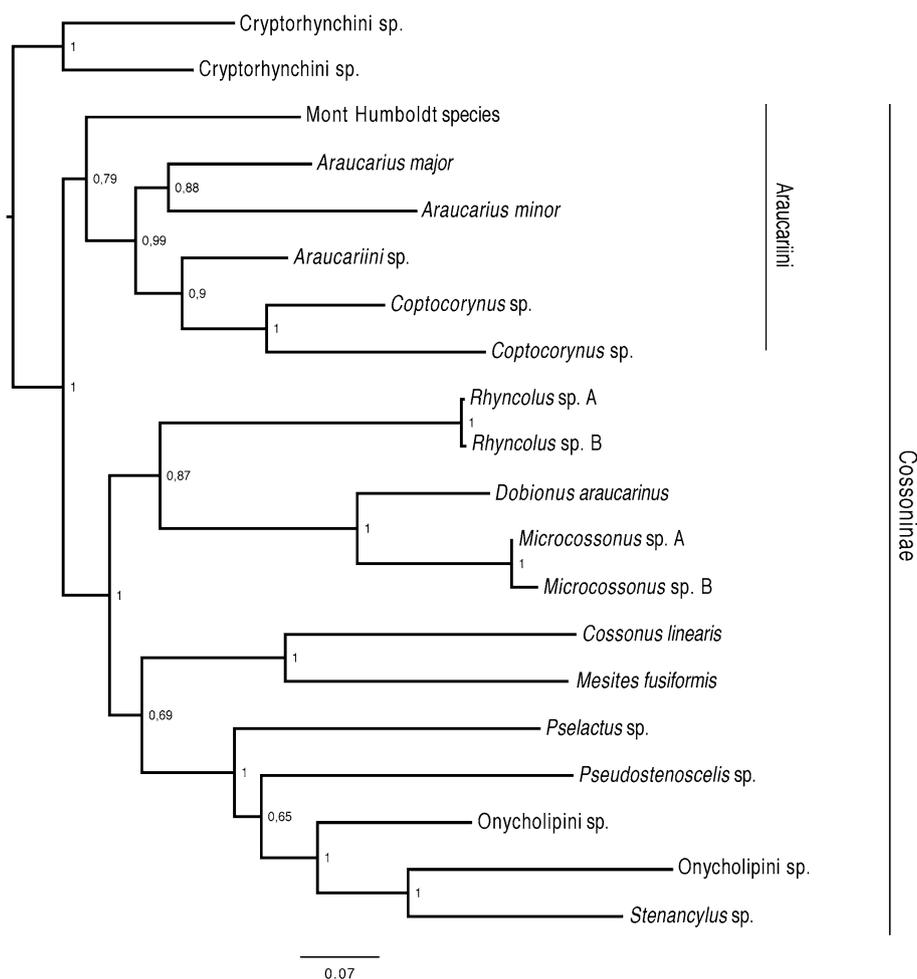
353 Rikkinen et al. R. Schmidt 2016. The pale mycelium grows
354 immersed in semi-solidified resin of *A. humboldtensis*
355 (Fig. 4a, lower left), and ascomata are formed when the
356 substrate solidifies. As the mycelium grows entirely sub-
357 merged in the resin and because individual hyphae grow in
358 random orientations, the fungus seems to utilize resin as a
359 food source. For more details on the ecology, anatomy and
360 taxonomy of *R. humboldtensis*, see Rikkinen et al. (2016).

361 While ascomata of *Resinogalea* were found in only a
362 small minority of resin flows on Mont Humboldt, almost all
363 hardening and solidified resin surfaces were colonized by a
364 highly conspicuous dematiaceous hyphomycete (Fig. 4b–
365 e). The dark hyphae of the fungus grew only on the hard-
366 ened resin surface and did not penetrate into semi-solidified
367 resin. Synnemata consisting of aggregated hyphae produce

simple acropetal chains of rounded to ovoid ornamented
368 conidia 4–7 μm long (Fig. 4e). Sometimes the conidio-
369 phores are reduced to mere conidiogenous cells with sim-
370 ple acropetal chains of more rounded conidia (Fig. 4d). On
371 the basis of ITS sequences, the fungus belongs to the
372 Mycosphaerellaceae, but its closer affinities remain
373 unresolved. 374

375 Resiniculous fungi represent a polyphyletic ecological
376 assemblage including, for example, many ascomycetes of the
377 order Mycocaliciales (e.g. Rikkinen 1999, 2003a, b; Rikkinen
378 et al. 2014, 2016; Tuovila et al. 2011a, b, 2012, 2013; Tuovila
379 2013). Many resinicolous mycocalicioids are highly substrate
380 specific, a feature most likely related to the unique chemical
381 compositions of many plant exudates (Lagenheim 2003).
382 *Chaenothecopsis neocaledonica* from *Agathis ovata* (C.

Fig. 5 50% majority rule consensus phylogram from Bayesian analyses (MrBayes) showing phylogenetic relationships of the Cossoninae based on nuclear ribosomal (LSU) and protein coding (CO1, ArgK, CAD) sequence data of 18 Cossoninae species and two Cryptorhynchinae species used as outgroup. **Numbers** at nodes indicate posterior probabilities (pp) for node support. **Node supports** of 1.0 pp and less are shown



383 Moore ex Vieill.) Warb. 1900 is the only resinicolous myco- 403
 384 calicioid fungus so far known from araucarian exudates 404
 385 (Rikkinen et al. 2014). However, considering the high diver- 405
 386 sity of Araucariaceae in New Caledonia, many new resini- 406
 387 colous fungi may still await discovery on the island. 407

388 A resinous community

389 *Araucaria humboldtensis* is the dominant tree species in 411
 390 the timberline forest of Mont Humboldt. The trees produce 412
 391 a steady supply of fresh resin induced by at least two wood- 413
 392 boring beetle species. The phylogenetic placement of the 414
 393 weevil species within the Araucariini tribe suggests a long- 415
 394 lasting interaction between the narrow endemic conifer 416
 395 host and the beetle species that has specialized to bore into 417
 396 its branches and feed on their internal tissue. Interestingly, 418
 397 the occurrence of *Resinogalea* further indicates that the 419
 398 beetle-induced resin outpourings must have been common 420
 399 and continuous enough to allow the evolution and contin- 421
 400 ued existence of a unique ascomycete species specific to 422
 401 this unusual substrate. It is also likely that *Resinogalea* 423
 402 *humboldtensis* and possibly the dematiaceous hyphomycete 424

are dispersed by adult beetles. The ascomata of *Resino-* 403
galea have long and slender stalks and well-developed 404
 mazaedia (spore masses), which both represent typical 405
 calicioid features that are suspected to promote insect 406
 dispersal. Mature ascospores accumulate into the maza- 407
 edium and are then easily attached to roaming insects 408
 (Rikkinen 1995, 2003a; Tuovila et al. 2011a; Prieto and 409
 Wedin 2013). Also, the widespread production of syn- 410
 nemata by the anamorphic stages of many ascomycetes 411
 (e.g. Seifert 1985) is undoubtedly partly explained by 412
 adaptations for animal dispersal. Thus, the two unique 413
 fungi on *A. humboldtensis* resin may depend on the wood- 414
 boring beetles, not only for the production of suitable sub- 415
 strate, but also in their dispersal. 416

Despite repeated efforts, we could not induce the 417
 ascospores of *Resinogalea humboldtensis* to germinate and 418
 were thus unable to culture the fungus. The dematiaceous 419
 hyphomycete did grow, but very slowly and exclusively on 420
 the original substrate, i.e. small pieces of *Araucaria hum-* 421
boldtensis resin. No growth was observed on sugar-based 422
 media or Canada balsam (Pinaceae resin). When small 423
 pieces of the natural substrate and sugar were provided, 424

425 growth was restricted to the resin. This strongly suggests an
426 inability to metabolize sugar-based carbohydrates and
427 exemplifies the level of substrate specialization in resini-
428 colous fungi. The inability to use Pinaceae resin together
429 with the apparent narrow endemism in New Caledonia
430 suggests that the dematiaceous hyphomycete may only
431 occur on the resin of this one *Araucaria* species or that it is
432 at least restricted to New Caledonia.

433 A concurrent example of extreme substrate specificity of
434 a resinicolous fungus to a narrowly endemic conifer host
435 was previously reported from California, where *Mycocalicium sequoiae*
436 only lives on the resinous exudate that
437 issues from the exposed heartwood of fire-scarred but still
438 living trunks of *Sequoiadendron giganteum* (Bonar 1971).
439 Two collections of the fungus have also been reported from
440 *Sequoia sempervirens*, but their identity should be con-
441 firmed by molecular methods.

442 We conclude that the wood-boring beetles that cause
443 highly conspicuous resin flows on *Araucaria humboldtensis*
444 are not introduced species and probably do not pose a
445 serious threat to the existence of the critically endangered
446 tree species. Conversely, they induce and maintain a con-
447 tinuum of substantial resin flows that apparently provide
448 the only substrate for two species of unique resinicolous
449 fungi. There is reason to believe that the ‘triangle associ-
450 ation’ between the endemic conifer host, the endemic
451 weevil and the two endemic fungi evolved in the humid
452 forests of New Caledonia and may be of considerable
453 antiquity. Divergence time estimates by Kranitz et al.
454 (2014) suggest that the New Caledonian *Araucaria* species
455 diversified in the Miocene–Pliocene between 19 and 3 Ma
456 and that *A. humboldtensis* appears to be approximately
457 5 Ma old, suggesting that the common history of the
458 association may date back to the early Pliocene or even
459 further.

460 Palaeoecological implications

461 We propose that the extant *Araucaria humboldtensis* forest
462 offers a model for a type of enhanced resin production in
463 ancient ‘amber forests’, i.e. past forest ecosystems from
464 which amber deposits derive.

465 The reasons for massive Mesozoic and Cenozoic amber
466 accumulations remain obscure. It has been suggested that
467 the evolution of certain wood-boring insect species and
468 subsequent large-scale insect outbreaks might have caused
469 substantial tree damage followed by enhanced resin release
470 (McKellar et al. 2011; Peris et al. 2015). Concurrently, it
471 has been suggested that Coleoptera were unlikely to have
472 been inducers for the resin outpourings that resulted in
473 early–middle Cretaceous ambers, based on the sparse
474 record of wood-boring beetle families such as Curculion-
475 idae, Cerambycidae or Buprestidae in these ambers (Peris

et al. 2016). However, this is based on the scarcity of adult
specimens preserved and does not consider the possibility
of larval stages boring into branchlets, which would have a
low probability of being engulfed by resin flows. Our
current observations from Mont Humboldt show that even
a moderate population of specialized insects can trigger
and maintain the continuous production of considerable
amounts of resin. Ambers are known to vary in size from
tiny droplets to massive pieces of up to 10 kg (e.g. Weit-
schat and Wichard 2002; Krumbiegel and Krumbiegel
2005), and their primary shape depends on resin viscosity
and how and where the resin was produced on the ancient
source trees. The shape and size of the resin droplets pro-
duced by *Araucaria humboldtensis* correspond closely to
those of certain amber pieces, such droplets from the Tri-
assic Heiligkreuz Formation in the Italian Dolomites
(Fig. 2d, Roghi et al. 2006a, b; Schmidt et al. 2006, 2012),
Late Cretaceous (Turonian–Santonian) of north-western
and southern France (Saint Martin et al. 2013; Néraudeau
et al. 2017) and from the Eocene of the Baltic area
(Fig. 2e).

The occurrence of Triassic amber exclusively in a nar-
row Carnian-aged time horizon exemplifies a probable
connection between enhanced resin production and climate
change (Schmidt et al. 2012), and a connection to the
Carnian Pluvial Event (Breda et al. 2009; Roghi et al.
2010), a global episode of atmospheric perturbation with
dramatic changes in a monsoonal climate due to massive
volcanism (Roghi et al. 2010; Preto et al. 2010; Dal Corso
et al. 2012). Previously, Langenheim (1994) suggested that
resin production can be enhanced in response to increased
water availability, and so on Mont Humboldt the contin-
uous high atmospheric humidity may well promote resin
exudation responses during insect infestations. We pre-
sume, however, that massive resin productions during
particular periods of Earth history were unlikely to be
caused by any single event or trigger, but more likely
reflect complex organismal interactions in humid forests,
involving not only trees and wood-boring insects but
potentially also many other resin-associated organisms,
including resinicolous ascomycetes. This is supported by
the fact that resinicolous *Chaenothecopsis* species have
been found in Palaeogene ambers of Europe (Beimforde
et al. 2014; Rikkinen and Poinar 2000; Tuovila et al. 2013),
demonstrating that their special mode of nutrition was
already developed at least 35 million years ago.

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