



HAL
open science

New species of *Iodes* fruits (Icacinaceae) from the early Eocene Le Quesnoy locality

Cédric del Rio, Gregory Stull, Dario de Franceschi

► **To cite this version:**

Cédric del Rio, Gregory Stull, Dario de Franceschi. New species of *Iodes* fruits (Icacinaceae) from the early Eocene Le Quesnoy locality. *Review of Palaeobotany and Palynology*, 2019, 262, pp.60-71. 10.1016/j.revpalbo.2018.12.005 . hal-02404789

HAL Id: hal-02404789

<https://hal.sorbonne-universite.fr/hal-02404789>

Submitted on 11 Dec 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 Title: New species of *Iodes* fruits (Icacinaceae) from the early Eocene Le Quesnoy locality,
2 Oise, France.

3 Cédric Del Rio^{1,2,*}, Gregory W. Stull³, Dario De Franceschi¹

4

5 ¹ CR2P - Centre de Recherche en Paléontologie - Paris, MNHN - Sorbonne Université -
6 CNRS, CP38, 57 rue Cuvier, 75231 Paris Cedex 05, France

7

8 ² ISYEB - Institut de Systématique, Évolution, Biodiversité, CNRS, MNHN, Sorbonne-
9 Université, EPHE, CP39, 57 rue Cuvier, 75231 Paris Cedex 05, France

10 ³ Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor,
11 Michigan, 48109, USA

12

13 * Author for correspondence, cedric.del-rio@edu.mnhn.fr

14 Abstract: The floristic diversity of the Le Quesnoy amber locality (Ypresian, Oise France)
15 remains understudied. Icacinaceae Miers, particularly, require careful study, as they are the
16 most abundant family in the site, with 185 nearly complete lignitic endocarps specimens and
17 numerous fragments. In this paper, we recognise three species of Icacinaceae, two of which
18 are new, that belong to the genus *Iodes*. Indeed, all *Iodes* species from this site have the
19 following diagnostic characters: a vascular bundle inside the endocarp wall, a reticulum of
20 external ridges, and papillae on the surface of the locule. *Iodes rigida* sp. nov differs from the
21 others in having a hole at the apex, a pattern of reticulation that delimits some areoles, an “I-
22 Beam” ridge structure, and punctuated and heterogeneous sessile, rounded papillae. *Iodes*
23 *acuta* sp. nov. is distinct from the others due to its unique apical outgrowth (composed of the
24 main ridge that runs from the base up to the apex and a protuberance from the keel merged), a
25 very thin wall, and sharp ridges. Therefore, these new species have a combination of new
26 morpho-anatomical characters never observed before and not found in extant *Iodes* species.
27 Despite some scarce differences, some specimens from Le Quesnoy are attributed to *I. parva*.
28 Finally, several seeds are recognized as Icacinaceae without particular affinity. These seeds
29 are elliptical in shape, lenticular in transverse section, and slightly asymmetrical to completely
30 asymmetrical at the apex. A review of the *Iodes* fossil record is provided. The significance of
31 endocarp ridge morphology is discussed in light of new fossils and extant data. These fossils
32 show affinities with representatives from other Eocene sites of Europe and with the Thanetian
33 Rivecourt site (Oise, France) and appear to have mixed affinities with the modern floras of
34 Asia and Africa. Other studies on this remarkable site, focusing on additional taxonomic
35 groups, are necessary to elucidate the relationship between Le Quesnoy and other floras from
36 the past and the present.

37

38 Key Words: endocarp, fossil, *Iodes*, new species, seed.

39 **1. Introduction**

40 Icacinaceae are a family of trees, shrubs, and climbers with a pantropical distribution (De La
41 Bâthie, 1952; Sleumer, 1971; Villiers, 1973). Traditionally, the family contained about 54
42 genera and 400 species (Sleumer, 1942). However, the lack of clear synapomorphies led to
43 confusions around the taxonomy and phylogeny of this group. Recent phylogenetic studies
44 using morphological and molecular data have greatly clarified the phylogeny of Icacinaceae,
45 allowing recognition of a monophyletic—and much reduced—circumscription of 23 genera
46 and about 150 species (Kårehed, 2001; Lens et al., 2008, Byng et al., 2014; Stull et al., 2015).
47 This clade, along with the family Oncothecaceae, is now placed in the order Icacinales (APG,
48 2016), which is sister to all other lamiids (Stull et al., 2015). The Icacinaceae s.s. are well
49 known in the fossil record in Paleogene localities from Europe, such as the London Clay flora
50 (Reid and Chandler, 1933; Chandler, 1961a, 1961b, 1962; Collinson, 1983; Cleal et al., 2001;
51 Stull et al., 2016), the Messel biota (Collinson et al., 2012), and the Dormaal Formation
52 (Fairon-Demaret and Smith, 2002). Remains from the Paleogene of North America are also
53 well documented (Crane et al., 1990, Manchester, 1994; Manchester, 1999, Pigg and Wher,
54 2002, Pigg et al., 2008, Rankin et al., 2008, Stull et al., 2011, Stull et al., 2012, Allen et al.,
55 2015). In addition, several fossils of the family are known from South America (Stull et al.,
56 2012) and Egypt (Manchester and Tiffney, 1993); additional material has been reported from
57 Africa (Chandler, 1954, Chester, 1955) and Japan (Tanai, 1990), but the affinities of these
58 fossils are more dubious.

59 The fossil record of the family is dominated by endocarps, which tend to be
60 taxonomically informative (Stull et al., 2016). Multiple clades of Icacinaceae are diagnosable
61 by fruit characters—for example, the genus *Iodes* Blume is characterized by elliptical to
62 globular endocarps, lenticular in transverse section, with an external reticular pattern, a
63 papillate layer on the inner surface (locule), and a vascular bundle running from the base to

64 the apex embedded in the endocarp wall. *Iodes*, which contains ~23 extant species, is the most
65 abundantly represented genus of Icacinaceae in the fossil record.

66 These endocarp features are present in numerous fossils from the Le Quesnoy site,
67 suggesting the presence of *Iodes* at this Paleogene locality. The faunal and floral diversity of
68 the Le Quesnoy amber locality (Ypresian, Oise, France) was first studied by Nel et al. (1999).
69 Particular elements of the flora have been examined; for example, there are studies focused on
70 flowers and pollen grains preserved in amber (De Franceschi et al., 2000, De Franceschi and
71 De Ploëg, 2003; Del Rio et al., 2017), lignitic fossil fruits and seeds (Nel et al., 1999), and
72 Menispermaceae endocarps (Jacques and De Franceschi, 2005). However, the diversity of the
73 flora remains understudied. In this paper, we describe two new species of *Iodes* based on
74 fossil endocarps and document a new occurrence of a species that was already described
75 recently from the Rivecourt site (Del Rio et al., 2018); in addition to the endocarp remains,
76 we also document multiple seeds specimens attributed to Icacinaceae, without specific
77 affinity. We discuss the morphological variation of modern and fossil *Iodes* endocarps,
78 establishing a context for assessing the systematic affinities of the new species.

79

80 **2. Material and methods**

81

82 **2.1 Material**

83 The lignitic fossil specimens were collected from Le Quesnoy locality (Houdancourt, Oise,
84 France) from 1996 to 2000, from the lignitic clay sediments of Le Quesnoy outcrop,
85 representing the lower Eocene. The sediments indicate that this site corresponds to an ancient
86 fluvial depositional environment (for location and geological setting, see De Franceschi and
87 De Ploëg, 2003; Smith et al., 2014). Based upon the mammalian fauna (e.g. *Teilhardina*,
88 *Landenodon* sp., *Paschatherium* sp. and *Palaeonictis* cf. *gigantea*; Nel et al., 1999), these

89 sediments are dated at MP7 (Lower Ypresian, ~56 Ma), with corroboration from
90 palynological studies (Nel et al., 1999; Cavagnetto, 2000). This corresponds to the Sparnacian
91 facies of the Lower Ypresian (Lower Eocene).

92 Approximately 185 nearly complete endocarps of Icacinaceae were collected, primarily
93 representing lignified samples, but some pyritized specimens were also obtained. In addition,
94 some lignitic fragments assigned to Icacinaceae were also collected. The fossils are kept in
95 the palaeobotanical collections of the Muséum national d'Histoire naturelle (MNHN) at Paris,
96 collection De Franceschi - De Ploëg. Endocarps of living species of *Iodes* were sampled from
97 herbarium specimens (Tab.1), obtained from the Muséum national d'Histoire naturelle de
98 Paris (P), the Royal Botanic Garden Kew (K), the Botanic Garden Meise (BR) and the
99 Missouri Botanical Garden (MO). We sampled 14 of the 23 extant species of *Iodes*, spanning
100 the biogeographic breadth of the genus, providing us a relatively comprehensive picture of its
101 morphological diversity. Voucher information is available in appendix.

102 103 **2.2 Method of collection**

104 The fruits were extracted and sieved from the lignitic clay sediments. They were slowly dried
105 after being treated with diluted hydrogen peroxide and washed in water and then they were
106 kept in dry conditions. Once dried, the different sediment fractions were sorted using a
107 binocular microscope (Mantis Elite). The pyritized samples are stored with a dehydration
108 agent (silica gel).

109 110 **2.3 Method of observation**

111 All specimens were studied with a binocular microscope (Wild M3Z) and imaged with a
112 Leica DFC 420 camera. Measurements were taken using the ImageJ Software (Rasband
113 2016). Cell diameters and papillae were measured 10 times for each species, using random
114 selections of the specimens. Multiple samples were coated with gold-palladium for

115 examination by Scanning Electron Microscopy (SEM), using a Jeol JCM6000 instrument,
116 facilitating observation of anatomical features, especially the endocarp wall layers and
117 papillae.

118

119 **2. Systematics**

120 The general fruit features of Icacinaceae are present in the species described here: bilateral
121 endocarps, usually elliptical, with an asymmetrical apex and containing a single-seeded. The
122 fossils show additional features generally associated with the *Iodeae* tribe (which is now
123 understood to be polyphyletic; see Stull et al., 2015): the presence of a keel surrounding the
124 endocarp, the pattern of ridges at the surface (which delimitate areoles), and papillae on the
125 inner endocarp surface. However, these features, combined with a vascular bundle inside the
126 endocarp wall and notably round papillae, suggest affinities with *Iodes*, which can be
127 distinguished from other genera of Icacinaceae based on this unique combination of
128 characters. Additionally, more subtle characters permit the recognition of three species, two
129 of which are newly described here.

130

131 Order- Icacinales Tiegh.

132 Family- Icacinaceae Miers

133 Genus- *Iodes* Blume

134 Species- *Iodes rigida* Del Rio and De Franceschi sp. nov.

135 Fig.1, 1-12

136

137 Diagnosis. Endocarp bilaterally symmetrical, elliptical to ovate, occasionally globular,
138 with a reticulate pattern of rectangular (I-Beam) ridges that delimit about 11 polygonal
139 areoles on each face, with few or no freely ending ridgelets. A keel surrounds the endocarp in

140 the plane of symmetry, with the thicker margin containing a vascular bundle embedded in the
141 endocarp wall. Endocarp possessing an apical hole. Endocarp wall about 0.26–0.50 mm thick
142 (excluding ridges; 0.43–0.58 mm including ridges). Inner endocarp surface densely covered
143 with regularly spaced, sessile papillae, rounded in shape with small punctuations/depressions
144 on the surface. Length of endocarp 3.72–9.29 mm, width 3.01–6.54mm.

145 Etymology. From *rigidus* (L = rigid), in reference to the strong ridges of the endocarp
146 structure.

147

148 Holotype. MNHN.F. 44593.

149 Stratigraphy. Early Eocene.

150

151 Type locality. Le Quesnoy (Oise, France).

152

153 Paratypes. MNHN.F.44547., 44548., 44555., 44557., 44558., 44560., 44561., 44563.,
154 44564., 44565., 44566., 44567., 44568., 44570., 44572., 44573., 44575., 44577., 44578.,
155 44579., 44580., 44581., 44582., 44583., 44584., 44585., 44586., 44587., 44588., 44589.,
156 44590., 44591., 44592., 44594., 44595., 44596., 44597., 44598., 44599., 44600., 44601.,
157 44602., 44603., 44604., 44606., 44607., 44608., 44609., 44610., 44611., 44612., 44613.,
158 44615., 44616., 44617., 44618., 44619., 44620., 44621., 44622., 44623., 44624., 44625.,
159 44626., 44627., 44629., 44630., 44631., 44632., 44633., 44635., 44637., 44640., 44641.,
160 44642., 44645., 44646., 44647., 44649., 44650., 44651., 44653., 44654., 44655., 44656.,
161 44657., 44658., 44659., 44661., 44662., 44663., 44665., 44666., 44667., 44670., 44672.,
162 44673., 44674., 44675., 44678., 44679., 44680., 44681., 44683., 44684., 44685., 44686.,
163 44688., 44689., 44690., 44691., 44692., 44693., 44695., 44697., 44698., 44699., 44703.,
164 44711., 44712., 44713., 44714., 44716., 44717.

165 Description. Endocarp bilaterally symmetrical, unilocular, single-seeded, elliptical to ovate
166 (Fig.1, 1–6), occasionally globular, lenticular in transverse section; length, 3.72–9.29 (avg.
167 6.25 mm; SD= 0.89, n=115), width 3.01–6.54 (avg. 4.79 mm; SD=0.73, n=110). Outer part of
168 endocarp with reticulate pattern of “I-Beam” ridges, a particular shape of rectangular ridges
169 with a channel on the median apical part of the surface corresponding to the trace left by the
170 outer vasculature at the boundary between endocarp and mesocarp (Fig.1, 7), occasionally
171 preserved. Each endocarp face generally includes five longitudinal ridges (Fig.1, 1–6); Ridges
172 without connexions or delimiting up to 20 polygonal areoles on each lateral face, avg. 11,
173 with few or no freely ending ridgelets. A keel surrounds the endocarp in the plane of
174 symmetry (Fig.1, 2) with the thicker margin containing a vascular bundle embedded in the
175 endocarp wall (Fig.1, 10). Endocarp possessing an apical hole (Fig.1, 4). Endocarp wall 0.26–
176 0.50 mm thick (avg. 0.38 mm; SD=0.1, n=4) excluding ridges, 0.43–0.58 mm thick (avg. 0.51
177 mm; SD=0.06, n=9) including ridges; see Fig.1, 8). Wall composed of packed, interlocking
178 digitate and sclerotic cells in a layer with about four units of cell rows; the outermost unit
179 consists of numerous apical cell rows, difficult to distinguish; the second unit corresponds to a
180 single row of isodiametrical cells, 0.039–0.104 mm in diameter; the basal sclerotic unit is
181 composed of numerous rows of periclinal cells, 0.019–0.050 mm in length. Inner endocarp
182 surface is densely covered with regularly spaced, sessile papillae, rounded in shape with small
183 punctuations on the surface (Fig.1, 11–12); the papillae correspond to the cell expansions of
184 the locule epidermal layer; papillae diameter 0.010–0.026 mm (MNHN.F.44601., 44607.,
185 44666., 44667., 44698., 44703.); the number of papillae per 0.25 mm² is between 290 and
186 570 (MNHN.F.44601., 44666., 44667., 44698., 44703.).

187

188 Remarks. This is the most abundant species at the Le Quesnoy site, with 125 endocarps
189 and a few fragments. The single row of isodiametric cells is a fragile zone (Fig.1, 8). Almost

190 all broken specimen show a ridge section with this layer; papillae are very heterogeneous in
191 form ranging from small to elongate to relatively large (Fig.1, 10 & 11). The pattern of ridges
192 is generally consistent across all specimens (Fig.2), but we show the extreme forms of this
193 species in Fig.2. The ridge pattern is composed first of one ridge, on the medial part of each
194 face, which begins at the base (or almost the base) and runs up two thirds of the length of the
195 endocarp (Fig.2). Two series of ridges (noted 2 & 2' and 3 & 3' on Fig.2) running along each
196 side complete the longitudinal ridges, with the secondary ones (2 & 2') well developed and
197 the third ones (3 & 3') more or less developed. The occurrence of all ridges depends on the
198 global shape of the endocarp. Punctuations in the papillae could correspond to an exchange
199 zone between endocarp and seed.

200

201 Systematic affinity. This species differs from others in having a hole at the apex (Fig.1, 4), a
202 pattern of reticulation that delimits some areoles (Fig.1, 1, 3 & 6), the “I-Beam” ridge
203 structure (Fig.1, 8), and the punctuated and heterogeneous sessile, rounded papillae (Fig.1,
204 12). Despite overlap in size, this species differs from *I. acuta* by having rectangular ridges and
205 endocarp walls twice as thick. It differs from *I. parva* in lacking horn-like protrusions and
206 possessing distinctive rectangular ridges. *Iodes rigida* differs from *I. bilinica*, *I. eocenica*, *I.*
207 *acutiformis*, *I. brownii*, *I. corniculata* and all the other species from Rivecourt site (Del Rio et
208 al., 2018) in having no horn-like protrusions but rather an apical hole. In addition, this species
209 differs from *I. bilinica* in size and in having no free-ending ridges; from *I. eocenica* in having
210 a clearly smaller size (3.7–9.3 mm vs 13.5–15 mm, Tab.1); from *I. acutiformis* in lacking an
211 acute apex and having rectangular, rather than sharp, ridges; from *I. brownii* by its different
212 pattern of ridges and distinct endocarp wall shape (?) and from *I. corniculata* in having
213 rectangular ridges. It differs from *I. occidentalis* (Allen et al., 2015) in having no free-ending
214 ridges, fewer areoles, and rectangular ridges. This species seems to be close to *I.*

215 *multireticulata* Reid and Chandler from the London Clay (Reid and Chandler, 1933) sharing
216 the apical hole and a pattern of reticulation without free-ending ridges (Stull et al., 2016).
217 However, specimens from Le Quesnoy are generally smaller in size, with a length of 3.7–9.3
218 mm compared to 8.0–12.5 mm for *I. multireticulata*. In addition, *I. rigida* has a maximum of
219 20 areoles per endocarp face, which is less than *I. multireticulata* (30–50 areoles per face).
220 The most important distinction is the shape of the ridges: the rectangular ridges of *I. rigida* do
221 not correspond to those described and illustrated for *I. multireticulata* (Reid and Chandler,
222 1933). Finally, the papillae diameter of *I. multireticulata* is more greater than that of *I. rigida*
223 (50 vs max 26 μm), but this last difference could be due to taphonomic bias. *I. germanica*
224 seems to be close to these new species but is typically smaller and shows more areoles and
225 less vertical ridges (Knobloch and Mai, 1986). However, the lack of detail provided for the
226 papillae and ridge characters in the original description of *I. germanica* makes difficult a
227 thorough comparison. The length of *Paleohosiea sulticensis* species (here considered as
228 potential *Iodes* species, see general discussion) is considerably greater than *I. rigida* (15–20
229 mm vs 3.7–9.3 mm). Finally, *Paleohosiea marchiaca* seems to be very close in shape and size
230 but has low, rounded ridges, which are distinct from the ridges of *I. rigida*.

231

232 Species - *Iodes acuta* Del Rio and De Franceschi sp. nov.

233 Fig.1, 13-24

234 Diagnosis. Endocarp bilaterally symmetrical, unilocular, single-seeded, elliptical to ovate,
235 with a reticulate pattern of sharp and sinuous ridges, which delimit about 17 polygonal areoles
236 on each face with few or no freely ending ridgelets. A keel surrounds the endocarp in the
237 plane of symmetry with the thicker margin containing a vascular bundle embedded in the
238 endocarp wall. Endocarp possessing an apical outgrowth composed of the main ridge that
239 runs from the base up to the apex and a protuberance from the keel merged. Endocarp wall

240 about 0.08–0.19 mm thick excluding ridges (0.18–0.39 mm including ridges). Inner endocarp
241 surface densely covered with regularly spaced more or less punctuated and sessile rounded
242 papillae. Length of endocarp about 5.8–8.0 mm, width about 3.61–5.42 mm.

243 Etymology. From *acutus* (L=sharpened, made sharp) in reference of the shape of ridges.

244 Holotype. MNHN.F.44571.

245 Stratigraphy. Early Eocene.

246

247 Type locality. Le Quesnoy (Oise, France).

248

249 Paratypes. MNHN.F.44551., 44553., 44554., 44576., 44605., 44614., 44634., 44668.,

250 44682., 44687., 44696., 44700., 44701., 44704., 44705., 44718., 44719.

251

252 Description. Endocarp bilaterally symmetrical, unilocular, single-seeded, elliptical to ovate
253 (Fig.1, 14–18), lenticular in transverse section; length 5.8–8.0 (avg. 6.91 mm; SD= 0.79,

254 n=12), width 3.61–5.42 (avg. 4.76 mm; SD=0.63, n=13). Outer part of endocarp with a

255 reticulate pattern of sharp and sinuous ridges (Fig.1, 19). Each face of the endocarp with 3–6

256 longitudinal ridges, which delimit 10–25 polygonal areoles on each lateral face, avg. 17, with

257 few or no freely ending ridgelets. A keel surrounds the endocarp in the plane of symmetry

258 (Fig.1, 14), with the thicker margin containing a vascular bundle embedded in the endocarp

259 wall (Fig.1, 22). Endocarp possessing an apical outgrowth (Fig.1, 16) composed of the main

260 ridge that runs from the base up to the apex and a protuberance from the keel merged;

261 Endocarp wall 0.08–0.19 mm thick (avg. 0.13 mm; SD=0.04, n=3) excluding ridges; 0.18–

262 0.39 mm thick (avg. 0.29 mm; SD=0.08, n=4) including ridges. Wall composed of packed

263 interlocking digitate and sclerotic cells with four units of unicellular and multicellular cell

264 rows (Fig.1, 20–21); the outermost unit corresponds to an apical sclerotic layer of numerous

265 cell rows, difficult to distinguish; the second unit corresponds to one row of isodiametric-
266 oriented cells, 0.035–0.041 mm in diameter; the basal sclerotic unit is composed of numerous
267 rows of periclinal cells. Inner endocarp surface densely covered with regularly spaced, more
268 or less punctuated, sessile papillae, rounded in shape (Fig.1, 23–24), which correspond to the
269 cell expansions of the locule epiderma layer; papillae diameter 0.010–0.018 mm
270 (MNHN.F.44554., 44668., 44705., 44718.); the number of papillae per 0.25 mm² is between
271 230 and 410 (MNHN.F. 44554., 44668.).

272

273 Remarks. This species is represented by 18 lignitic fossils from Le Quesnoy. Two
274 morphotypes are remarkable, one elongate (Fig.1, 18) and one more elliptical with a thicker
275 and more delicate keel (Fig.1, 13-17). Despite these conspicuous features, the anatomical data
276 allow consideration of these two shapes as an intraspecific variation, showing the great
277 plasticity of this species. The wall is exceptionally thin for an icacinaceous endocarp. We
278 show numerous mycelium filaments between papillae (Fig.1, 23-24). These filaments have
279 the same lignitic nature of endocarp, indicating that the mycelium represents a probable
280 saprophytic consumption before fossilisation.

281

282 Systematic affinity. This new species is distinct from the others due to its unique apical
283 outgrowth, composed of the main ridge that runs from the base up to the apex and a
284 protuberance from the keel merged (Fig.1, 16), a very thin wall (Fig.1, 20-21), and sharp
285 ridges (Fig.1, 19). It differs from *I. rigida* and *I parva* by its sharper ridges. *Iodes acuta* shares
286 this shape of ridges with *I. acutiformis*, *I.bilinica*, *I.sinuosa* and *I. tubulifera*, all species from
287 European Eocene sites; other species have clearly rounded or rectangular ridges (Tab. 1). *I.*
288 *acutiformis* has a thicker endocarp wall (200 µm vs max. 130 µm) and an acute apex, which is
289 not found in *I. acuta*. In addition, the papillae seem to be denser in *I. acutiformis*, but we do

290 not have information about the shape and diameter of the papillae for comparison. *I. acuta*
291 differs from *I. bilinica* (Collinson et al., 2012) in overall size (5.8–8.0 mm vs 9.0–16.0 mm
292 length), the absence of free-ending ridges, and endocarp thickness (for *I. bilinica*, 650 µm,
293 Tab.1). *I. germanica* is smaller than *I. acuta* and is not well described, making it difficult to
294 more thoroughly assess the affinities between these two species.

295 The shape of the ridges in transverse section of the new species (Fig.1, 20) resembles that of *I.*
296 *sinuosa* from the Rivecourt site (Del Rio et al., 2018), suggesting potential affinities, despite
297 the differences in apex morphology, overall size, endocarp wall thickness, and papillae
298 density. Finally, *I. tubulifera* has a greater size and shows tubular papillae not found in *I.*
299 *acuta*.

300

301 *Species - Iodes parva* Del Rio, Thomas and De Franceschi

302 Fig.3, 1-12

303

304 Stratigraphy. Late Paleocene

305 Additional stratigraphy. Early Eocene

306

307 Type locality. Rivecourt (Oise, France).

308 Additional locality. Le Quesnoy (Oise, France)

309

310 Specimens: MNHN.F.44549., 44550., 44552., 44556., 44562., 44569., 44628., 44638.,

311 44639., 44648., 44660., 44706., 44707., 44709., 44710., 44730.

312

313 Description (Le Quesnoy specimens). Endocarp bilaterally symmetrical, unilocular,

314 single-seeded. Endocarp shape elliptical to ovate (Fig.3, 1–6), lenticular in transverse section;

315 length 4.27–7.10, avg. 5.47 mm (SD= 0.95, n=15), width 3.20–5.48, avg. 4.34 mm (SD=0.77,
316 n=14). Outer part of the endocarp with a reticulate pattern of rounded and thin ridges (Fig.3,
317 7), each face of the endocarp with 3–6 longitudinal ridges, which delimit 9–23 polygonal
318 areoles on each lateral face, avg. 17, with few or no freely ending ridgelets. A keel surrounds
319 the endocarp in the plane of symmetry (Fig.3, 2), with the thicker margin containing a
320 vascular bundle embedded in the endocarp wall. Endocarp possessing a symmetrical pair of
321 horn-like protrusions compressed on the keel (Fig.3, 1–6, arrows), positioned eccentrically
322 and subapically on the apical endocarp faces, each with a central pit. Endocarp wall 0.10–
323 0.17, avg. 0.13 mm (SD=0.05, n=2) thick (excluding ridges, 0.21–0.32, avg. 0.26 mm
324 (SD=0.08, n=2) including ridges). Wall composed of packed interlocking digitate and
325 sclerotic cells with four units of unicellular and multicellular layers (Fig.3, 8); the outermost
326 unit corresponds to an apical sclerotic layer of numerous cell rows, difficult to distinguish and
327 often absent by abrasion; the second unit corresponds to one row of isodiametric cells; the
328 basal sclerotic unit is composed of numerous cell rows. Inner endocarp surface densely
329 covered with regularly spaced, sessile, rounded papillae (Fig.3, 10–12), which correspond to
330 the cell expansions of the locule epidermal layer; papillae diameter 0.014–0.020 mm
331 (MNHN.F.44706., 44709.); the number of papillae per 0.25 mm² is between 300 and 500
332 (MNHN.F.44706., 44709.). Testa with rectangular to polygonal cells, 0.020–0.027 X 0.008–
333 0.014 mm.

334

335 Remarks. This species is represented by 16 fossils from Le Quesnoy. They are very
336 different from the others specimens from Le Quesnoy in having horn-like protrusions (Fig.3,
337 4). The wall and ridges are not well preserved on the endocarps (Fig.3, 7-8), whereas the
338 papillae are well preserved and clearly lack punctuations on the surface (Fig.3, 11-12). These

339 fossils are the most decayed among *Iodes* remains examined here; however, the seeds are well
340 preserved and include testa remains.

341

342 Sytematic affinity. Specimens with horn-like protrusions are included within our concept
343 of *I. parva* (Fig.3, 1-12). Minor quantitative differences are noted: the wall and ridges are
344 smaller, papillae are wider and the density is lower on Le Quesnoy specimens compared to
345 the Rivecourt ones. However, the wall of the Le Quesnoy specimens is poorly preserved
346 compared to those of Rivecourt (Fig.3, 8). The different size could be a consequence of
347 crushing of the cells during the taphonomic process for the Le Quesnoy specimens. In
348 contrast, papillae cells of *I. parva* from Rivecourt are retracted and non-touching, whereas the
349 same layer of specimens from Le Quesnoy is uniform and cells are contiguous. This cell
350 retraction could explain the smaller size of papillae in the Rivecourt endocarps (Del Rio et al.,
351 2018). Differences in papillae density remain problematic, although the lower values in *I.*
352 *parva* from Rivecourt correspond to the higher values in the Le Quesnoy specimens. Overall,
353 the specimens from these two sites show high levels of affinity, supporting their recognition
354 as a single species.

355

356 Icacinaceae *Incertae Sedis* sp.

357 Fig.3, 13–18

358

359 Description. Seeds elliptical in shape (Fig.3, 13–15), lenticular in transverse section, slightly
360 asymmetrical to completely asymmetrical at the apex; length 6.31–8.56, avg. 7.52 mm (SD=
361 0.7, n=10), width 4.67–6.00, avg. 5.49 mm (SD=0.37, n=10). Outer surface smooth (Fig.3,
362 16–17); anatomical structure unknown (Fig.3, 18).

363

364 Specimens. MNHN.F.44720., 44721., 44722., 44723., 44724., 44725., 44726., 44729.,
365 44731., 44732., 44733.

366

367 Remarks. Ten mineralized seeds represent this type. Due to mineral preservation (Fig.3,
368 18), it is difficult to distinguish the hilum and the micropyle, but the asymmetrical shape of
369 the apex is a clue for the position of both structures (Fig.3, 13-15). A trace surrounds the seed
370 (Fig.3, 17), probably due to the shape of the bilateral endocarp that embeds it. The trace left
371 by the raphe is absent for all the specimens, probably a result of the taphonomic processes.
372 The wall is mineralized and thin (Fig.3, 16).

373

374 Systematic affinity Mineralized seeds found in Le Quesnoy are very similar in shape with
375 seeds of Icacinaceae documented from the Dormaal Formation (Fairon-Demaret and Smith,
376 2002). However, the specimens from Le Quesnoy are bigger than the Dormaal's specimens.
377 We suspect a close affinity between these taxa, but without anatomical information, it is
378 impossible to determine. The size of these seeds may indicate a species of Icacinaceae with
379 much bigger endocarps than the other species from the Le Quesnoy site, but we could not find
380 remains of the corresponding endocarp.

381

382 **4. Discussion**

383 **4.1 Review of the *Iodes* fossil record**

384 In the light of these new discoveries, we present a review of *Iodes* fossil record (following on
385 Stull et al., 2016). The recognition of *Iodes* is based on three diagnostic characters: the ridges
386 at the surface, papillae on the locule surface, and the presence of a vascular bundle inside the
387 endocarp wall. Indeed, *Iodes* is the only genus in the family to have all three of these

388 characters (Stull et al., 2011, Stull et al. 2016). In North America, three species share these
389 characters: *Iodes brownii* from Eocene localities in Wyoming, Utah, Oregon, and Colorado
390 (Allen et al., 2015, Stull et al., 2016); *I. occidentalis* from the Eocene Bridger Formation of
391 Wyoming (Allen et al., 2015) and *I. multireticulata* from the Eocene Clarno Formation of
392 Oregon. *Iodes chandlerae*, from the Clarno Formation, although its locule casts show a
393 papillate, reticulately faceted surface, the endocarp wall is not preserved so it remains
394 unknown whether the funicle passed through the wall as in *Iodes*, or outside of it as in other
395 Iodeae.s. (Stull et al., 2016); therefore, we regard this as a dubious generic identification. In
396 addition, *Croomiocarpum mississippiensis* from the early-middle Eocene Tallahatta Formation
397 of Mississippi is very similar to *Iodes* in having a vascular bundle inside the endocarp wall
398 and a reticulate pattern of endocarp ridges (Stull et al., 2011). It mainly differs by its thick
399 wall (about 2 mm including ridges) and the absence of papillae, although the lack of papillae
400 might be due to taphonomic degradation, as noted by Stull et al. (2011).

401 The size of the endocarp wall (with ridges) is very uncommon in fossil species of *Iodes* but
402 not aberrant: the wall thickness (including ridges) of *Iodes bilinica* reaches 1 mm (Stull et al.,
403 2016) and 1.5 mm for *I. rivecourtensis* (Del Rio et al., 2018). In addition, we also found in
404 modern *Iodes* species endocarp walls reaching 1 mm thick (*I. cirrhosa*, *I. balansae*, and *I.*
405 *yatesii*, Tab.1). Thus, we consider it as a probable species of *Iodes* despite the lack of papillae
406 (but also of cell preservation).

407 The fossil genus *Iodicarpa* from the Clarno Formation (Manchester, 1994) is cited as
408 close to, or potentially included with, *Iodes* (Allen et al., 2015, Stull et al., 2016), given that
409 members of this fossil genus possess papillae and a vascular bundle embedded in the
410 endocarp wall. Both diagnostic characters are only found together in *Iodes*. However, the size
411 of the specimens (26–56 mm in length, 20–35 mm in width) and the ornamentation (veinlike
412 reticulum of groves) is unusual for the modern and fossil species of *Iodes*. Indeed, only two

413 modern species (*I. balansae* and *I. yatesii*, Tab. 1) are as long as the species included in
414 *Iodicarpa*. However, these two modern species are less than 17 mm in width. Among the
415 current species, only *I. seguinii* has a smooth ornamentation but also a vascular bundle in a
416 gutter and no papillae (Tab. 1). Thus, we do not have final argument to include or exclude
417 these species in *Iodes*. Consistent with previous studies, we consider this genus as closely
418 related to *Iodes* or included inside the clade but with extinct morphology (regarding its
419 distinct ornamentation type, compared to described fossil and modern species of *Iodes*). An
420 *Iodes* sp. was illustrated from the Chuckanut Formation of Washington (Pigg and Wher,
421 2002). However, the specimen seems to be an endocarp impression with no anatomical
422 information available. Although it conforms morphologically to tribe Iodeae, we consider this
423 occurrence as a dubious record of *Iodes*.

424 In Europe, *Iodes* is represented by 12 fossil species: *I. germanica* from Cretaceous of
425 Eilseben and Palaeocene of Gona (Germany; Knobloch and Mai, 1986, Mai, 1987), *I.*
426 *multireticulata*, *I. eocenica*, *I. corniculata*, *I. hordwellensis*, and *I. acutiformis* from various
427 sites of the well-known Eocene London Clay Formation (Reid and Chandler, 1933, Stull et
428 al., 2016) *I. bilinica* from the Eocene Messel Biota, the Eocene of Bohemia, and from the
429 London Clay Formation (Chandler, 1925; Kvaček and Bůžek, 1995; Collinson, 2012). And
430 finally *Iodes tubulifera*, *I. sinuosa*, *I. rivecourtensis*, *I. reidii* and *I. parva* from the Paleocene
431 of Rivecourt site (Del Rio et al., 2018; Tab.1). Here, we add two new species, *I. rigida* and *I.*
432 *acuta*, which appear closely related to species from the Paleogene of Europe, and particularly
433 from the Paris Basin. These species add to our understanding of the historical diversity of
434 *Iodes* in Europe, and help establish connections among European Paleogene floras.

435 *Palaeohosiea* (Kvaček and Bůžek, 1995) possesses the three major diagnostic
436 characters of *Iodes* with no significant other distinguishing features (Allen et al., 2015). Thus,
437 we consider all species of this genus as members of *Iodes* and include them in our

438 comparisons: *P. marchiaca* and *P. suleticensis* from the Paleocene and Oligocene of Bohemia
439 (Kvaček and Bůžek, 1995). In addition, *Hosiea pterojugata* from the Palaeocene of Gona,
440 Germany (Mai, 1987), also has all key diagnostic characters of *Iodes* genus, although the
441 specimen descriptions are relatively minimal.

442 Chandler (1961) attributed another fossil from Southern England to *Iodes*, as *Iodes* sp.,
443 but we consider this placement equivocal. The specimen has papillae and a reticulate pattern
444 of ridges. It is very small, about 4.5 mm in length, which is unknown for modern members of
445 *Iodes* (see. Tab.1), but we have described other fossil examples of small *Iodes* (Del Rio et al.,
446 2018). However, the specimen is a locule cast, indicating that the endocarp is at least slightly
447 larger than 4.5 mm. The position of the vascular bundle is unknown as only a locule cast
448 remains. Because the genus *Hosiea* also possesses reticulate ridges and papillate locule
449 linings, we hesitate to attribute this fossil to *Iodes* given the unknown position of the vascular
450 bundle. *Iodes* sp. from the Dormaal formation possesses a reticulation pattern “obliterated by
451 encrustation of sand” and papillae inside the locule (Fairon-Demaret and Smith, 2002).
452 However, the specimen is very decayed; therefore, it is difficult to decide if this specimen
453 belongs to *Iodes* genus or other similar genera, such as *Hosiea*.

454 An *Iodes* from the Miocene of Yunnan (China) has been mentioned (Stull Obs. Pers.) but not
455 formally published. A second *Iodes* species from the Miocene of Turkey seems to have been
456 studied but not published (Duperon, com. Pers.). Therefore, there are no published records of
457 *Iodes* from areas other than North America and Europe.

458 In conclusion, the *Iodes* genus has an extensive fossil record, ranging from the Late
459 Cretaceous to the Miocene, with notable abundance and diversity in the Northern Hemisphere
460 during the Paleogene. The diversity of fossil remains from the European Eocene in particular
461 is comparable to modern diversity, distributed across tropical Africa, Madagascar, and Asia.

462

463 **4.2 Significance of the ridges**

464 The ridges at the surface seem to be formed by the development of anticlinally oriented cells.
465 However, this same anatomical development can yield distinct morphological shapes. For the
466 *Iodes* species, we identified three major shapes: angular (more or less rectangular), sharp, and
467 rounded. In addition, we show an important disparity in terms of ridge thickness, from 180 μm
468 for *Iodes acuta* to more than 2 mm for *Croomiocarpon mississippiensis*. Finally, the ridges are
469 more or less connected at the surface and form a reticulum or a diffuse pattern. These three
470 characters help to differentiate species in extant as well as extinct species (Tab. 1).

471 In extant species, these characters seem to be significant in species delimitation (Tab.1).
472 In addition, we noticed some geographic patterns of ridge morphology and organisation. Asian
473 species tend to have rectangular and strong ridges mostly forming diffuse patterns (see Fig.4,
474 1-4). The ridges mostly have a median channel, which corresponds to the imprint of the external
475 vasculature (Fig.4, arrows). The African species tend to bear rounded to sharp ridges, weaker
476 in structure, and mostly forming a close reticular pattern with free ending ridges in the areoles.
477 Only two species show a median channel on the ridges (Fig.4, 5-6).

478 In fossil *Iodes* species from Europe and North America, we found all types of ridge
479 shapes and great variation in their thickness. These differences were traditionally considered
480 significant for species delimitation. Our review of extant species confirm this position (Tab. 1).
481 The reticulation patterns observed in fossil specimens seems to be more limited. We found
482 reticulation patterns mostly formed by polygonal areoles and without free ending ridges.
483 Without taking into account the shape of the ridges, the fossil record seems to show a general
484 reticulation pattern of ridges that is only found in few extant species (e.g. *Iodes africana* &
485 *Iodes klaineana*).

486 In our site, the ridges of *I. rigida* are more similar to some modern Asian rather than
487 African species in having a median channel and a rectangular shape (e.g. *Iodes ovalis*, *I.*

488 *scandens*, *I. yatesii* and *I. balansae*, Fig.4, 1-4). Two modern species from Africa, *I.*
489 *kamerounensis* and *I. seretii*, have clear channels on the ridges but not the characteristic
490 rectangular shape (Fig.4, 5-6). Ridges like those of *Iodes acuta* were found in the European
491 fossil record (e.g. *Iodes acutiformis*, *I. bilinica*, *I. sinuosa* & *I. tubulifera*) but in the living
492 species only in *I. perrieri* from Madagascar (with a very different reticulation, Tab.1). Finally,
493 *I. parva* has rounded ridges and a reticular pattern of ridges, which is more similar to African
494 species. However, this species was considered beforehand as close to Asian species because it
495 possesses a pair of horn-like protrusions (Del Rio et al., 2018). Collectively, the species from
496 Le Quesnoy show characters found today in both Africa and Asia, which may indicate that
497 these areas represent refugia for lineages that originally diversified in the Northern Hemisphere
498 (Wolfe, 1975).

499

500 **5. Conclusion**

501 All species studied here possesses remarkably well preserved anatomical and
502 morphological characters, including a reticulate pattern of ridges, a vascular bundle embedded
503 in the endocarp wall, and a papillate locule surface, which allow us to consider them as part of
504 *Iodes*. Of these species, two species are new: *I. rigida* sp. nov. (showing I-beam ridges, no
505 horn-like protrusions sub-apically, and punctuated and heterogeneous papillae) and *I. acuta*
506 (showing a unique and complex apex, a very thin wall, and sharp ridges). *I. parva* is
507 recognised in this site, despite some minor differences with the specimens from Rivecourt
508 (Del Rio et al., 2018).

509 The two news species of Icacinaceae described here increase the diversity of the
510 family known from the Eocene of Europe. Our review of the *Iodes* fossil record, presented
511 above, outlines the great diversity of forms through time for this genus, in Europe and North

512 America, and highlight previously described fossil species that also likely belong to this
513 genus.

514 The species from Le Quesnoy, like most of the fossils known from Europe, appear to
515 have affinities with Eocene fossils from North America. However, they also show close
516 connections to other sites from the Paleocene of France and the Eocene of Europe more
517 broadly. Our analysis of the patterns of ridge anatomy and organisation suggests that *Iodes*
518 species from the Le Quesnoy site share affinities with extant species from both Africa and
519 Asia.

520 This study demonstrates the significance of the Le Quesnoy fossil assemblage for
521 systematic, paleoecology, and paleobiogeographic research. In particular, the exceptional
522 anatomical preservation allows detailed comparisons of the Le Quesnoy material with fossils
523 from other European floras as well as with extant species. Others studies on this remarkable
524 site, centred on other groups, are necessary to more fully understand the affinities of Le
525 Quesnoy with other modern and paleofloras

526

527 **Acknowledgements**

528 The fossils were collected during fieldwork by the “amber team” of MNHN, with the help of
529 Lafarge-Granulat Cie, and we thank the Langlois-Meurinne family for giving the
530 authorization to work on their property. This work was supported by a grant from Agence
531 Nationale de la Recherche under the LabEx ANR-10-LABX-0003-BCDiv, in the program
532 “Investissements d’avenir” n_ ANR-11-IDEX-0004-02 and by the CR2P (UMR 7207).

533

534 **References**

535 Allen, S. E., Stull, G. W., Manchester, S. R., 2001. Icacinaceae from the Eocene of western
536 North America. *Am. J. of bot.*, 102(5), 725–744.

- 537 APG, 2016. An update of the Angiosperm Phylogeny Group classification for the orders and
538 families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 141(4), 399–436.
- 539 Byng, J.W., Bernardini, B., Joseph, J.A., Chase, M.W., Utteridge, T., 2014. Phylogenetic
540 relationships of Icacinaceae focusing on the vining genera. *Bot. J. Linn. Soc.* 176(3),
541 277–294.
- 542 Cavagnetto, C.G., 2000. La palynoflore d'un gisement d'ambre de l'Eocène basal du Bassin
543 Parisien (Le Quesnoy, France). *Palaeontographica Abteilung B* 255(4-6), 147–171.
- 544 Chandler, M.E.J., 1962. The Lower tertiary floras of Southern England. II. Flora of the Pipe-
545 Clay Series of Dorset (Lower Bagshot). British Museum of Natural History, London.
546 176 pp.
- 547 Chandler, M.E.J., 1961a. Plant remains of the Hengistbury and Barton Beds. British Museum
548 of Natural History, London. 238 pp.
- 549 Chandler, M.E.J., 1961b. The Lower tertiary floras of Southern England. I. British Museum of
550 Natural History, London. 354 pp.
- 551 Chandler, M.E.J., 1954. Some Upper Cretaceous and Eocene fruits from Egypt (with
552 appendices by M.Y. Hassan and M. I. Youssef. *Br. Mus. Nat. Hist. Bull. Geol.* 2, 149–
553 187.
- 554 Chandler, M.E.J., 1925. The Upper Eocene flora of Hordle, Hants, *Palaeontographical Society*
555 monographs, London. 52 pp.
- 556 Chester, K. I. M., 1955. Some plant remains from the Upper Cretaceous and Tertiary of West
557 Africa. *Ann Mag Nat Hist* 8(91), 498–504.
- 558 Cleal, C.J., Thomas, B.A., Batten, D.J., Collinson, M.E., 2001. Mesozoic and Tertiary
559 paleobotany of Great Britain., *Geological Conservation Review Series*, Joint Nature
560 Conservation Committee. ed. Peterborough, UK. 335 pp.
- 561 Collinson, M.E., 1983. Fossil Plants of the London Clay. The *Palaeontological association*,

- 562 London. 121 pp.
- 563 Collinson, M.E., Manchester, S.R., Wilde, V., 2012. Fossil fruit and seeds of the Middle
564 Eocene Messel biota, Germany, *Abh. Senckenb. Ges. Naturforsch. Stuttgart*. 251 pp.
- 565 Crane, P.R., Manchester, S.R., Dilcher, D.L., 1990. A preliminary survey of fossil leaves and
566 well-preserved reproductive structures from the Sentinel Butte Formation (Paleocene)
567 near Almont, North Dakota. *Geology* 20, 1–63.
- 568 De Franceschi, D., De Ploëg, G., 2003. Origine de l'ambre des faciès sparnaciens (Éocène
569 inférieur) du Bassin de Paris: le bois de l'arbre producteur. *Geodiversitas* 25(4), 633–
570 647.
- 571 De Franceschi, D., Dejax, J., De Ploëg, G., 2000. Extraction du pollen inclus dans l'ambre
572 [Sparnacien du Quesnoy (Oise), bassin de Paris]: vers une nouvelle spécialité de la
573 paléo-palynologie. *Comptes Rendus Académie Sci.-Ser. IIA-Earth Planet. Sci.* 330(3),
574 227–233.
- 575 De La Bâthie, P., 1952. Icacinaceae, In: *Flore de Madagascar et Des Comores*. Firmin-Didot et
576 Cie, Paris, France, pp. 1–45.
- 577 Del Rio, C., Haevermans, T., De Franceschi, D., 2017. First record of an Icacinaceae Miers
578 fossil flower from Le Quesnoy (Ypresian, France) amber. *Sci. Rep.* 7, 11099.
- 579 Del Rio, C., Thomas, R., De Franceschi, D., 2018. Fruits of Icacinaceae Miers from the
580 Paleocene of the Paris Basin (Oise, France). *Earth Environ Sci Trans R Soc Edinb.*
581 Accepted. (DOI: 10.1017/S1755691018000221).
- 582 Fairon-Demaret, M., Smith, T., 2002. Fruits and seeds from the Tienen Formation at Dormaal,
583 Palaeocene–Eocene transition in eastern Belgium. *Rev. Palaeobot. Palynol.* 122(1-2),
584 47–62.
- 585 Jacques, F.M.B., De Franceschi, D., 2005. Endocarps of Menispermaceae from Le Quesnoy
586 outcrop (Sparnacian facies, Lower Eocene, Paris Basin). *Rev. Palaeobot. Palynol.*

587 135(1-2), 61–70.

588 Kårehed, J., 2001. Multiple origin of the tropical forest tree family Icacinaceae. *Am. J. Bot.*
589 88(12), 2259–2274.

590 Knobloch, E., Mai, D.H., 1986. Monographie der Furche und Samen in der Kreide von
591 Mitteleuropa. Vydal Ustredni ustav geologicky, Praha. 219 pp.

592 Kvaček, Z., Bůžek, Č., 1995. Endocarps and foliage of the flowering plant family Icacinaceae
593 from the Tertiary of Europe. *Tert. Res.* 15(3), 121–138.

594 Lens, F., Kårehed, J., Baas, P., Jansen, S., Rabaey, D., Huysmans, S., Hamann, T., Smets, E.,
595 2008. The wood anatomy of the polyphyletic Icacinaceae sl., and their relationships
596 within asterids. *Taxon* 57(2), 525–552.

597 Mai, D.H., 1987. Neue Früchte und Samen aus paläozänen Ablagerungen Mitteleuropas.
598 *Feddes Repert.* 98, 197–229.

599 Manchester, S.R., 1999. Biogeographical relationships of North American Tertiary Floras.
600 *Ann. Mo. Bot. Gard.* 86(2), 472–522.

601 Manchester, S.R., 1994. Fruits and seeds of the Middle Eocene nut beds flora, Clarno
602 Formation, Oregon, *Palaeontographica Americana*. Paleontological Research
603 Institution, New York. 205 pp.

604 Manchester, S.R., Tiffney, B.H., 1993. Fossil fruits of *Pyrenacantha* and related *Phytocreneae*
605 (*Icacinaceae*) in the Paleogene of North America, Europe, and Africa. In *American*
606 *Journal of Botany Abstracts* 80, 91.

607 Nel, A., de Plöeg, G., Dejax, J., Dutheil, D., De Franceschi, D., Gheerbrant, E., Godinot, M.,
608 Hervet, S., Menier, J.-J., Augé, M., Bignot, G., Cavagnetto, C., Duffaud, S., Gaudant, J.,
609 Hua, S., Jpsang, A., de Lapparent de Broin, F., Pozzi, J.-P., Paicheler, J.-C., Beuchet,
610 F., Rage, J.-C., 1999. Un gisement sparnacien exceptionnel à plantes, arthropodes et
611 vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France). *Comptes Rendus Académie*

- 612 Sci. - Ser. IIA - Earth Planet. Sci. 329, 65–72.
- 613 Pigg, K.B., Manchester, S.R., DeVore, M.L., 2008. Fruits of Icacinaceae (Tribe Iodeae) from
614 the Late Paleocene of western North America. *Am. J. Bot.* 95(7), 824–832.
- 615 Pigg, K.B., Wher, W.C., 2002. Tertiary flowers, fruits, and seeds of Washington State and
616 adjacent area-Part III. *Wash. Geol.* 30(3/4), 1–24.
- 617 Rankin, B.D., Stockey, R.A., Beard, G., 2008. Fruits of Icacinaceae from the Eocene Appian
618 Way Locality of Vancouver Island, British Columbia. *Int. J. Plant Sci.* 169(2), 305–314.
- 619 Rasband, W. S., 2017. “ImageJ Website.” <https://imagej.nih.gov/ij/>.
- 620 Reid, E.M., Chandler, M.E.J., 1933. *The London Clay Flora*. The British Museum (Natural
621 History), London. 561 pp.
- 622 Sleumer, H., 1971. Icacinaceae, In: *Flora Malesiana*. CGGJ van Steenis, Noordhoff, Leyden,
623 7(1), 1–87.
- 624 Smith, T., Quesnel, F., De Plöeg, G., De Franceschi, D., Métais, G., De Bast, E., Solé, F., Folie,
625 A., Boura, A., Claude, J., Dupuis, C., Gagnaison, C., Iakovleva, A., Martin, J., Maubert,
626 F., Prieur, J., Roche, E., Storme, J.-Y., Thomas, R., Tong, H., Yans, J., Buffetaut, E.,
627 2014. First Clarkforkian equivalent land mammal age in the Latest Paleocene Basal
628 Sparnacian Facies of Europe: fauna, flora, paleoenvironment and (bio)stratigraphy.
629 *PLoS ONE* 9(1), 1–20.
- 630 Soudry, D., Gregor, H.-J., 1997. *Jodes israelii* sp. nov.: a huge phosphate-mineralized
631 icacinacean fructification from the Late Cretaceous of the Negev, southern Israel.
632 *Cretac. Res.* 18(2), 161–178.
- 633 Stull, G.W., Adams, N.F., Manchester, S.R., Sykes, D., Collinson, M.E., 2016. Revision of
634 Icacinaceae from the Early Eocene London Clay flora based on X-ray micro-CT.
635 *Botany* 94(9), 713–745.
- 636 Stull, G.W., Duno de Stefano, R., Soltis, D.E., Soltis, P.S., 2015. Resolving basal lamiid

- 637 phylogeny and the circumscription of Icacinaceae with a plastome-scale data set. *Am. J.*
638 *Bot.* 102(11), 1794–1813. *Botany* 94, 713–745.
- 639 Stull, G.W., Herrera, F., Manchester, S.R., Jaramillo, C., Tiffney, B.H., 2012. Fruits of an “Old
640 World” tribe (Phytocreneae; Icacinaceae) from the Paleogene of North and South
641 America. *Syst. Bot.* 37(3), 784–794.
- 642 Stull, G.W., Moore, B.R., Manchester, S.R., 2011. Fruits of Icacinaceae from the Eocene of
643 Southeastern North America and their biogeographic implications. *Int. J. Plant Sci.*
644 172(7), 935–947.
- 645 Tanai, T., 1990. Euphorbiaceae and Icacinaceae from the Paleogene of Hokkaido, Japan. *Bull*
646 *Natn Sci Mus Tokyo SerC* 16(3), 91–118.
- 647 Villiers, J.-F., 1973. Icacinaceae, In: *Flore Du Cameroun*. A. Aubréville et J-F. Leroy, Paris,
648 France, pp. 3–100.
- 649 Wolfe, J.A., 1975. Some aspects of plant geography of the Northern Hemisphere during the
650 Late Cretaceous and Tertiary. *Ann. Mo. Bot. Gard.* 62(2), 264–279.
- 651

652 CAPTION

653 **Figure 1.**

654 1-12. *Iodes rigida* Del Rio and De Franceschi sp. nov.

655 1. Lateral view of endocarp showing the reticulate pattern of ridges, Holotype specimen
656 (MNHN.F.44593.).

657 2. Same in dorsal view showing the keel surrounding the fruit.

658 3. Same in lateral view showing the second face of endocarp.

659 4. Same in apical view showing the hole.

660 5. Same in basal view showing the trace left by the peduncle.

661 6. Lateral view of another specimen (MNHN.F.44564.) showing a comparable reticulum
662 of ridges.

663 7. SEM view of ridges showing trace left by vascular bundles (MNHN.F.44655.).

664 8. SEM transverse view of wall and ridge (MNHN.F.44697.).

665 9. SEM transverse view showing the basal sclerotic layer and locule epidermal layer with
666 papillae in contact with seed cells. (MNHN.F.44607.).

667 10. SEM view of the vascular bundle (arrow) inside the endocarp wall (MNHN.F.44601.).

668 11. SEM view of the papillae on the locule lining.

669 12. Same with magnification showing punctuation under papillae.

670

671 13-24. *Iodes acuta* Del Rio and De Franceschi sp. nov.

672 13. Lateral view of endocarp showing the reticulum of ridges, Holotype specimen
673 (MNHN.F.44571.).

674 14. Same in dorsal view showing the keel surrounding the fruit.

675 15. Same in lateral view showing the second face of the endocarp.

676 16. Same in apical view showing the hole.

- 677 17. Same in basal view showing the trace left by the peduncle.
- 678 18. SEM lateral view of another specimen (MNHN.F.44696.) showing reticulum of sharp
679 ridges.
- 680 19. SEM view of reticulum of sharp ridges (MNHN.F.44705.).
- 681 20. Same in transverse view of wall and ridges.
- 682 21. Same with magnification focused on cell layers.
- 683 22. View of the vascular bundle (arrow) inside the endocarp wall (MNHN.F.44701.).
- 684 23. Same with magnification showing mycological filaments.
- 685 24. Same with magnification focused on non-punctuated papillae.
- 686 Scale bar: 5 mm = 1-6, 13-18; 1 mm = 22; 500 μm = 7, 19; 200 μm = 8, 10, 20; 50 μm = 9,
687 11, 21, 23; 20 μm = 24; 5 μm = 12.

688

689 **Figure 2.** Reticulation pattern of *Iodes rigida*. (1) MNHN.F.44593, (2) MNHN.F.44557. and
690 (3) MNHN.F.44621. Scale bar: 5 mm.

691

692 **Figure 3.**

693 1-12. *I. parva* Del Rio, Thomas and De Franceschi

- 694 1. Lateral view of endocarp showing the reticulum of ridges and sub-apical horn-like
695 protrusions, (MNHN.F.44562.).
- 696 2. Same in dorsal view showing the keel surrounding the fruit.
- 697 3. Same in lateral view showing the second face of endocarp.
- 698 4. Same in apical view showing the ridges and sub-apical horn-like protrusions.
- 699 5. Same in basal view showing the trace left by the peduncle.
- 700 6. Lateral view of another specimen (MNHN.F.44556.).

701 7. SEM view of reticulum of ridges showing tearing of primary layer (MNHN.F.44628.).

702 8. Same in transverse view of wall and ridge.

703 9. Same with a view of the locule epidermal layering showing remnant testa in contact

704 with the endocarp.

705 10. SEM view of locule epiderma layer showing numerous sessile, rounded papillae

706 (MNHN.F.44709.)

707 11. Same with magnification.

708 12. Same with magnification showing unpunctuated cells under papillae.

709

710 13-18. Icacinaceae *insertae sedis*

711 13. Lateral view of seed showing smooth surface and asymmetrical apex

712 (MNHN.F.44725.).

713 14. Other example in the same configuration (MNHN.F.44724.).

714 15. Other example in the same configuration (MNHN.F.44723.).

715 16. SEM view of broken apex of seeds (MNHN.F.44731.).

716 17. Same in apical view showing trace surrounding the seed.

717 18. Same in lateral view showing the mineralized surface.

718

719 Scale bar: 5 mm = 1-6, 13-15; 1 mm = 16; 500 μm = 7, 17; 200 μm = 8, 10; 100 μm = 9; 50

720 μm = 11; 20 μm = 12, 18.

721

722 **Figure 4.** Shape of ridges of modern *Iodes* species. Rectangular with (1) *Iodes balansae*, (2)

723 *Iodes yatesii*, (3) *Iodes scandens* and (4) *Iodes ovalis*; and mostly rounded with (5) *Iodes*

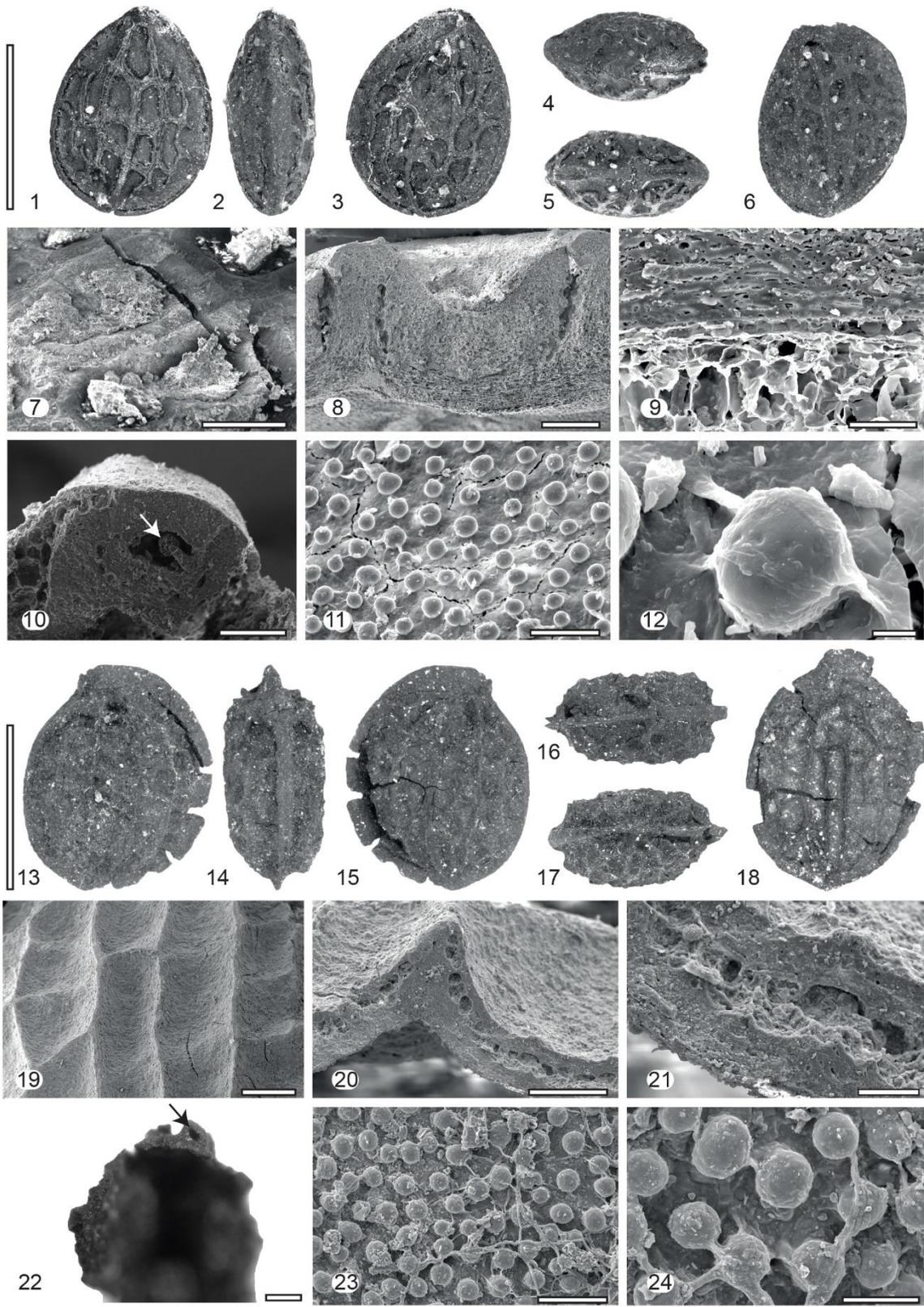
724 *seretii* and (6) *Iodes kamerounensis*. Arrow = trace left by vascular bundle (sometimes still

725 visible) Scale bars: 500 μm .

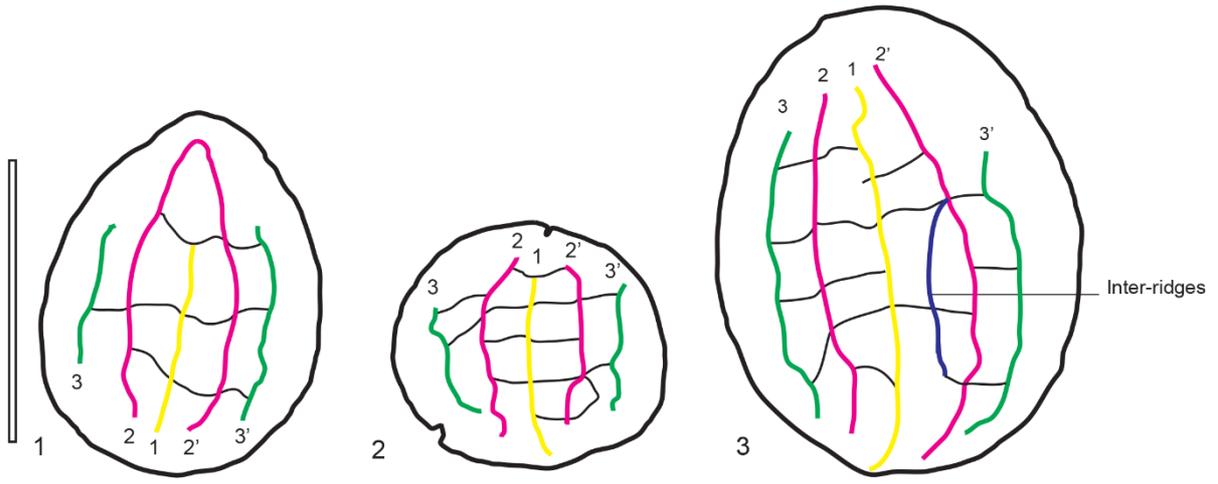
726

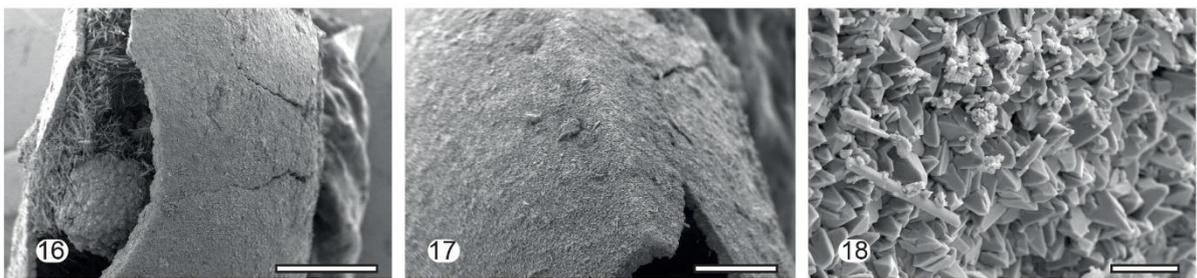
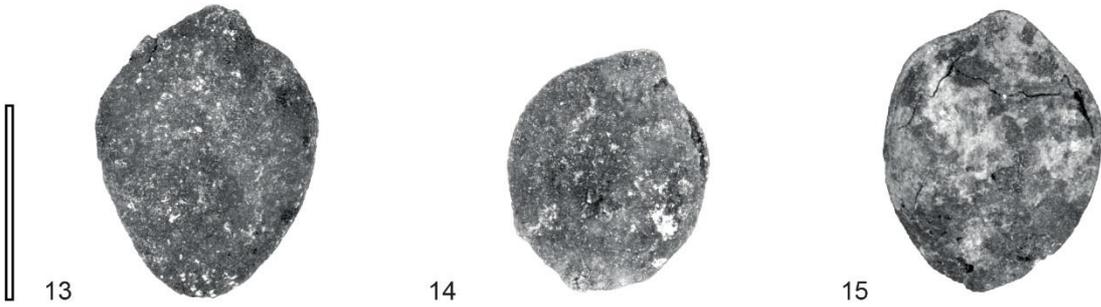
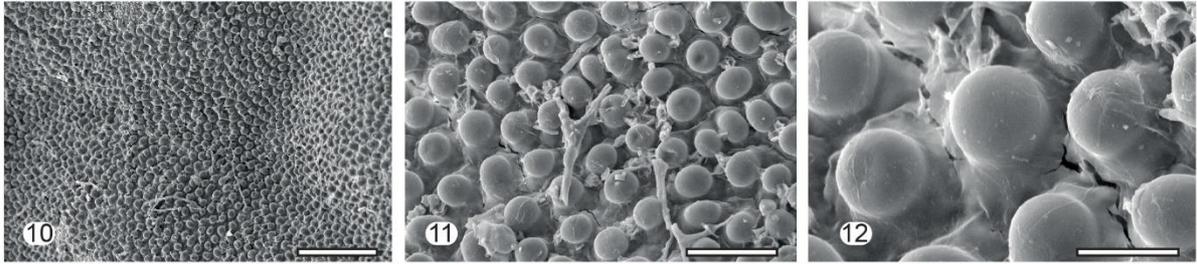
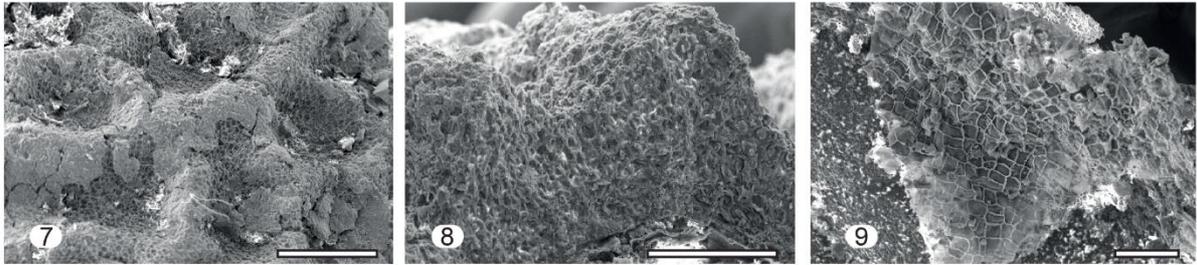
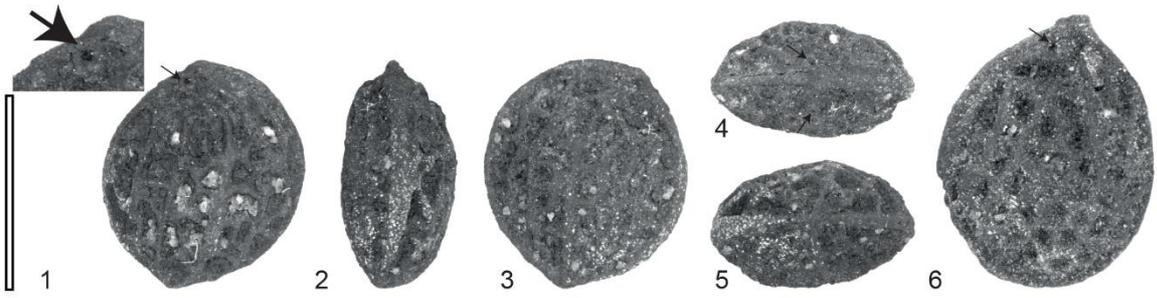
727 **Appendix**

- 728 *Iodes africana* **Welw. ex Oliv.** R.P. Tisserant s.n., Oubangui, 1948, MNHN-P-P03951984;
729 R.P. Klaine 3505, Gabon, 1904, MNHN-P-P03951995. *Iodes balansae* **Gagnep.** KUN
730 0647593 (KUN). *Iodes cirrhosa* **Turcz.** B. Hayata 672, “Indo-chine”, 1921, MNHN-P-
731 P06672331. *Iodes kamerunensis* **Engl.** G.A. Zenker 2032, Cameroon, 1899, MNHN-P-
732 P03951972. *Iodes klaineana* **Pierre** R.P. Klaine 3064, Gabon, 1902, MNHN-P-P04472306.
733 *Iodes liberica* **Stapf** J.G. Adam 3833, Guinea, 1949, MNHN-P-P04472332. *Iodes*
734 *madagascariensis* **Baill.** Chapelier s.n., Madagascar, s.d., MNHN-P-P04472113; McPherson
735 18809 (MO). *Iodes ovalis* **Blume** Hiep HLF 203 (MO). *Iodes perrieri* **Sleumer** Perrier De La
736 Bâthie 17843, Madagascar, 1926, MNHN-P-P04472108. *Iodes philippinensis* **Merr.** A.D.E.
737 Elmer 16418, Phillipines, 1916, MNHN-P-P04504850. *Iodes scandens* (**Becc.**) **Utteridge**
738 **and Byng** No voucher (MO). *Iodes seguinii* (**H.Lév.**) **Rehder** Abbé Cavalerie 3932, Chine,
739 1913, MNHN-P-P05279333. *Iodes seretii* (**De Wild.**) **Boutique** D. Thomas and M. Etuge 63,
740 Cameroon, s.d., BR0000015596772 (BR). *Iodes yatesii* **Merr.** Burley 1577 (K).



742





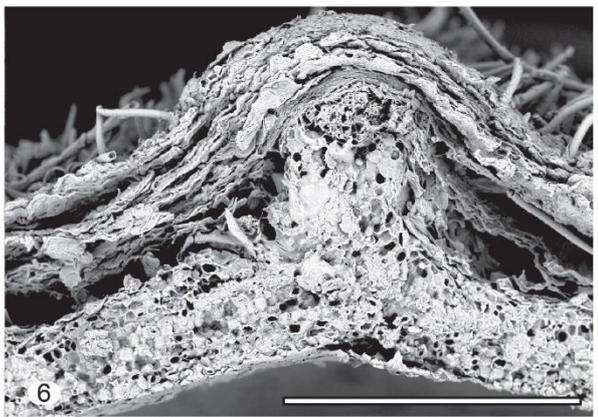
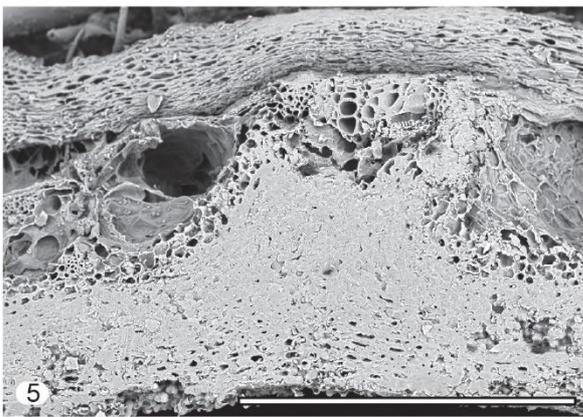
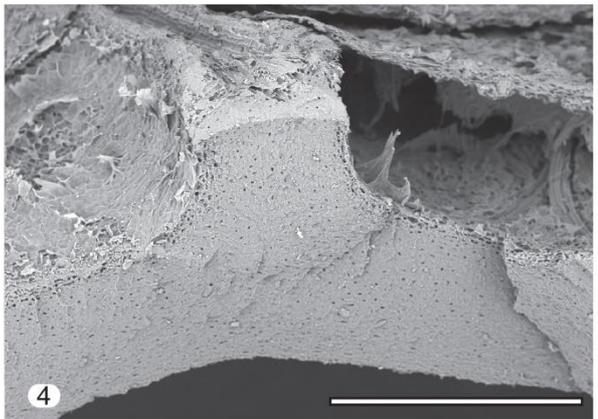
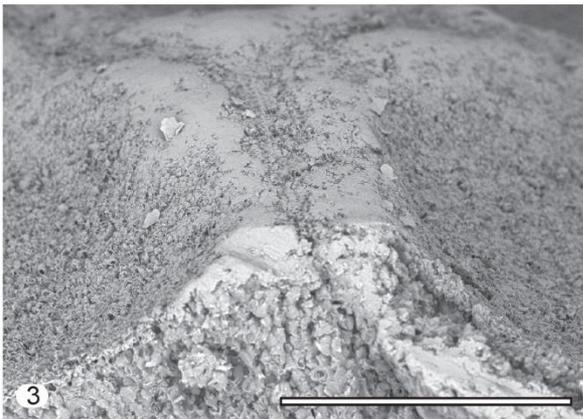
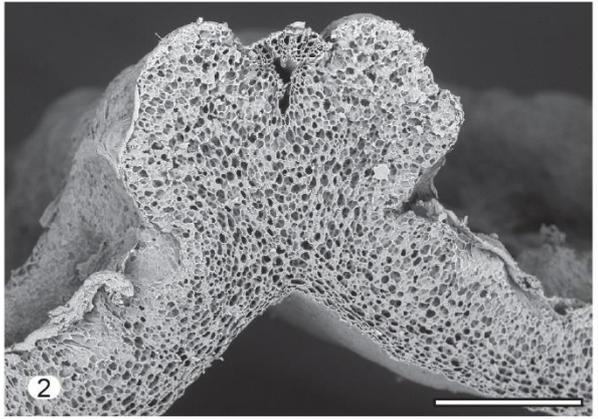
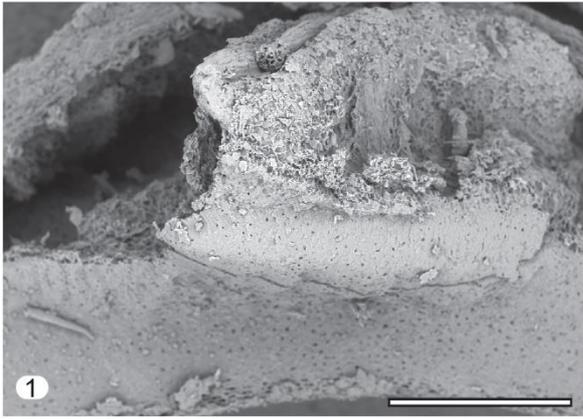


Table 1. Comparative table of features of fossil and modern endocarps of *Iodes*

Species	Endocarp length (mm)	Endocarp width (mm)	Endocarp thickness (mm)	Endocarp ornamentation	Endocarp ridging pattern	Apex vascular structure	Freely ending ridgelets	Number of areoles	Shape of ridges	Ridges at the point of the base	Ridges vertically	Thickness of endocarp wall (μm)
<i>Croomiocarpon mississippiensis</i> Stull, Manchester & Moore	20	18	?	Ridged	Reticulate	Absent (Bulge)	Rare or absent	9–11	Angular	1	3	1140–1160
<i>Hosiea pterojugata</i> Mai	4–6	4–5	?	Ridged	Reticulate	?	Rare or absent	?	?	?	?	?
<i>Iodes acuta</i> Del Rio & De Franceschi	5.8–8.0	3.6–5.4	?	Ridged	Reticulate	Absent (Bulge)	Rare or absent	10–25	Sharp	2	3 & 6	80–130
<i>Iodes acutiform</i> (is?) Chandler	6	3.5–4	?	Ridged	Reticulate	Horns	Rare or absent	15–15	Sharp	?	4 & 3	200
<i>Iodes africana</i> Welw. ex Oliv.	10.8–11.7	8.5–9.1	4.5	Ridged	Reticulate	Absent	Present	21–25	Rounded	6	3	154–171
<i>Iodes balansae</i> Gagnep.	32.7	15.2	?	Ridged	Diffuse & Reticulate	Horns	Present	?	Angular	2	3	434–450
<i>Iodes bilinica</i> (Ettingshausen) Stull, Adams, Manchester et Collinson	9–16	7–11	5–6	Ridged	Reticulate	Pores	Present	?	Sharp	2	3 & 5	650–650
<i>Iodes brownii</i> (Berry) Stull, Adams, Manchester et Collinson	7.5–9.5	5–7.5	?	Ridged	Reticulate	Horns	Rare or absent	20–25	Rounded (?)	2	5 & 6 & 7	300–400

<i>Iodes cirrhosa</i> Turcz.	12.6	9.5	4.5	Ridged & Rugose	Diffuse		Not applicable	Not applicable	Rounded	0 & 2	2	381–405
<i>Iodes corniculata</i> Reid & Chandler	8–9	5.5–7.0	4	Ridged	Reticulate	Horns	Not applicable	15–20	Rounded	2	3 & 4	?
<i>Iodes eocenica</i> Reid et Chandler	13.5–15	12.0	5–6	Ridged	Reticulate	Horns	Rare or absent	?	Rounded	2	2	?
<i>Iodes germanica</i> Knobloch & Mai	4–5	2.6–3.2	?	Ridged	Reticulate	Absent (?)	Rare or absent	20	?	?	2 & 3	?
<i>Iodes kamerunensis</i> Engl.	10.9	9	7.5	Ridged	Reticulate	Absent	Present	1–3	Rounded	2	1	154–181
<i>Iodes klaineana</i> Pierre	12.1	7.6	6.3	Ridged	Reticulate	Absent	Present	13–15	Rounded	2	3	128–173
<i>Iodes liberica</i> Stapf	10.4	7.1	7	Ridged	Diffuse	Absent	Not applicable	Not applicable	Sharp	2	1	138–172
<i>Iodes madagascariensis</i> Baill.	7.6–8	4.6	4.3	Ridged	Reticulate	Absent	Rare or absent	About 80	Rounded	4	2 & 3	165–201
<i>Iodes multireticulata</i> Reid et Chandler	8–12.5	4–7.5	3.4	Ridged	Reticulate	Absent	Rare or absent	30–50	Rounded	2	4 & 5	?
<i>Iodes occidentalis</i> S.E. Allen, Stull & Manchester	7.1	6.2	?	Ridged	Reticulate	Absent	Present	26	Rounded	2	4 & 3	640
<i>Iodes ovalis</i> Blume	17.8	11	8.6	Ridged & Rugose	Reticulate	Horns	Present	3–4	Angular	2	3	314–375
<i>Iodes parva</i> Del Rio, Thomas & De Franceschi	4.4–6	3.5–5.2	2.6–3.5	Ridged	Reticulate	Horns	Rare or absent	11–20	Rounded	2	4 & 5 & 6	160–260

<i>Iodes perrieri</i> Sleumer	11.5	10.9	9.2	Ridged	Diffuse	Pores	Not applicable	Not applicable	Sharp	4	2	317–338
<i>Iodes philippinensis</i> Merr.	12.4	6–7.6	5–6.5	Ridged	Diffuse	Horns	Not applicable	Not applicable	Rounded	0 & 2	2	229–282
<i>Iodes redii</i> Del Rio, Thomas & De Franceschi F	9.2–10.8	6.7–7.5	2.9–4.6	Ridged	Reticulate	Horns	Rare or absent	9–19	Rounded	4	4 & 5	250–270
<i>Iodes rigida</i> Del Rio & De Franceschi	3.7–9.3	3.0–6.5	?	Ridged	Reticulate	Absent	Rare or absent	0–20	Angular	2	5	260–500
<i>Iodes rivecourtensis</i> Del Rio, Thomas & De Franceschi	8.2–12.0	6.3–9.9	2.8–5.9	Ridged	Reticulate	Horns/Pores	Rare or absent	8–22	Rounded	2	4 & 5 & 6	320–700
<i>Iodes scandens</i> (Becc.) Utteridge & Byng	14.7	12.9	11.2	Ridged	Reticulate	Horns	Present	13–18	Angular	2	2 & 3	502–564
<i>Iodes seguinii</i> (H, Lév.) Rehder	16.5	11.0	8.1	Smooth	Not applicable	Absent	Not applicable	Not applicable	Not applicable	0	0	173–226
<i>Iodes seretii</i> (De Wild.) Boutique	11.6	8.7	5.9	Ridged	Reticulate	Absent	Rare or absent	23–25	Rounded & Angular	6	3 & 4	227–245
<i>Iodes sinuosa</i> Del Rio, Thomas & De Franceschi	4.6–5.3	3.7	2.5	Ridged	Reticulate	Horns	Rare or absent	16–17	Sharp	2	3 & 4	220–240
<i>Iodes tubulifera</i> Del Rio, Thomas & De Franceschi	10	6	2	Ridged	Reticulate	Horns	Rare or absent	21	Sharp	2	5	260
<i>Iodes yatesii</i> Merr.	33.8	17	10.7	Ridged	Reticulate	Pores	Present	7–8	Angular	2	3	258–322

<i>Palaeohosiea marchiaca</i> (Mai) Kvaček & Bůžek	6–10	4–7	?	Ridged	Reticulate	Horns (?)	Rare or absent	?	?	?	?	?
<i>Palaeohosiea suleticensis</i> Kvaček & Bůžek	15–20	13–16	?	Ridged	Reticulate	Absent (?)	Rare or absent	?	?	1(?)	2 & 3	?
Species	Thickness of endocarp wall with ridges (µm)	Diameter of papillae (µm)	Density of papillae (µm)	Cell composition of endocarp wall	Orientation of endocarp wall cells	Geological period	Geographical sampling	References				
<i>Croomiocarpon mississippiensis</i> Stull, Manchester & Moore	2200–2500	?–?	?–?	?	?	Eocene	North America	Stull et al., 2011				
<i>Hosiea pterojugata</i> Mai	?	?	?	?	?	Paleocene	Europe	Mai, 1987				
<i>Iodes acuta</i> Del Rio & De Franceschi	180–390	10–18	230–410	Divided into distinctive layers	Isodiametric & Periclinal	Eocene	Europe	This study				
<i>Iodes acutiform</i> (is?) Chandler	?	?	900–1600	?	?	Eocene	Europe	Chandler, 1962				
<i>Iodes africana</i> Welw. ex Oliv.	268–277	14.3–17.4	810–840	Divided into distinctive layers	Periclinal & Isodiametric	Extant	Africa	This study				
<i>Iodes balansae</i> Gagnep.	543–1311	20	?	Divided into distinctive layers	Periclinal & Isodiametric	Extant	Asia	This study				
<i>Iodes bilinica</i> (Ettingshausen) Stull, Adams, Manchester et Collinson	1000	?	?	?	?	Eocene	Europe	Chandler, 1925, Kvaček and Bůžek, 1995, Collinson, 2012				
<i>Iodes brownii</i> (Berry) Stull, Adams,	?	30	?	?	?	Eocene	North America	Allen et al., 2015, Stull et al., 2016				

Manchester et
Collinson

<i>Iodes cirrhosa</i> Turcz.	813–1064	8.6–15.3	462	Divided into distinctive layers	Isodiametric & Periclinal	Extant	Asia	This study
<i>Iodes corniculata</i> Reid & Chandler	?	?	?	?	?	Eocen e	Europe	Reid and Chandler, 1933
<i>Iodes eocenica</i> Reid et Chandler	?	16	?	?	?	Eocen e	Europe	Reid and Chandler, 1933
<i>Iodes germanica</i> Knobloch & Mai	?	?	?	?	?	Cretac eous	Europe	Knobloch and Mai, 1986, Mai, 1987
<i>Iodes kamerunensis</i> Engl.	460–470	?	?	Homogeneous	Isodiametric	Extant	Africa	This study
<i>Iodes klaineana</i> Pierre	300–360	?	?	Divided into distinctive layers	Isodiametric & Periclinal	Extant	Africa	This study
<i>Iodes liberica</i> Stapf	257–266	?	?	Divided into distinctive layers	Isodiametric & Periclinal	Extant	Africa	This study
<i>Iodes madagascariensis</i> s Baill.	227–265	13.3	?	Divided into distinctive layers	Periclinal & Isodiametric	Extant	Madagascar	This study
<i>Iodes multireticulata</i> Reid et Chandler	?	50	?	?	?	Eocen e	Europe	Reid and Chandler, 1933
<i>Iodes occidentalis</i> S.E. Allen, Stull & Manchester	?	30–50	99–180	?	?	Eocen e	North America	Allen et al., 2015
<i>Iodes ovalis</i> Blume	490	9.2–11.8	?	Divided into distinctive layers	Isodiametric & Periclinal	Extant Paleoc ene & Eocen e	Asia	This study
<i>Iodes parva</i> Del Rio, Thomas & De Franceschi	400–560	10–14	510–1060	Divided into distinctive layers	Isodiametric & Periclinal		Europe	Del Rio et al., accepted
<i>Iodes perrieri</i> Sleumer	340–426	12.3–18	448	Divided into distinctive layers	Isodiametric & Periclinal	Extant	Madagascar	This study

<i>Iodes philippinensis</i> Merr.	360–387	?	?	Divided into distinctive layers	Isodiametric & Periclinal	Extant	Asia	This study
<i>Iodes redii</i> Del Rio, Thomas & De Franceschi F	800	?	?	Divided into distinctive layers	Isodiametric & Periclinal	Paleocene	Europe	Del Rio et al., accepted
<i>Iodes rigida</i> Del Rio & De Franceschi	430–580	10–26	290–570	Divided into distinctive layers	Isodiametric & Periclinal	Eocene	Europe	This study
<i>Iodes rivecourtensis</i> Del Rio, Thomas & De Franceschi	380–1590	13–17	126–260	Divided into distinctive layers	Isodiametric & Periclinal	Paleocene	Europe	Del Rio et al., accepted
<i>Iodes scandens</i> (Becc.) Utteridge & Byng	652–672	?	?	Divided into distinctive layers	Periclinal & Anticlinal	Extant	Asia	No voucher (MO).
<i>Iodes seguinii</i> (H. Lév.) Rehder	?	?	?	Homogeneous	Periclinal	Extant	Asia	This study
<i>Iodes seretii</i> (De Wild.) Boutique	320–386	11.8–13.7	?	Divided into distinctive layers	Isodiametric & Periclinal	Extant	Africa	BR0000015596772
<i>Iodes sinuosa</i> Del Rio, Thomas & De Franceschi	350–390	11–15	600	Divided into distinctive layers	Isodiametric & Periclinal	Paleocene	Europe	Del Rio et al., accepted
<i>Iodes tubulifera</i> Del Rio, Thomas & De Franceschi	380	16–19	270	Divided into distinctive layers	Isodiametric & Periclinal	Paleocene	Europe	Del Rio et al., accepted
<i>Iodes yatesii</i> Merr.	430–959	?	?	Divided into distinctive layers	Isodiametric & Periclinal	Extant	Asia	This study
<i>Palaeohosiea marchiaca</i> (Mai) Kvaček & Bůžek	?	16–25	?	?	?	Paleocene	Europe	Kvaček and Bůžek, 1995
<i>Palaeohosiea sulticensis</i> Kvaček & Bůžek	?	15–20	?	?	?	Oligocene	Europe	Kvaček and Bůžek, 1995