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

Cédric Del Rio[1, 2, *], Gregory W. Stull[3], Dario De Franceschi[1]

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

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

[3] Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, 48109, USA

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

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

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

1. Introduction

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

The fossil record of the family is dominated by endocarps, which tend to be taxonomically informative (Stull et al., 2016). Multiple clades of Icacinaceae are diagnosable by fruit characters—for example, the genus *Iodes* Blume is characterized by elliptical to globular endocarps, lenticular in transverse section, with an external reticular pattern, a papillate layer on the inner surface (locule), and a vascular bundle running from the base to the apex embedded in the endocarp wall. *Iodes*, which contains ~23 extant species, is the most abundantly represented genus of Icacinaceae in the fossil record.

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

2. Material and methods

2.1 Material

The lignitic fossil specimens were collected from Le Quesnoy locality (Houdancourt, Oise, France) from 1996 to 2000, from the lignitic clay sediments of Le Quesnoy outcrop, representing the lower Eocene. The sediments indicate that this site corresponds to an ancient fluvial depositional environment (for location and geological setting, see De Franceschi and De Ploëg, 2003; Smith et al., 2014). Based upon the mammalian fauna (e.g. *Teilhardina*, *Landenodon* sp., *Paschatherium* sp. and *Palaeonictis* cf. *gigantea*; Nel et al., 1999), these sediments are dated at MP7 (Lower Ypresian, ~56 Ma), with corroboration from palynological studies (Nel et al., 1999; Cavagnetto, 2000). This corresponds to the Sparnacian facies of the Lower Ypresian (Lower Eocene).

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

2.2 Method of collection

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

2.3 Method of observation

All specimens were studied with a binocular microscope (Wild M3Z) and imaged with a Leica DFC 420 camera. Measurements were taken using the ImageJ Software (Rasband 2016). Cell diameters and papillae were measured 10 times for each species, using random selections of the specimens. Multiple samples were coated with gold-palladium for examination by Scanning Electron Microscopy (SEM), using a Jeol JCM6000 instrument, facilitating observation of anatomical features, especially the endocarp wall layers and papillae.

2. Systematics

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

Order- Icacinales Tiegh.

Family- Icacinaceae Miers

Genus- *Iodes* Blume

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

Fig.1, 1-12

Diagnosis. Endocarp bilaterally symmetrical, elliptical to ovate, occasionally globular, with a reticulate pattern of rectangular (I-Beam) ridges that delimit about 11 polygonal areoles on each face, with few or no freely ending ridgelets. A keel surrounds the endocarp in the plane of symmetry, with the thicker margin containing a vascular bundle embedded in the endocarp wall. Endocarp possessing an apical hole. Endocarp wall about 0.26–0.50 mm thick (excluding ridges; 0.43–0.58 mm including ridges). Inner endocarp surface densely covered with regularly spaced, sessile papillae, rounded in shape with small punctuations/depressions on the surface. Length of endocarp 3.72–9.29 mm, width 3.01–6.54mm.

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

Holotype. MNHN.F. 44593.

Stratigraphy. Early Eocene.

Type locality. Le Quesnoy (Oise, France).

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

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

Remarks. This is the most abundant species at the Le Quesnoy site, with 125 endocarps and a few fragments. The single row of isodiametric cells is a fragile zone (Fig.1, 8). Almost all broken specimen show a ridge section with this layer; papillae are very heterogeneous in form ranging from small to elongate to relatively large (Fig.1, 10 & 11). The pattern of ridges is generally consistent across all specimens (Fig.2), but we show the extreme forms of this species in Fig.2. The ridge pattern is composed first of one ridge, on the medial part of each face, which begins at the base (or almost the base) and runs up two thirds of the length of the endocarp (Fig.2). Two series of ridges (noted 2 & 2’ and 3 & 3’ on Fig.2) running along each side complete the longitudinal ridges, with the secondary ones (2 & 2') well developed and the third ones (3 & 3') more or less developed. The occurrence of all ridges depends on the global shape of the endocarp. Punctuations in the papillae could correspond to an exchange zone between endocarp and seed.

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

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

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

Fig.1, 13-24

Diagnosis. Endocarp bilaterally symmetrical, unilocular, single-seeded, elliptical to ovate, with a reticulate pattern of sharp and sinuous ridges, which delimit about 17 polygonal areoles on each face with few or no freely ending ridgelets. A keel surrounds the endocarp in the plane of symmetry with the thicker margin containing a vascular bundle embedded in the endocarp wall. Endocarp possessing an apical outgrowth composed of the main ridge that runs from the base up to the apex and a protuberance from the keel merged. Endocarp wall about 0.08–0.19 mm thick excluding ridges (0.18–0.39 mm including ridges). Inner endocarp surface densely covered with regularly spaced more or less punctuated and sessile rounded papillae. Length of endocarp about 5.8–8.0 mm, width about 3.61–5.42 mm.

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

Holotype. MNHN.F.44571.

Stratigraphy. Early Eocene.

Type locality. Le Quesnoy (Oise, France).

Paratypes. MNHN.F.44551., 44553., 44554., 44576., 44605., 44614., 44634., 44668., 44682., 44687., 44696., 44700., 44701., 44704., 44705., 44718., 44719.

Description. Endocarp bilaterally symmetrical, unilocular, single-seeded, elliptical to ovate (Fig.1, 14–18), lenticular in transverse section; length 5.8–8.0 (avg. 6.91 mm; SD= 0.79, n=12), width 3.61–5.42 (avg. 4.76 mm; SD=0.63, n=13). Outer part of endocarp with a reticulate pattern of sharp and sinuous ridges (Fig.1, 19). Each face of the endocarp with 3–6 longitudinal ridges, which delimit 10–25 polygonal areoles on each lateral face, avg. 17, with few or no freely ending ridgelets. A keel surrounds the endocarp in the plane of symmetry (Fig.1, 14), with the thicker margin containing a vascular bundle embedded in the endocarp wall (Fig.1, 22). Endocarp possessing an apical outgrowth (Fig.1, 16) composed of the main ridge that runs from the base up to the apex and a protuberance from the keel merged; Endocarp wall 0.08–0.19 mm thick (avg. 0.13 mm; SD=0.04, n=3) excluding ridges; 0.18–0.39 mm thick (avg. 0.29 mm; SD=0.08, n=4) including ridges. Wall composed of packed interlocking digitate and sclerotic cells with four units of unicellular and multicellular cell rows (Fig.1, 20–21); the outermost unit corresponds to an apical sclerotic layer of numerous cell rows, difficult to distinguish; the second unit corresponds to one row of isodiametric-oriented cells, 0.035–0.041 mm in diameter; the basal sclerotic unit is composed of numerous rows of periclinal cells. Inner endocarp surface densely covered with regularly spaced, more or less punctuated, sessile papillae, rounded in shape (Fig.1, 23–24), which correspond to the cell expansions of the locule epiderma layer; papillae diameter 0.010–0.018 mm (MNHN.F.44554., 44668., 44705., 44718.); the number of papillae per 0.25 mm^2 is between 230 and 410 (MNHN.F. 44554., 44668.).

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

Systematic affinity. This new species is distinct from the others due to its unique apical outgrowth, composed of the main ridge that runs from the base up to the apex and a protuberance from the keel merged (Fig.1, 16), a very thin wall (Fig.1, 20-21), and sharp ridges (Fig.1, 19). It differs from I. *rigida* and *I parva* by its sharper ridges. *Iodes acuta* shares this shape of ridges with *I. acutiformis*, *I.bilinica*, *I.sinuosa* and *I. tubulifera*, all species from European Eocene sites; other species have clearly rounded or rectangular ridges (Tab. 1). *I. acutiformis* has a thicker endocarp wall (200 µm vs max. 130 µm) and an acute apex, which is not found in *I. acuta*. In addition, the papillae seem to be denser in *I. acutiformis,* but we do not have information about the shape and diameter of the papillae for comparison. *I. acuta* differs from *I. bilinica* (Collinson et al., 2012) in overall size (5.8–8.0 mm vs 9.0–16.0 mm length), the absence of free-ending ridges, and endocarp thickness (for *I. bilinica*, 650 µm, Tab.1). *I. germanica* is smaller than *I. acuta* and is not well described, making it difficult to more thoroughly assess the affinities between these two species.

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

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

Fig.3, 1-12

Stratigraphy. Late Paleocene

Additional stratigraphy. Early Eocene

Type locality. Rivecourt (Oise, France).

Additional locality. Le Quesnoy (Oise, France)

Specimens: MNHN.F.44549., 44550., 44552., 44556., 44562., 44569., 44628., 44638., 44639., 44648., 44660., 44706., 44707., 44709., 44710., 44730.

Description (Le Quesnoy specimens). Endocarp bilaterally symmetrical, unilocular, single-seeded. Endocarp shape elliptical to ovate (Fig.3, 1–6), lenticular in transverse section;

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

Remarks. This species is represented by 16 fossils from Le Quesnoy. They are very different from the others specimens from Le Quesnoy in having horn-like protrusions (Fig.3, 4). The wall and ridges are not well preserved on the endocarps (Fig.3, 7-8), whereas the papillae are well preserved and clearly lack punctuations on the surface (Fig.3, 11-12). These fossils are the most decayed among *Iodes* remains examined here; however, the seeds are well preserved and include testa remains.

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

Icacinaceae *Incertae Sedis* sp.

Fig.3, 13–18

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

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

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

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

4. Discussion

4.1 Review of the *Iodes* fossil record

In the light of these new discoveries, we present a review of *Iodes* fossil record (following on Stull et al., 2016). The recognition of *Iodes* is based on three diagnostic characters: the ridges at the surface, papillae on the locule surface, and the presence of a vascular bundle inside the endocarp wall. Indeed, *Iodes* is the only genus in the family to have all three of these characters (Stull et al., 2011, Stull et al. 2016). In North America, three species share these characters: *Iodes brownii* from Eocene localities in Wyoming, Utah, Oregon, and Colorado (Allen et al., 2015, Stull et al., 2016); *I. occidentalis* from the Eocene Bridger Formation of Wyoming (Allen et al., 2015) and *I. multireticulata* from the Eocene Clarno Formation of Oregon. *Iodes chandlerae*, from the Clarno Formation, although its locule casts show a papillate, reticulately faceted surface, the endocarp wall is not preserved so it remains unknown whether the funicle passed through the wall as in *Iodes*, or outside of it as in other Iodeae.s. (Stull et al., 2016); therefore, we regard this as a dubious generic identification. In addition, *Croomiocarpum missippiensis* from the early-middle Eocene Tallahatta Formation of Mississippi is very similar to *Iodes* in having a vascular bundle inside the endocarp wall and a reticulate pattern of endocarp ridges (Stull et al., 2011). It mainly differs by its thick wall (about 2 mm including ridges) and the absence of papillae, although the lack of papillae might be due to taphonomic degradation, as noted by Stull et al. (2011).

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

The fossil genus *Iodicarpa* from the Clarno Formation (Manchester, 1994) is cited as close to, or potentially included with, *Iodes* (Allen et al., 2015, Stull et al., 2016), given that members of this fossil genus possess papillae and a vascular bundle embedded in the endocarp wall. Both diagnostic characters are only found together in *Iodes*. However, the size of the specimens (26–56 mm in length, 20–35 mm in width) and the ornamentation (veinlike reticulum of groves) is unusual for the modern and fossil species of *Iodes*. Indeed, only two modern species (*I. balansae* and *I. yatesii*, Tab. 1) are as long as the species included in *Iodicarpa*. However, these two modern species are less than 17 mm in width. Among the current species, only *I. seguinii* has a smooth ornamentation but also a vascular bundle in a gutter and no papillae (Tab. 1). Thus, we do not have final argument to include or exclude these species in *Iodes*. Consistent with previous studies, we consider this genus as closely related to *Iodes* or included inside the clade but with extinct morphology (regarding its distinct ornamentation type, compared to described fossil and modern species of *Iodes*). An *Iodes* sp. was illustrated from the Chuckanut Formation of Washington (Pigg and Wher, 2002). However, the specimen seems to be an endocarp impression with no anatomical information available. Although it conforms morphologically to tribe Iodeae, we consider this occurrence as a dubious record of *Iodes*.

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

Palaeohosiea (Kvaček and Bůžek, 1995) possesses the three major diagnostic characters of *Iodes* with no significant other distinguishing features (Allen et al., 2015). Thus, we consider all species of this genus as members of *Iodes* and include them in our comparisons: *P. marchiaca* and *P. suleticensis* from the Paleocene and Oligocene of Bohemia (Kvaček and Bůžek, 1995). In addition, *Hosiea pterojugata* from the Palaeocene of Gona, Germany (Mai, 1987), also has all key diagnostic characters of *Iodes* genus, although the specimen descriptions are relatively minimal.

Chandler (1961) attributed another fossil from Southern England to *Iodes*, as *Iodes* sp., but we consider this placement equivocal. The specimen has papillae and a reticulate pattern of ridges. It is very small, about 4.5 mm in length, which is unknown for modern members of *Iodes* (see. Tab.1), but we have described other fossil examples of small *Iodes* (Del Rio et al., 2018). However, the specimen is a locule cast, indicating that the endocarp is at least slightly larger than 4.5 mm. The position of the vascular bundle is unknown as only a locule cast remains. Because the genus *Hosiea* also possesses reticulate ridges and papillate locule linings, we hesitate to attribute this fossil to *Iodes* given the unknown position of the vascular bundle. *Iodes* sp. from the Dormaal formation possesses a reticulation pattern "obliterated by encrustation of sand" and papillae inside the locule (Fairon-Demaret and Smith, 2002). However, the specimen is very decayed; therefore, it is difficult to decide if this specimen belongs to *Iodes* genus or other similar genera, such as *Hosiea*.
An *Iodes* from the Miocene of Yunnan (China) has been mentioned (Stull Obs. Pers.) but not formally published. A second *Iodes* species from the Miocene of Turkey seems to have been studied but not published (Duperon, com. Pers.). Therefore, there are no published records of *Iodes* from areas other than North America and Europe.

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

4.2 Significance of the ridges

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

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

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

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

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

5. Conclusion

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

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

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

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

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

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CAPTION

Figure 1.

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

1. Lateral view of endocarp showing the reticulate pattern of ridges, Holotype specimen (MNHN.F.44593.).
2. Same in dorsal view showing the keel surrounding the fruit.
3. Same in lateral view showing the second face of endocarp.
4. Same in apical view showing the hole.
5. Same in basal view showing the trace left by the peduncle.
6. Lateral view of another specimen (MNHN.F.44564.) showing a comparable reticulum of ridges.
7. SEM view of ridges showing trace left by vascular bundles (MNHN.F.44655.).
8. SEM transverse view of wall and ridge (MNHN.F.44697.).
9. SEM transverse view showing the basal sclerotic layer and locule epidermal layer with papillae in contact with seed cells. (MNHN.F.44607.).
10. SEM view of the vascular bundle (arrow) inside the endocarp wall (MNHN.F.44601.).
11. SEM view of the papillae on the locule lining.
12. Same with magnification showing punctuation under papillae.

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

13. Lateral view of endocarp showing the reticulum of ridges, Holotype specimen (MNHN.F.44571.).
14. Same in dorsal view showing the keel surrounding the fruit.
15. Same in lateral view showing the second face of the endocarp.
16. Same in apical view showing the hole.

17. Same in basal view showing the trace left by the peduncle.
18. SEM lateral view of another specimen (MNHN.F.44696.) showing reticulum of sharp ridges.
19. SEM view of reticulum of sharp ridges (MNHN.F.44705.).
20. Same in transverse view of wall and ridges.
21. Same with magnification focused on cell layers.
22. View of the vascular bundle (arrow) inside the endocarp wall (MNHN.F.44701.).
23. Same with magnification showing mycological filaments.
24. Same with magnification focused on non-punctuated papillae.

Scale bar: 5 mm = 1-6, 13-18; 1 mm = 22; 500 µm = 7, 19; 200 µm = 8, 10, 20; 50 µm = 9, 11, 21, 23; 20 µm = 24; 5 µm = 12.

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

Figure 3.

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

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

7. SEM view of reticulum of ridges showing tearing of primary layer (MNHN.F.44628.).
8. Same in transverse view of wall and ridge.
9. Same with a view of the locule epidermal layering showing remnant testa in contact with the endocarp.
10. SEM view of locule epiderma layer showing numerous sessile, rounded papillae (MNHN.F.44709.)
11. Same with magnification.
12. Same with magnification showing unpunctuated cells under papillae.

13-18. Icacinaceae *insertae sedis*

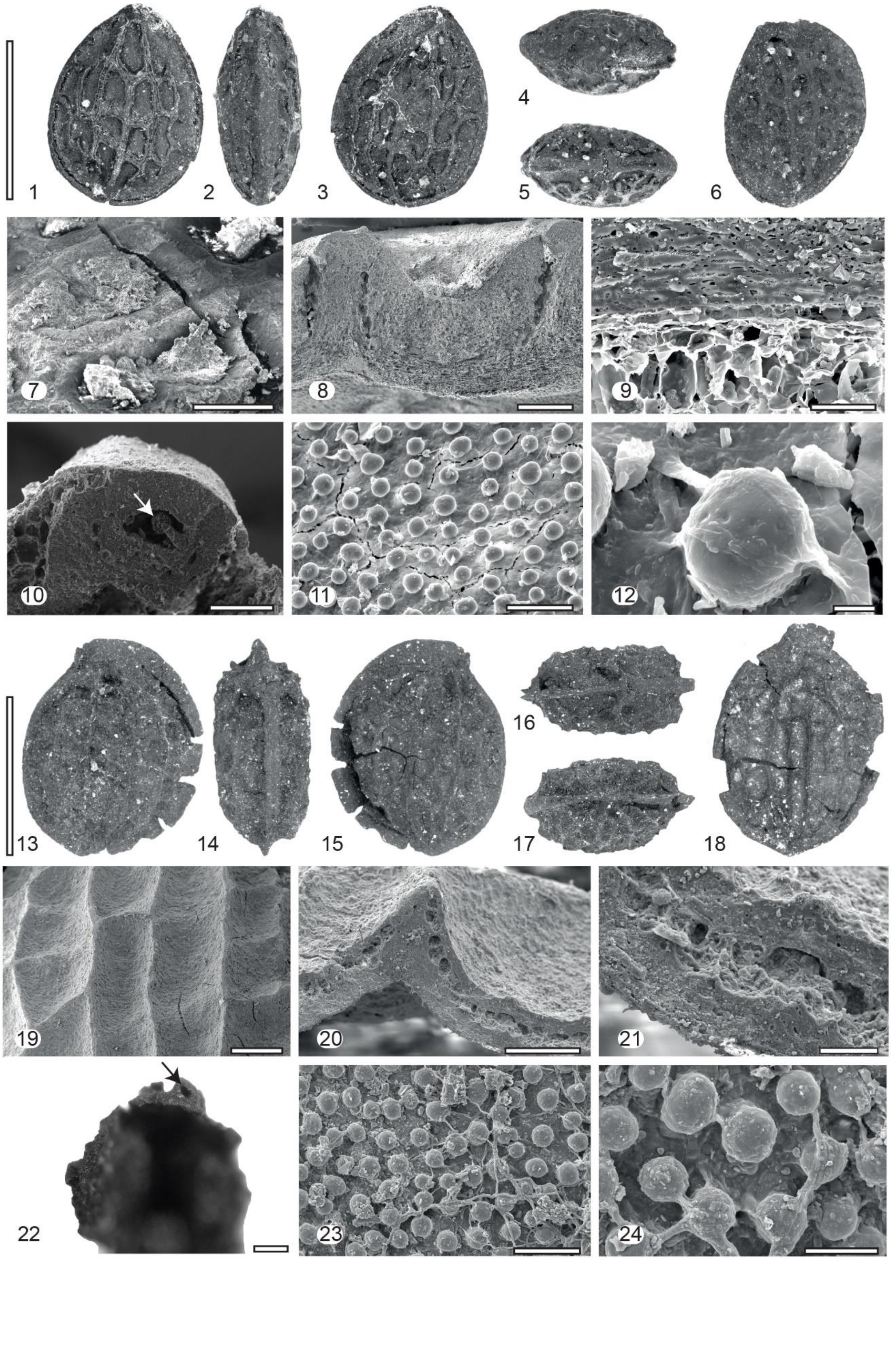
13. Lateral view of seed showing smooth surface and asymmetrical apex (MNHN.F.44725.).
14. Other example in the same configuration (MNHN.F.44724.).
15. Other example in the same configuration (MNHN.F.44723.).
16. SEM view of broken apex of seeds (MNHN.F.44731.).
17. Same in apical view showing trace surrounding the seed.
18. Same in lateral view showing the mineralized surface.

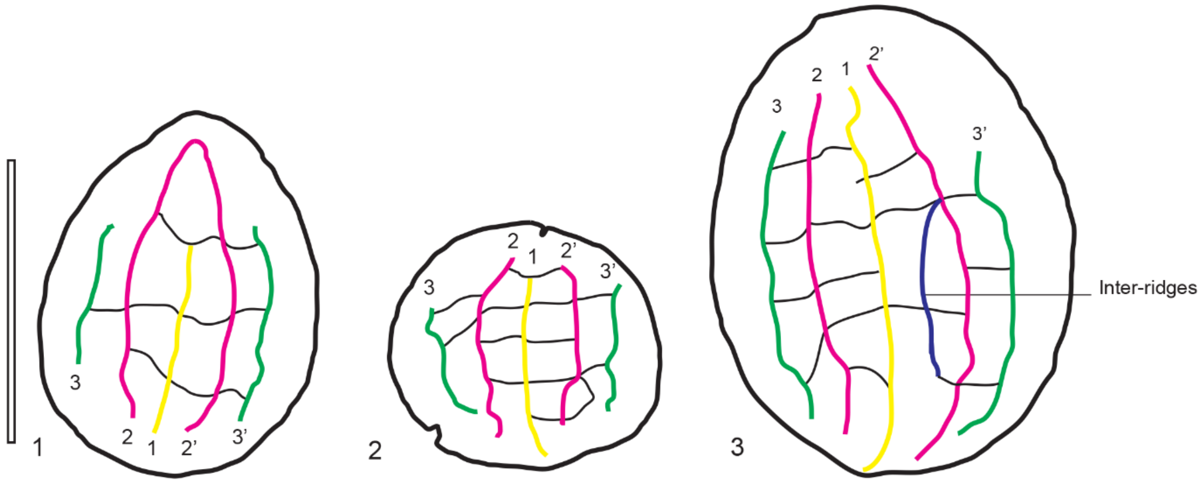
Scale bar: 5 mm = 1-6, 13-15; 1 mm = 16; 500 µm = 7, 17; 200 µm = 8, 10; 100 µm = 9; 50 µm = 11; 20 µm = 12, 18.

Figure 4. Shape of ridges of modern *Iodes* species. Rectangular with (1) *Iodes balansae*, (2) *Iodes yatesii*, (3) *Iodes scandens* and(4) *Iodes ovalis*; and mostly rounded with (5) *Iodes seretii* and(6) *Iodes kamerounensis*. Arrow = trace left by vascular bundle (sometimes still visible) Scale bars: 500 µm.

Appendix

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





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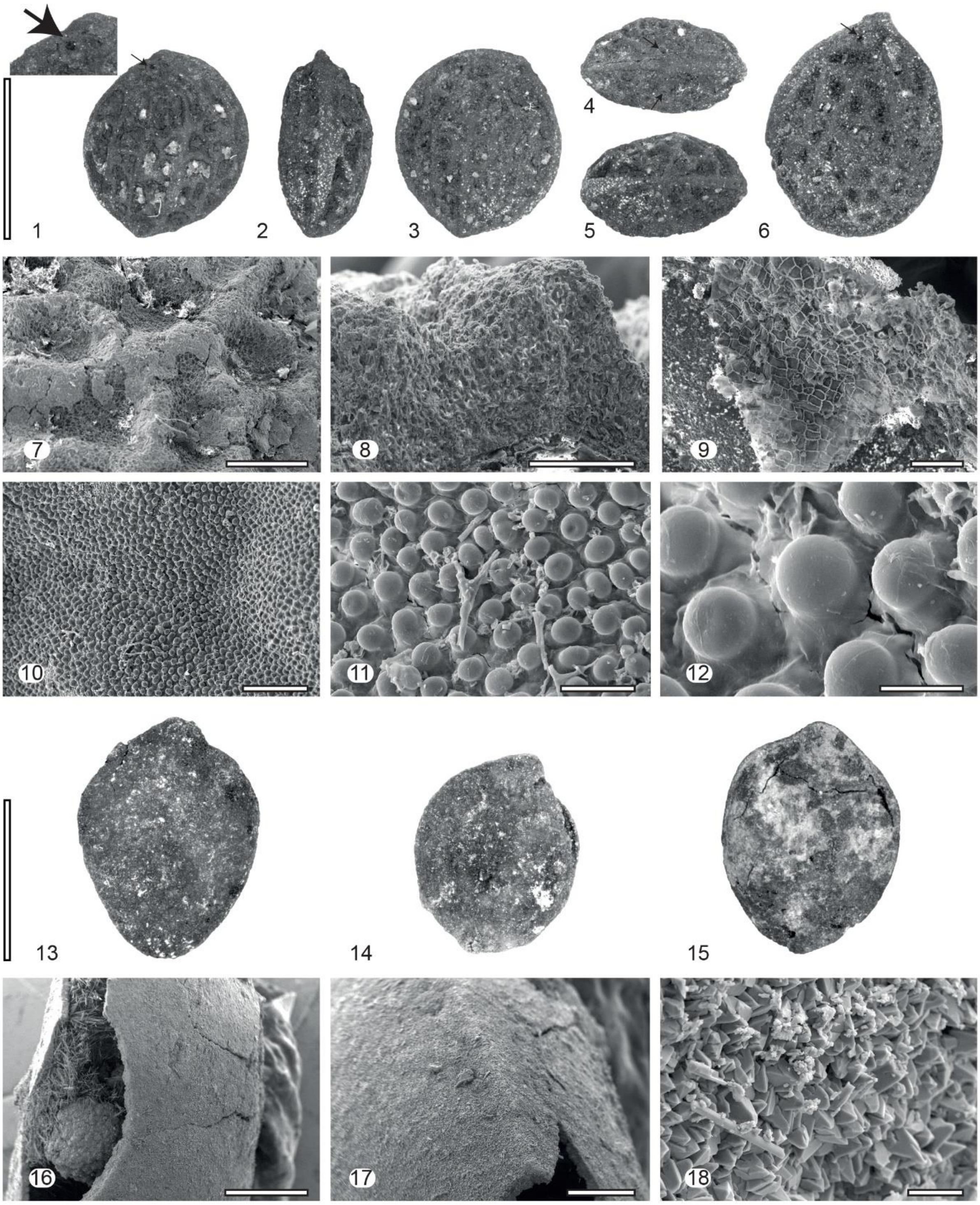
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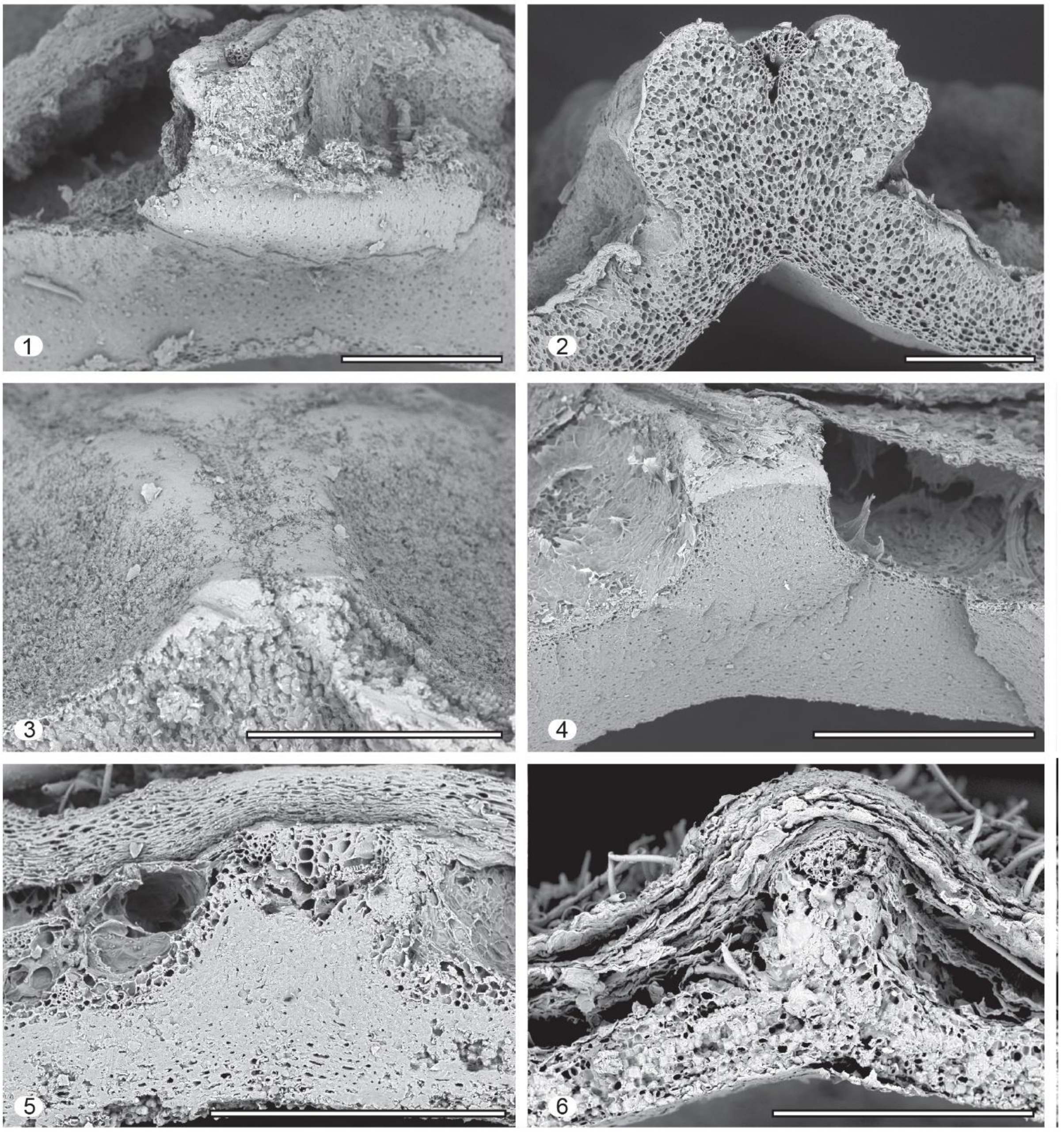
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Table 1. Comparative table of features of fossil and modern endocarps of *Iodes*

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)
Croomiocarpon missippiensis Stull, Manchester & Moore	20	18	?	Ridged	Reticulate	Absent (Bulge)	Rare or absent	9–11	Angular	1	3	1140–1160
Hosiea pterojugata Mai	4–6	4–5	?	Ridged	Reticulate	?	Rare or absent	?	?	?	?	?
***Iodes acuta* 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**
Iodes acutiform(is?) Chandler	6	3.5–4	?	Ridged	Reticulate	Horns	Rare or absent	15–15	Sharp	?	4 & 3	200
Iodes africana Welw. ex Oliv.	10.8–11.7	8.5–9.1	4.5	Ridged	Reticulate	Absent	Present	21–25	Rounded	6	3	154–171
Iodes balansae Gagnep.	32.7	15.2	?	Ridged	Diffuse & Reticulate	Horns	Present	?	Angular	2	3	434–450
Iodes bilinica (Ettingshausen) Stull, Adams, Manchester et Collinson	9–16	7–11	5–6	Ridged	Reticulate	Pores	Present	?	Sharp	2	3 & 5	650–650
Iodes brownii (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

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

Iodes perrieri Sleumer	11.5	10.9	9.2	Ridged	Diffuse	Pores	Not applicable	Not applicable	Sharp	4	2	317–338
Iodes philippinensis Merr.	12.4	6–7.6	5–6.5	Ridged	Diffuse	Horns	Not applicable	Not applicable	Rounded	0 & 2	2	229–282
Iodes redii 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
***Iodes rigida* Del Rio & De Franceschi**	**3.7–9.3**	**3.0–6.5**	**?**	**Ridged**	**Reticulat e**	**Absent**	**Rare or absent**	**0–20**	**Angular**	**2**	**5**	**260–500**
Iodes rivecourtensis 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
Iodes scandens (Becc.) Utteridge & Byng	14.7	12.9	11.2	Ridged	Reticulate	Horns	Present	13–18	Angular	2	2 & 3	502–564
Iodes seguinii (H, Lév.) Rehder	16.5	11.0	8.1	Smooth	Not applicable	Absent	Not applicable	Not applicable	Not applicable	0	0	173–226
Iodes seretii (De Wild.) Boutique	11.6	8.7	5.9	Ridged	Reticulate	Absent	Rare or absent	23–25	Rounded & Angular	6	3 & 4	227–245
Iodes sinuosa 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
Iodes tubulifera Del Rio, Thomas & De Franceschi	10	6	2	Ridged	Reticulate	Horns	Rare or absent	21	Sharp	2	5	260
Iodes yatesii Merr.	33.8	17	10.7	Ridged	Reticulate	Pores	Present	7–8	Angular	2	3	258–322

Palaeohosiea marchiaca (Mai) Kvaček & Bůžek	6–10	4–7	?	Ridged	Reticulate	Horns (?)	Rare or absent	?	?	?	?	?
Palaeohosiea suleticensis 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	Geologica l period	Geographical sampling	References
Croomiocarpon missippiensis Stull, Manchester & Moore	2200-2500	?–?	?–?	?	?	Eocene	North America	Stull et al., 2011
Hosiea pterojugata Mai	?	?	?	?	?	Paleocene	Europe	Mai, 1987
***Iodes acuta* Del Rio & De Franceschi**	**180–390**	**10–18**	**230–410**	**Divided into distinctive layers**	**Isodiametric & Periclinal**	**Eocene**	**Europe**	**This study**
Iodes acutiform(is?) Chandler	?	?	900–1600	?	?	Eocene	Europe	Chandler, 1962
Iodes africana Welw. ex Oliv.	268–277	14.3–17.4	810–840	Divided into distinctive layers	Periclinal & Isodiametric	Extant	Africa	This study
Iodes balansae Gagnep.	543–1311	20	?	Divided into distinctive layers	Periclinal & Isodiametric	Extant	Asia	This study
Iodes bilinica (Ettingshausen) Stull, Adams, Manchester et Collinson	1000	?	?	?	?	Eocene	Europe	Chandler, 1925, Kvaček and Bůžek, 1995, Collinson, 2012
Iodes brownii (Berry) Stull, Adams,	?	30	?	?	?	Eocene	North America	Allen et al., 2015, Stull et al., 2016

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

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