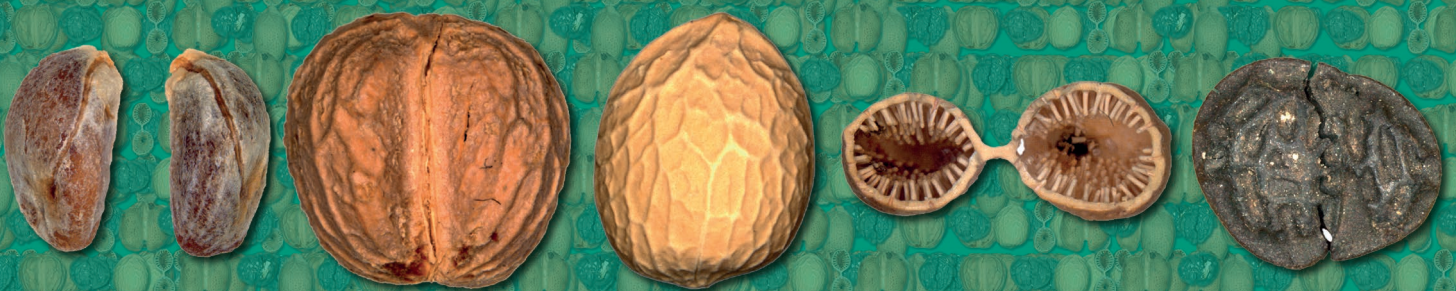


An abnormally twinned fossil fruit  
of *Iodes* Blume (Icacinaceae)  
from Rivecourt (Thanetian, Oise, France)

Cédric DEL RIO & Dario DE FRANCESCHI



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ISSN (imprimé / *print*): 1280-8571/ ISSN (électronique / *electronic*): 1639-4798

# An abnormally twinned fossil fruit of *Iodes* Blume (Icacinaceae) from Rivecourt (Thanetian, Oise, France)

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Submitted on 12 June 2018 | accepted on 12 October 2018 | published on 11 March 2019

Del Rio C. & De Franceschi D. 2019. — An abnormally twinned fossil fruit of *Iodes* (Icacinaceae) from Rivecourt (Thanetian, Oise, France). *Adansonia*, sér. 3, 41 (3): 25-28. <https://doi.org/10.5252/adansonia2019v41a3>. <http://adansonia.com/41/3>

## ABSTRACT

The Rivecourt site (Thanetian from Oise, France) includes about 70 endocarp specimens distributed among five *Iodes* Blume species. Of the 36 specimens of *Iodes rivecourtenis* Del Rio, Thomas & De Franceschi one has an abnormal morphology. It is divided in two locules rather than one, and two apical apertures per face in contrast to normal specimen possessing only one per face. Icacinaceae Miers is a family with one carpel and two pendulous ovules where only one becomes mature. Here we have cases of two fused carpels, revealed by a wall between the twin lateral parts and by the four apertures, probably corresponding to the vascularisation of the four ovules. Finally, we hypothesize that the two functional locules found here may correspond to a partial reversion of ancestral characters of the fruit.

## KEY WORD

*Iodes*,  
ovules,  
teratology,  
endocarp,  
twinned-fruit.

## RÉSUMÉ

*Un fruit fossile anormalement jumelé du genre Iodes Blume (Icacinaceae) provenant de Rivecourt (Thanétien, Oise, France).*

Le site de Rivecourt (Thanétien de l’Oise, France) montre environ 70 spécimens d’endocarpes répartis en cinq espèces de *Iodes* Blume. Parmi les 36 spécimens d’*Iodes rivecourtenis* Del Rio, Thomas & De Franceschi, l’un d’entre eux est divisé en deux parties latérales, avec deux ouvertures sur chaque face, contre une seule pour les spécimens habituels. Les fleurs des Icacinaceae portent un carpelle à une loge contenant deux ovules pendants, dont un seul atteint la maturité. Ici nous avons le cas de deux carpelles accolés, révélés par une paroi séparant les deux parties similaires et par les quatre ouvertures, correspondant probablement à la vascularisation des quatre ovules. Finalement, nous émettons l’hypothèse que ces deux loges fonctionnelles trouvées ici pourraient correspondre à une réversion partielle de l’état ancestral du fruit.

## MOTS CLÉS

*Iodes*,  
ovules,  
téatologie,  
endocarpe,  
fruits jumelés.

## INTRODUCTION

The Rivecourt site, from the Paleocene (Thanetian, Oise, France; Smith *et al.* 2014) shows numerous fruits, endocarp and seeds preserved as lignite. About 70 of these conform to the genus *Iodes* Blume of the Icacinaceae and have been placed in 5 species (Del Rio *et al.* 2019). *Iodes* is easily recognisable in the fossil record by the elliptical shape of the endocarp, the ridged ornamentation at the surface, a primary vascular bundle inside the wall and running to the base up to the apex, and rounded papillae in the locule surface. In addition, all *Iodes* species from Rivecourt have more or less compressed horn-like pair of subapical endocarp protrusions (apertures), a feature probably linked to the vascularisation of the ovules and only found in Asian modern species but lacking in the African members (Stull *et al.* 2016). Among the 36 specimens of *Iodes rivecourtenis* Del Rio, Thomas & De Franceschi, one specimen caught our attention. Numbered as Riv. PPB19 and figured in the overview of the Rivecourt site (Smith *et al.* 2014: fig. 4T), this specimen shows quite exceptional and “abnormal” characters which led us to research the origin and significance of these particularities.

## MATERIAL AND METHODS

The lignitic fossil endocarp Riv. PPB19 is housed at the Muséum national d’Histoire naturelle of Paris for study and will be held at the Musée Vivenel in Compiègne (Oise, France) for permanent storage. This specimen was studied in detail and compared with extant specimens from the Herbarium of Paris (P) fruits. Among the herbarium material, three sheets were sampled for special fruits illustrating the rare morphology described here, *Iodes africana* Welw. ex Oliv. (*R.P. Tisserant s.n.*, [P03951984] and *R.P. Klaine 3505* [P03951995]) and *Pyrenacantha vogelianna* Baill. (*R.P. Sacleux 1873b* [P04472242]).

The fossil and extant specimens were studied with a binocular microscope (Wild M3Z) and imaged with a Leica DFC 420 camera.

## RESULTS

The endocarp (Fig. 1A-D) shows two adjacent raised apical apertures (compressed horn-like protrusions *sensu* Del Rio *et al.* 2019) on each face. A total of four, as seen on the endocarp apex (Fig. 1D) *versus* only two of these “horn-like” protrusions in usual specimens (Fig. 1E). Moreover, the endocarp is divided laterally into two twin parts (Fig. 1C) and thus presents two locules; one of them has a seed inside still preserved. The locule of the other part remains unopened so the presence of a seed can only be inferred. The bipartite configuration correlates with the unusual wideness of this specimen (ratio length/wide = 0.82) compared to the usual type (ratio l/w = 1.14).

This fossil fruit is affected by teratology, but this is not an isolated case. We found, among the more than 4000 fruit

specimens of Icacinaceae *s.s.* (Stull *et al.* 2015) present in the Paris Herbarium (P), two comparable examples, which indicate a low rate of occurrence of the “siamese-twins” (roughly 0.5 ‰). In *Iodes africana* (Fig. 1F-H), only one specimen, among the 404 specimens (max 2.5‰) has two locules clearly divided into two lateral parts (Fig. 1F); all locules contain a developed seed (Fig. 1G). This abnormal endocarp is wider than the standard single-seeded type (Fig. 1H) characteristic of the family. In *Pyrenacantha vogeliana* Baill. (Fig. 1I-K), we also found an abnormal specimen, among 147 present in herbarium (max 6.8‰). In this specimen, the endocarp is clearly divided into two parts (Fig. 1I, J). In cross section, we observe a wall separating the two parts. Each locule possesses tubercles positioned as in the usual type (Fig. 1J).

## DISCUSSION

A similar case of twinned endocarp has been mentioned in the fossil record in the London Clay outcrops for *Iodes multireticulata* Reid & Chandler (see in particular Reid & Chandler 1933: pl. 15, fig. 8) within one hundred specimens. In other sites with numerous Icacinaceae fossils specimens, we do not find other cases (Knobloch & Mai 1986; Manchester 1994; Collinson *et al.* 2012).

Since extant Icacinaceae Miers is a family with two pendulous ovules, where only one reaches the maturity (Kårehed 2001), Reid and Chandler proposed that the development of the two ovules causes the abnormal development of the endocarp. The alternative hypothesis of two accrescent carpel fused is rejected by the fractioning of the London Clay specimen, which show no evidence of a carpel wall between the twin parts. However, in the absence of seeds and modern comparisons, they cannot conclude.

In our case, we found two symmetrical units of endocarp linked by a wall in the specimen Riv. PPB19 and in extant species (see in particular Fig. 1J). This observation led us to consider that these fruits were developed from two fused ovaries, each with two ovules instead of that the maturity of the two ovules. Furthermore, the sub-apical apertures here named “horns” are considered as “the point of entry of two vascular bundles into the locule (supplying the two apical ovules characteristic of icacinaceous fruits)” (Allen *et al.* 2015). Here we have four horn-like protrusions, which is in accordance with the hypothesis of two carpels and four ovules with only one reaching the maturity in each carpel. However, the role of these apical structures remains partially unresolved and development studies in extant *Iodes*, which have horns, is necessary.

The species of Icacinaceae *s.s.* (Stull *et al.* 2015) have only one locule. These cases reported here in the past and modern Icacinaceae species demonstrate that some abnormal fruits with two locules, both functional, exist (Fig. 1G). The sister group of Icacinaceae (Stull *et al.* 2015) is Oncothecaceae, which have 1-2 ovules in five locules (Morat & Veillon 1988). This configuration seems to be ancestral in lamiid groups (Sauquet *et al.* 2017). Therefore, the ancestral character of the Icacinaceae

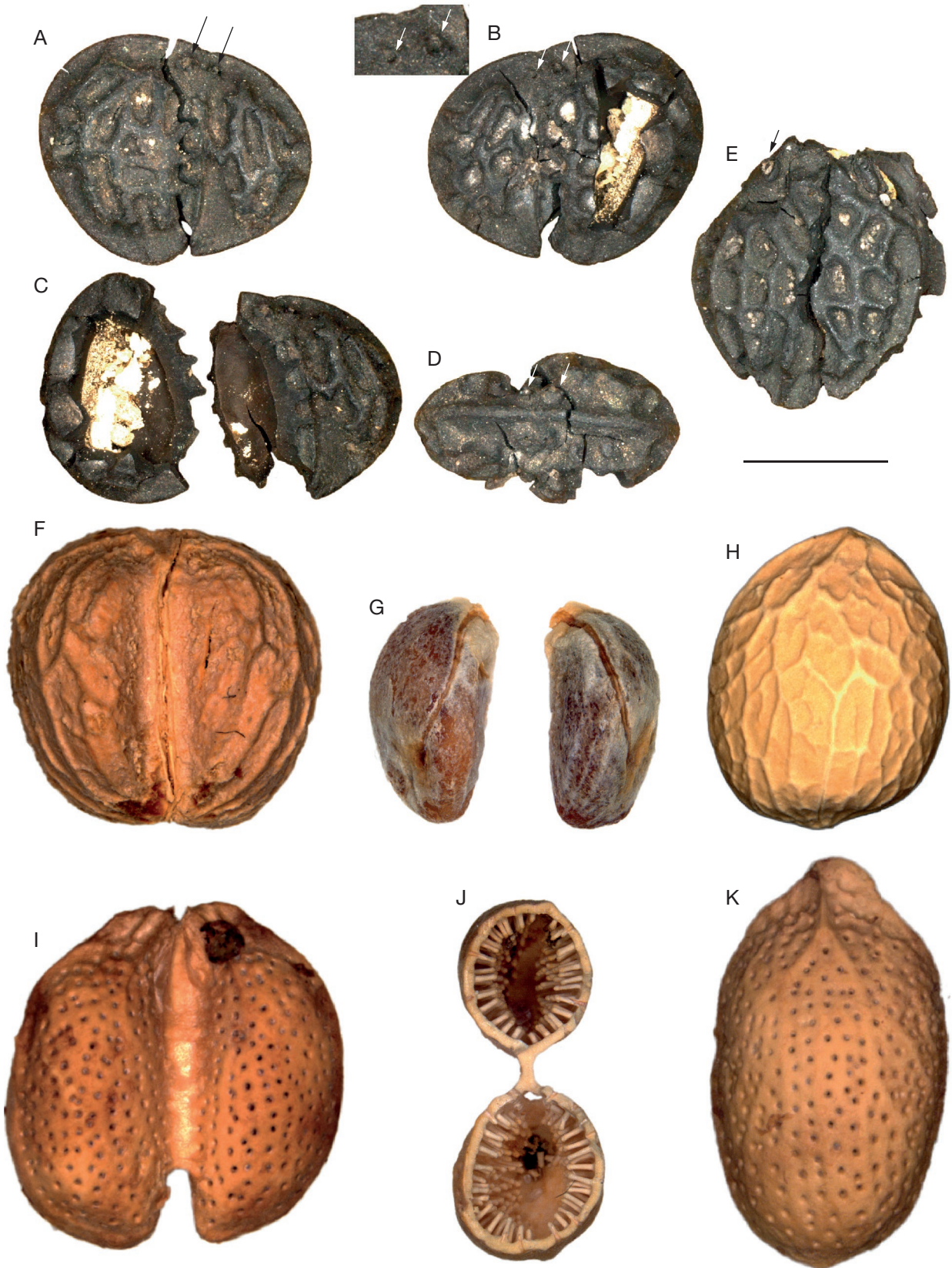


FIG. 1. — **A-D**, Abnormal *Iodes rivecourtensis* Del Rio, Thomas & De Franceschi specimen (Riv. PPB19.); **A, B**, lateral view showing the lightly raised apertures (arrows); **C**, broken parts showing one of the two locules, in cream color the remnants of a seed still embedded in the endocarp; **D**, same in apical view showing the four horn-like protrusions (arrows); **E**, *Iodes rivecourtensis* usual type (Riv. PPB 156.) showing one horn-like protrusion (arrow); **F, G**, abnormal *Iodes africana* Welw. ex Oliv. specimen (P03951995); **F**, lateral view showing the clear two twin parts; **G**, two mature seeds from the abnormal fruit; **H**, standard single-seeded fruit of *Iodes africana* (P03951984); **I, J**, abnormal *Pyrenacantha vogeliana* Baill. (P04472242); **I**, lateral view showing the clear two parts; **J**, cross section of the abnormal fruit; **K**, usual fruit of *Pyrenacantha vogeliana* (P04472242). Scale bar: 5 mm.

(*sensu* Stull *et al.* 2015) could be fruits with five locules. The fruit with one locule appear to be apomorphic of Icacinaceae and the evolution of this fruits in the Icacinaceae family seems linked to the loss of locules. Thus the two functional locules found here may correspond to a partial reversion of ancestral characters, reversion shared by at least the clade III and IV in the Icacinaceae family (*sensu* Stull *et al.* 2015). We should note also that the state “two carpels” is frequent in lamiids (Borraginales, Lamiales, Gentianales, Solanales, etc.).

### Acknowledgements

We thank Lafarge Granulats for logistic help to carry out the excavation on the Rivecourt site, the Musée Vivienel for allowing us to study of the fossil specimens, and the staff of the Paris Herbarium (MNHN P) for the modern endocarp sample loan and access to herbarium sheets. We are grateful to Steven Manchester and an anonymous referee for their fruitful suggestions, which notably improved the manuscript. This work was supported by a grant from Agence Nationale de la Recherche under the LabEx ANR-10-LABX-0003-BCDiV, in the program “Investissements d’avenir” n\_ ANR-11-IDEX-0004-02 and by the CR2P.

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*Submitted on 12 June 2018;  
 accepted on 12 October 2018;  
 published on 11 March 2019.*