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First endocarp record of *Miquelia* (Icacinaceae) from the late Miocene of northern Vietnam and its phytogeographical and paleoecological implications

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ABSTRACT

Abundant fossil records of Icacinaceae have been documented in the Northern Hemisphere; however, they are rare in the paleotropics where the family is most diverse today. As such, the evolutionary history of the family remains incomplete. In this study, we describe a newly discovered endocarp of Icacinaceae from the late Miocene of northern Vietnam, namely *Miquelia yenbaiensis* N.B. Hung, J. Huang & S.F. Li sp. nov. The identification is based on detailed morphological observations conducted using a reflected light microscope, together with extensive comparisons with both modern and fossil endocarps of the Phytocreneae. *Miquelia yenbaiensis* is characterized by sharp, thin, and reticulate ridges, with five main longitudinal ridges, and primarily circular pits arranged in longitudinal lines, with approximately 110–120 pits per face. The fossil examined in our study represents the first fossil record of *Miquelia*, indicating that this genus existed in northern Vietnam since at least the late Miocene. Additionally, our fossil finding provides the most recent fossil record of the Phytocreneae as well as the Icacinaceae, extending their historical range into tropical Asia during the late Miocene. *Miquelia yenbaiensis* likely inhabited a wet tropical ecosystem with a multi-stratified forest in the Yen Bai Basin during the late Miocene.

1. Introduction

The Icacinaceae are a pantropical family of asterid angiosperms comprising 23 genera and approximately 160 species (Stull et al., 2015, 2020a; Jongkind and Lachenaud, 2019). This family includes trees, shrubs, and woody climbers that predominantly inhabit lowland rainforests, though a few species have adapted to temperate or arid environments (Peng and Howard, 2008; Potgieter and Duno, 2016). Although most modern species occur in the tropics, the family has a rich fossil record in temperate regions of the Northern Hemisphere (Del Rio and De Franceschi, 2020a). Icacinaceae fossils are documented extensively from the Paleogene of North America (e.g., Wolfe, 1977; Manchester, 1994; Pigg and Wehr, 2002; Rankin et al., 2008; Stull et al., 2011, 2012; Allen et al., 2015; Atkinson, 2022) and Europe (e.g., Reid and Chandler, 1933; Chandler, 1961; Collinson et al., 2012; Stull et al., 2016; Del Rio et al., 2017, 2019a, 2019b; Del Rio and De Franceschi, 2020b). In addition, few fossil occurrences of the family are also reported from the Paleogene of Africa (e.g., Stull et al., 2020b), Asia (e.g., Hofmann et al., 2019; Del Rio et al., 2022), and Australia (Rozefelds et al., 2021) and the early Miocene of Africa (Collinson et al., 2009). The oldest reliable fossil record of the family is recovered from the early to the middle Campanian (Upper Cretaceous) of western North America (Atkinson, 2022).

Phylogenetic analyses of the chloroplast genome have previously

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placed Icacinaceae as a sister group to Oncothecaceae, with these two groups collectively designated as sisters to the remaining lamiids (Stull et al., 2015). Conversely, recent nuclear phylogenomic analyses of asterids have recovered Icacinaceae as a sister group to the core lamiids, while Oncothecaceae have been recognized as a sister group to both lamiids and campanulids (Stull et al., 2020a). All genera previously in Icacinaceae were placed into the clade Icacinoideae with the exception of *Cassinopsis* Sond. Additionally, four major clades were identified within Icacinoideae, each characterized by unique geographic distributions and morphological traits (Stull et al., 2015). The first clade is characterized by trees or shrubs comprising the Neotropical genus *Mappia* Jacq. and the Asiatic genus *Nothapodytes* Blume. The second clade consists of scandent shrubs or lianas belonging to two American genera *Casimirella* Hassl. and *Leretia* Vell. and two other African genera *Icacina* A. Juss. and *Lavigeria* Pierre. The third clade comprises the paleotropical genus *Iodes* Blume and the small Asiatic genus *Mappianthus* Hand.-Mazz., characterized by climbers with opposite leaves and distinctive tendrils. The last clade is the largest and most morphologically heterogeneous, including the remaining paleotropical genera.

Within the largest clade, five extant genera of the tribe Phytocreneae, including *Miquelia* Meisn., *Phytocrene* Wall., *Pyrenacantha* Wight, *Sarcostigma* Wight & Arn., and *Stachyanthus* Engl. form a subclade differentiated from others by pitted endocarps excepting *Sarcostigma* with smooth endocarps (Stull et al., 2015). Additionally, four fossil genera, *Manchesteria* Stull & Rozefelds (Rozefelds et al., 2021), *Palaeophytocrene* Reid & Chandler (Reid and Chandler, 1933), *Perforatocarpum* (Chandler) Stull, Adams, Manchester & Collinson (Reid and Chandler, 1933; Stull et al., 2016), and *Stizocarya* Reid & Chandler (Reid and Chandler, 1933), are also placed in this group based on endocarp morphology. The present-day distribution of the Phytocreneae is confined to tropical regions of Africa, Southeast Asia, India, and Papua New Guinea (Fig. 1) (Sleumer, 1971). Nevertheless, no fossil record of the Phytocreneae has been reported from its extant geographic ranges, despite their extensive occurrences in various Paleogene floras across Europe (Reid and Chandler, 1933; Chandler, 1961; Collinson et al., 2012; Stull et al., 2016; Del Rio and De Franceschi, 2020b), the Americas (Wolfe, 1977; Manchester, 1994; Pigg and Wehr, 2002; Rankin et al., 2008; Stull et al., 2011, 2012; Atkinson, 2022; Poore et al., 2023), Africa (Stull et al., 2020b), and Australia (Rozefelds et al., 2021) (Fig. 1). The different patterns observed in the modern and fossil distributions suggest a complex biogeographic history for the Phytocreneae. Meanwhile, the lack of a fossil record in the extant distribution limits our understanding of the evolutionary and biogeographic history of the clade. For example, abundant Paleogene occurrences of the Phytocreneae in mid-latitudes of the Northern Hemisphere indicate the expansion of the clade when global temperature was warm (Poore et al., 2023). Additionally, fossil records of the Phytocreneae from the Eocene of Australia suggest that they had spread widely by the middle Eocene (Rozefelds et al., 2021). Furthermore, Rozefelds et al. (2021) also suggested that “regional extinction/extirpation since the Eocene, likely driven by post-Eocene climatic cooling” has largely shaped the modern distribution of the Phytocreneae. However, it is not known when the Phytocreneae established their modern distribution in the Paleotropics, underscoring the importance of studying the group’s fossil record within it’s current geographic range.

Miquelia comprises ten extant species, primarily found in Southeast Asia and India (https://powo.science.kew.org/). The genus typically consists of woody climbers and features a distinctive endocarp surface characterized by a reticulum of prominent longitudinal and transverse ridges that define areolae, each surrounding one to several pits (Del Rio et al., 2020; Stull et al., 2020b). Recent phylogenetic analysis placed *Miquelia* as a sister to *Phytocrene* (Stull et al., 2015), a genus that likely originated from the Northern Hemisphere (Stull et al., 2011). In contrast to other fossil-rich genera in the clade, such as *Phytocrene*, *Pyrenacantha*, and *Palaeophytocrene* (e.g., Manchester, 1994; Stull et al., 2011, 2012, 2016, 2020b; Collinson et al., 2012; Poore et al., 2023), there is no documented fossil record of *Miquelia* to our current knowledge (Del Rio and De Franceschi, 2020a). Therefore, any fossil record of *Miquelia* would provide significant insights into the phytogeography and paleoecology of the genus as well as the evolutionary history of the Phytocreneae.

In this study, we report the first endocarp fossil record of *Miquelia*, namely *Miquelia yenbaiensis* N.B. Hung, J. Huang & S.F. Li sp. nov., originating from the late Miocene of northern Vietnam. We observed the morphological features of the fossil using a reflected light microscope and extensively compared them with those of modern and fossil endocarps of the Phytocreneae. Additionally, we discuss the phytogeography and paleoecology of *M. yenbaiensis*, which greatly extends our

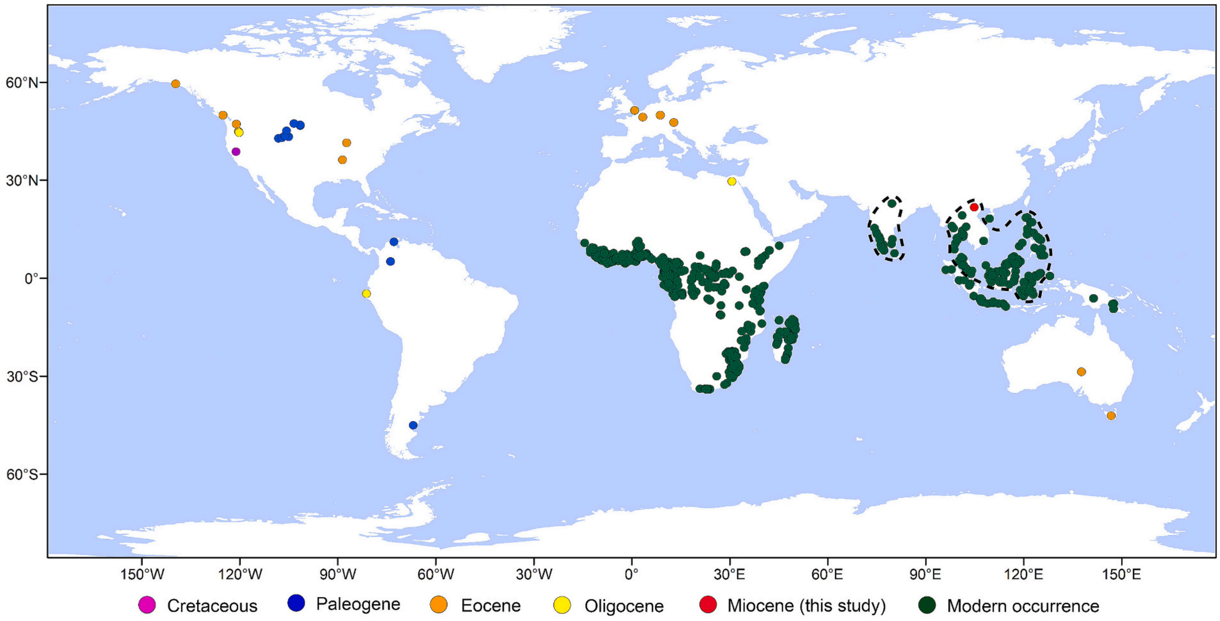

Fig. 1. Fossil and extant distribution of the Phytocreneae. Modern occurrences of the Phytocreneae were obtained from GBIF, while its fossil records were referenced from previously published works (e.g., Del Rio and De Franceschi, 2020a; Stull et al., 2020a; Rozefelds et al., 2021; Atkinson, 2022; Poore et al., 2023). The dashed lines indicate the modern distribution of *Miquelia*.

understanding and offers extensive perspectives on the evolutionary history, biogeography, and paleoecology of the Phytocreneae.

2. Material and methods

2.1. Geological setting

The fossil specimen was obtained from the fine-grained sandstones of the Co Phuc Formation, exposed in an inactive claystone mine in the Tuy Loc commune, located approximately 3 km northwest of Yen Bai City, Yen Bai Province, northern Vietnam (21°43’24.06” N, 104°51’5.43″ E, Figs. 1, 2). The Co Phuc Formation consists of lacustrine deposits characterized by fine-grained sandstones, siltstones, and claystone, lying conformably upon the coarse-grained sediments of breccia boulderstones and conglomerates of the Van Yen Formation (Tran and Trinh, 1975; Tong and Vu, 2011). These sedimentary successions are well-exposed around Yen Bai City, along both sides of the Red River valley, in the Yen Bai Basin, which is located at the distal part of the Red River fault zone separating the Indochina and South China blocks (Fig. 2).

The age of the Co Phuc Formation was assigned to the late Miocene based on a preliminary paleobotanical investigation (Tran and Trinh, 1975), supported by recent studies on lithology and sedimentary environment (Wysocka and Świerczewska, 2003, 2005, 2010), the evolutionary history of the Red River system (Hoang et al., 2009), and paleobotany (Aung et al., 2020; Nguyen et al., 2022, 2023, 2024). During our four field investigations (2020–2022), more than 300 plant megafossils were excavated from another outcrop in the Yen Bai Basin,

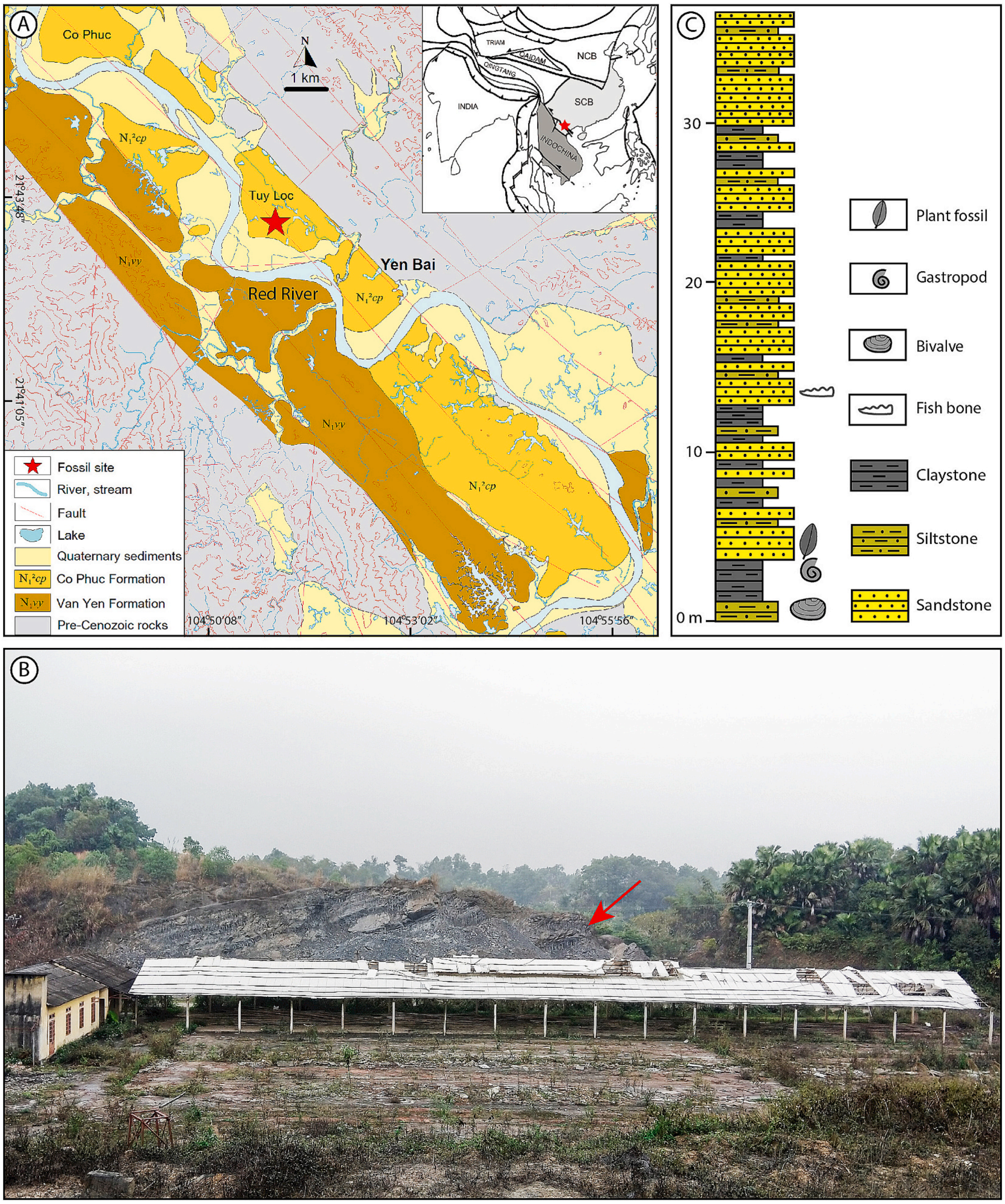

Fig. 2. Location and stratigraphy of the fossil site. A. Map showing the geology of the Yen Bai Basin and the location of the fossil site (adapted from Pham, 2010 and Nguyen et al., 2005). B. A photograph showing the exposure in an inactive claystone mine (the red arrow indicates the fossil-bearing layer). C. Stratigraphic column of the Co Phuc Formation at the fossil study site. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

about 6 km south of the current studied fossil site. These plant fossils represent various organs such as leaves, fruits, and stems (Nguyen et al., 2024). A preliminary biodiversity analysis shows that these fossils represent 40 morphotypes dominated by Fabaceae, Fagaceae, and Lauraceae, followed by Sapindaceae, Annonaceae, Euphorbiaceae, Anacardiaceae, Hernandiaceae, Malvaceae, and Betulaceae, indicative of a tropical environment (Nguyen et al., 2024).

2.2. Morphological observations

Only a single endocarp, preserved as compression in fine-grained sandstone, was collected and investigated in this study. The specimen, with the endocarp remnant attached, was initially examined under a reflected light microscope and photographed using a digital camera (Nikon D850) with a micro Nickkor 105-mm lens to capture its original preservation. The endocarp remnant was then carefully removed using a needle to reveal the outer surface of the endocarp. Meanwhile, the tiny fragments of the endocarp remnant were collected for observation under an SEM to examine the details of the inner endocarp, but no papilla were observed. The specimen, showing the impression of the endocarp, was observed and photographed again using the same microscope and digital camera. The measurements were performed on digital photographs using ImageJ software (https://imagej.nih.gov/ij/).

The fossil was morphologically compared with endocarps of both extant and fossil genera in the Phytocreneae described in the literature (e.g., Manchester, 1994; Stull et al., 2011, 2012, 2016, 2020b; Collinson et al., 2012; Del Rio et al., 2020; Rozefelds et al., 2021; Atkinson, 2022; Poore et al., 2023). We conducted a thorough examination of all available extant fruits in the genus *Miquelia* based on records obtained from the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/), the Royal Botanic Gardens, Kew (http://powo.science.kew.org/), and the PhytoImages (http://www.phytoimages.siu.edu/index.html). Voucher and additional information related to comparative material illustrated in this paper are available in Appendix A following the recommendation made by Del Rio (2023). Figures were made using the software Photoshop CS6 and Adobe Illustrator CS6. The distribution occurrences of extant *Miquelia*, as well as other genera of the Phytocreneae, were downloaded from GBIF. The climate range of extant *Miquelia* was calculated with the R package "Dismo," using the downloaded occurrence data and bioclimatic data from WorldClim (https://www.worldclim.org/).

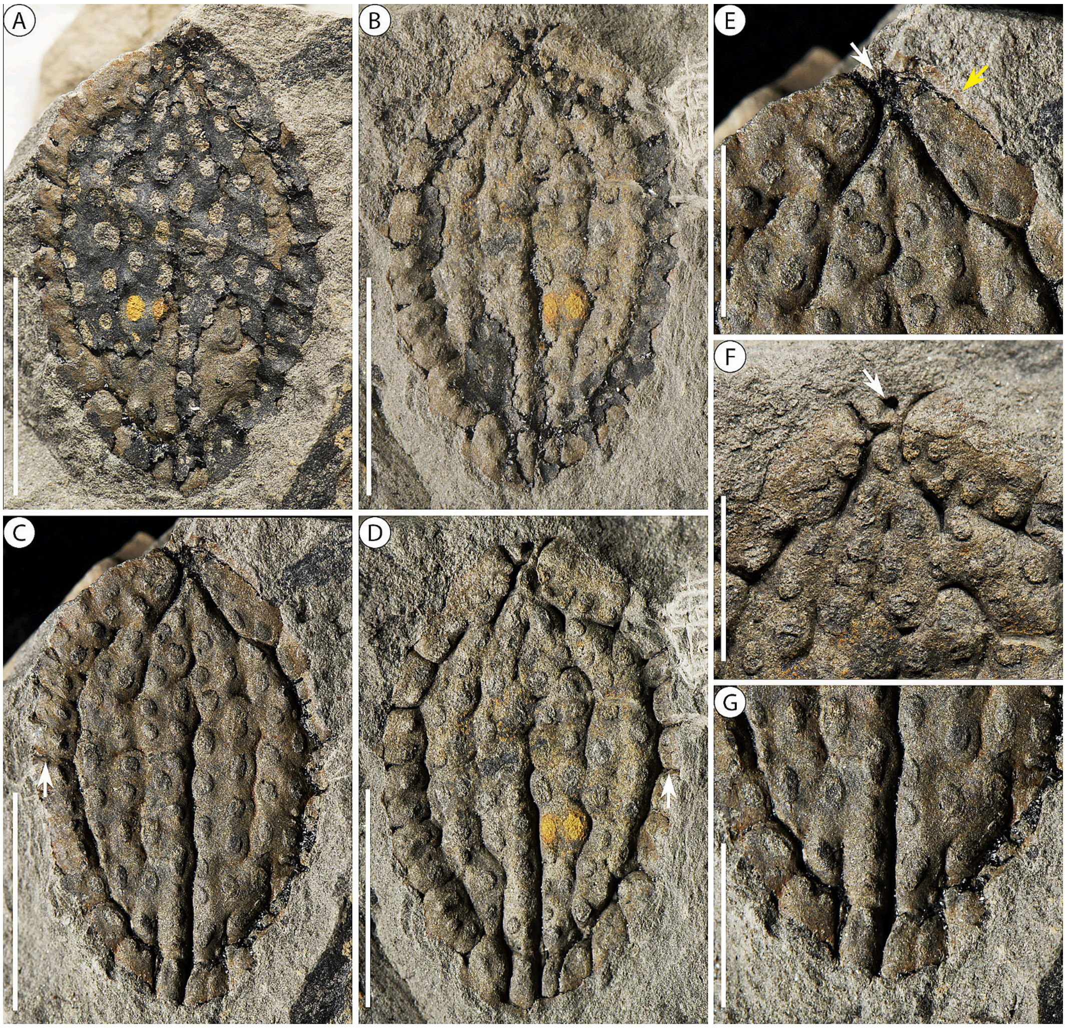

Fig. 3. Compression and impression of the endocarp of *Miquelia yenbaiensis* from the late Miocene of northern Vietnam (No. YB02–042). A, B. Compression of endocarp and its counterpart showing shape, ridges, and pits. C, D. Impressions of endocarp after removing the remnant of endocarp showing lateral view and opposite lateral view with circular and occasionally ovoid or elliptic pits, longitudinal ridges, and transverse ridges (arrow). E. Enlargement of apex showing the entrance of the primary vascular bundle (white arrow) and the keel (yellow arrow). F. Enlargement of apex showing the impression of a horn-like protrusion (arrow). G. Enlargement of base showing ridges and pits. Scale bars, A–D = 10 mm; E–G = 5 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3. Systematics

Order: Icacinales Tiegh. ex Reveal

Family: Icacinaceae Miers

Genus: ***Miquelia*** Meisn.

Species: *Miquelia yenbaiensis* N.B. Hung, J. Huang & S.F. Li sp. nov.

Etymology: The designation '*yenbaiensis*' indicates the location of the fossil specimen found in Yen Bai City, Yen Bai Province.

Locality: Tuy Loc commune, Yen Bai City, Yen Bai Province, northern Vietnam (21°43'24.06" N; 104°51'5.43″ E).

Holotype: YB02–042 (Fig. 3), designated here.

Stratigraphic horizon and age: Lower part of the Co Phuc Formation, late Miocene.

Repository: Centre for Earth Sciences, Vietnam National Museum of Nature, Vietnam Academy of Science and Technology, Hanoi.

Diagnosis: Endocarp bivalved, elliptic in face view, with a pitted and ridged outer surface. Apex slightly asymmetrical and base symmetrical. Ridges sharp, thin (ca. 0.1–0.5 mm in width), and reticulate, forming irregular areoles with five prominent longitudinal ridges. Pits circular, occasionally ovoid or elliptic, ca. 0.2–1.0 mm in diameter, longitudinally organized, 10–14 pits longitudinally, 8–10 pits transversally, and about 110–120 pits per face. A horn-like protrusion (probably a pair of horn-like protrusions) positioned centrically and subapically on the endocarp face.

Description: Endocarp bilaterally symmetrical, elliptical in lateral view, 21.9 mm in length, 13.6 mm in width, with a length to width ratio of 1.6:1 (Fig. 3A–D). A thin keel encircles the endocarp in the plane of symmetry (Fig. 3E). Apex slightly asymmetrical and rounded in lateral view (Fig. 3A–F), base symmetrical and rounded (Fig. 3A–D, G). The apex shows subapical entrance of the primary vascular bundle (Fig. 3E). The outer surface pitted and ridged (Fig. 3A–G). Ridges sharp, thin (ca. 0.1–0.5 mm in width), and reticulate, with five main longitudinal ridges (Fig. 3A–D); the median ridge stout and high at the base (ca. 0.5 mm in width and 1 mm in height), gradually becoming thinner and lower near the apex, running from the point of the base up to 4/5 of the endocarp's length (Fig. 3A–G); the two outermost lateral ridges running parallel with the keel and meeting at the apex, each connected with 9–10 transverses ridges enclosing one or two areoles (ended by the keel) (Fig. 3A–D); the two lateral ridges between the median ridge and the outermost lateral ridges connecting with the outermost lateral ridges at the apex, running parallel with the median ridge and reaching the keel at the base (Fig. 3A–D). Pits circular, occasionally ovoid or elliptic, 0.2–1.0 mm in diameter, and organized in longitudinal lines with two pits between two adjacent main longitudinal ridges, 10–14 pits longitudinally and 8–10 pits transversally, about 110–120 pits per face (Fig. 3A–D). Endocarp possesses a horn-like protrusion (probably a pair of horn-like protrusions) positioned centrically and subapically on the endocarp face (Fig. 3F).

4. Discussion

4.1. Morphological comparison

The fossil specimen from northern Vietnam presented here is characterized by having a bilateral symmetry, a slightly asymmetrical apex and symmetrical base, a keel surrounding the endocarp in the plane of symmetry, and a ridged and pitted surface. These features are consistent with typical endocarps of Icacinaceae (Del Rio et al., 2020). In addition, the pitted endocarp further supports its affinity with those of the Phytocreneae (Del Rio et al., 2020; Stull et al., 2020b) (Fig. 4) comprising

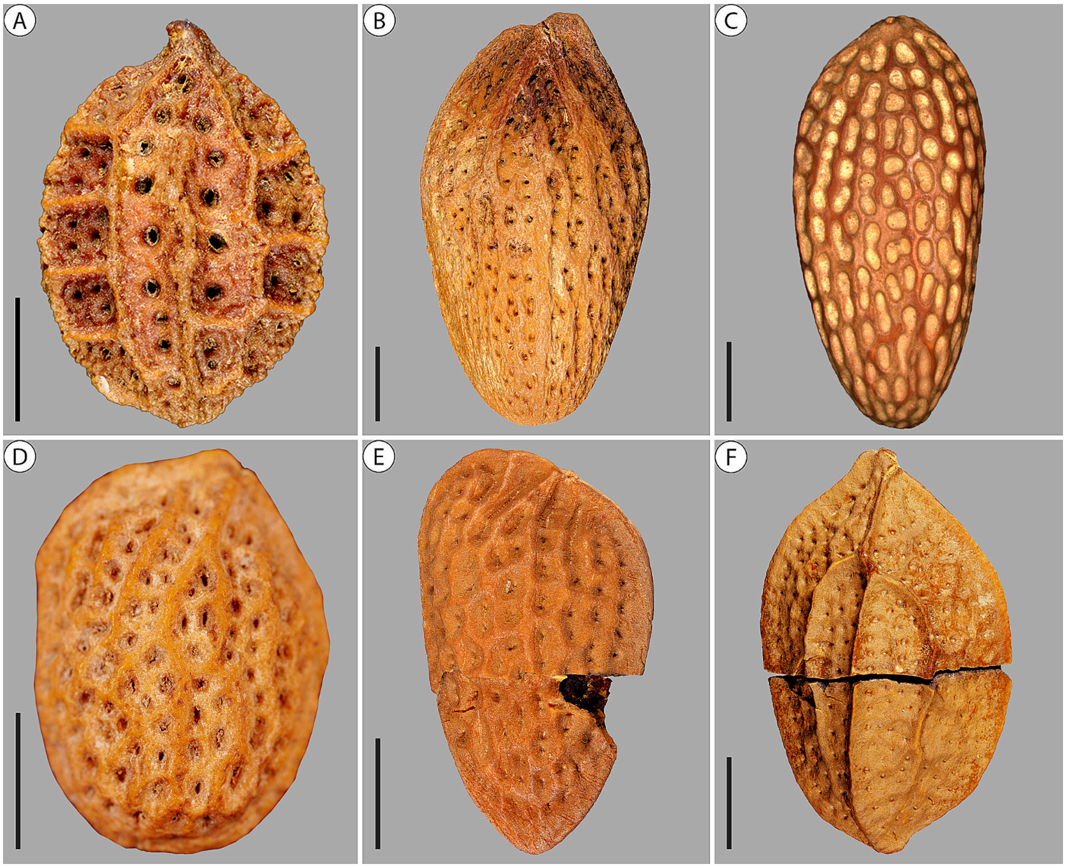

Fig. 4. Selected endocarps of Phytocreneae for morphological comparison with current fossil (adapted from Del Rio et al., 2020). A. *Miquelia caudata* King (Mohd, Shah & Sidek 1168). B. *Phytocrene hirsuta* Blume (O. Beccari HB.2497/98). C. *Phytocrene oblonga* Wall. (s. col. s.n.; P). D. *Pyrenacantha thomsoniana* (Bail.) Byng & Utteridge (M. Le Testu 1038). E. *Pyrenacantha soyauxii* (Engl.) Byng & Utteridge (R.P. Klaine 1469). F. *Stachyanthus zenkeri* Engl. (Carvalho 3626). Scale bars = 5 mm.

five extant genera and four fossil genera as previously mentioned. Moreover, our fossil shares the most similar morphological features to those of *Miquelia*, with typical longitudinally arranged pits, prominent longitudinal and transverse ridges, and a horn-like protrusion positioned centrically and subapically on the endocarp face (Figs. 4A, 5C, D). It can be readily distinguished from other genera in the Phytocreneae based on the pitted and ridged patterns of the endocarp.

Pyrenacantha represents the most diverse group within the Phytocreneae and varies in overall size, surface patterns (pit and ridge arrangement), and tubercle morphology (Stull et al., 2020b). They differ from the current fossil by having no ridge or randomly arranged or less longitudinally arranged pits, and rounded and thin or large ridges delimiting a reticulate pattern enclosing each pit in an areola (Del Rio et al., 2020) (Fig. 4D, E). In addition, the endocarps of *Pyrenacantha* have no horn-like protrusion on the outer surface (Del Rio et al., 2020). *Stachyanthus* features endocarps characterized by randomly arranged pits, a larger number of pits per face (153–184), smaller pit size (0.1–0.6 mm in diameter), and faintly apparent ridges in a diffuse pattern (Del Rio et al., 2020) (Fig. 4F). In contrast, the current fossil has longitudinally arranged pits with 110–120 pits per face, larger pit size (0.2–1.0 mm in diameter), and prominent ridges. The endocarps of *Phytocrene* exhibit dense ridges (e.g., *P. hirsuta* Blume and *P. oblonga* Wall.) (Fig. 4B, C) or sometimes limited to two lateral ridges only present in the apical third to half of the endocarp length (e.g., *P. macrophylla* (Blume) Blume, and *P. palmata* Wall.) (Del Rio et al., 2020). *Palaeophytocrene*, *Perforatocarpum*, *Stizocarya*, and *Manchesteria* have endocarps that differ from our fossil by having a smooth outer surface or faintly apparent ridges and randomly or less longitudinally arranged pits (e.g., Manchester, 1994; Stull et al., 2016; Rozefelds et al., 2021; Poore et al., 2023). Conversely, our fossil is characterized by longitudinally arranged pits and prominent longitudinal and transverse ridges.

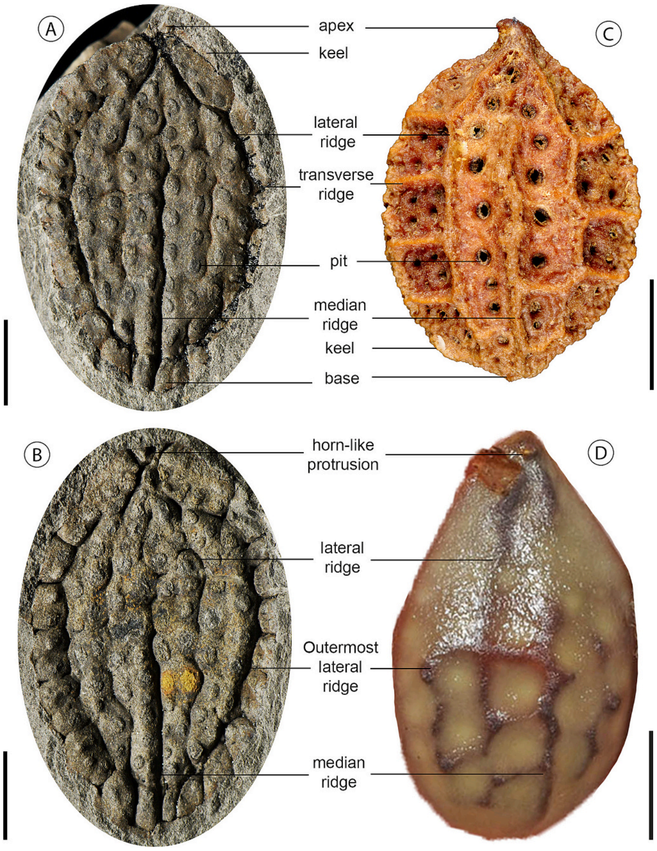

Fig. 5. Morphological comparison of endocarps of fossil and extant species of *Miquelia*. A, B. Impression of *M. yenbaiensis*. C. Lateral view of *M. caudata* (Mohd, Shah & Sidek 1168). D. Lateral view of *M. reticulata* Merr. (adapted from Pelser et al., 2011 onwards, DOL131136). Scale bars = 5 mm.

Collectively, the endocarps of *Miquelia* are often ornamented with well-arranged longitudinal pits and thin, sharp longitudinal and transverse ridges, bearing a strong morphological resemblance to those of our fossil (Figs. 4A, 5C, D). Specifically, the fossil endocarp of *Miquelia* also features a median longitudinal ridge running from the point of the base upwards but not reaching the point of the apex (as seen in *M. caudata* King; Fig. 5C), or five longitudinal ridges and a horn-like protrusion positioned centrically and subapically on the endocarp face (as seen in *M. reticulata* Merr.; Pelser et al., 2011, DOL131136; Fig. 5D). These diagnostic features directly associate our fossil with *Miquelia*. There are few documentations of extant *Miquelia* fruit in the literature (e.g., Stull et al., 2012, 2020b; Del Rio et al., 2020; Rozefelds et al., 2021) as well as available material in Herbaria. Detailed morphological comparison of our fossil with the four available endocarps of extant species of *Miquelia* indicates that our fossil can be distinguished from extant species of *Miquelia* by having two pits between two adjacent longitudinal ridges and a larger number of pits per endocarp face (110–120 compared to 12–48) (Table 1). Additionally, extant species of *Miquelia* have an acute apex, unlike our fossil, which has a rounded apex (Table 1). Therefore, we describe the endocarp record collected from the late Miocene of northern Vietnam as a new species, *Miquelia yenbaiensis*, providing the first fossil evidence of the genus.

4.2. Phytogeographical implications

Miquelia comprises ten extant species mainly distributed in Southeast Asia, with a disjunct distribution extending to India (https://powo.science.kew.org/). Of these, three modern species, *M. thorelii* Gagnep., *M. umbellata* Gagnep. and *M. paniculata* Gagnep., are documented in Vietnam (Pham, 1999). The presence of the *Miquelia* fossil in northern Vietnam indicates that this genus has been present in the region since at least the late Miocene. This suggests that the genus has been a part of the Southeast Asian flora since that time, offering an understanding of the historical biogeography and climatic conditions of the area during the Miocene.

Within the Phytocreneae, two extant genera, *Phytocrene* and *Pyrenacantha*, and four extinct genera, *Manchesteria*, *Palaeophytocrene*, *Perforatocarpum*, and *Stizocarya* are represented in the fossil record (e.g., Reid and Chandler, 1933; Chandler, 1961; Wolfe, 1977; Manchester, 1994; Rankin et al., 2008; Stull et al., 2011, 2012, 2016, 2020b; Collinson et al., 2012; Rozefelds et al., 2021; Atkinson, 2022; Poore et al., 2023). Three other extant genera, *Miquelia*, *Sarcostigma* and *Stachyanthus*, have not yet been documented in the fossil record. In addition, all fossil occurrences of the Phytocreneae are recovered from the Cretaceous and Paleogene of America, Europe, northern Africa, and southern Australia (see Table 1 in Del Rio and De Franceschi, 2020a; Stull et al., 2020b; Rozefelds et al., 2021; Atkinson, 2022; Poore et al., 2023) (Fig. 1). Our fossil discovery extends the historical range of the Phytocreneae as well as the family Icacinaceae to tropical Asia in the late Miocene, providing the youngest known fossil record of the family. This finding also represents the first fossil record of *Miquelia*, offering valuable insights into the migration patterns and information for understanding the evolutionary history of the Phytocreneae across different geographical regions.

Currently, Indo-Malesia, tropical Africa, and Madagascar are home to the Phytocreneae (Fig. 1) (Sleumer, 1971). However, their fossil records, which include numerous findings from the Paleocene and Eocene of America, Europe and Australia (e.g., Reid and Chandler, 1933; Manchester, 1994; Stull et al., 2011, 2012, 2016; Rozefelds et al., 2021; Poore et al., 2023) and the Oligocene of Egypt (Stull et al., 2020b), indicate a much broader historical distribution for the Phytocreneae (Fig. 1). The oldest known reliable fossil record of the clade, namely *Palaeophytocrene chicoensis* Atkinson, has been reported from the late Cretaceous of western North America (Atkinson, 2022), suggesting that

Table 1
Morphological comparison of endocarps of fossil and extant species of *Miquelia*.

Species	Endocarp length (mm)	Endocarp width (mm)	Endocarp shape	Endocarp apex	Endocarp base	Endocarp surface ornamentation	Endocarp ridging pattern	Shape of ridges	Number of vertical ridges	Pit pattern	Pit size (mm)	Pit number (in length)	Pit number (in width)	Number of pits per face	Reference
Miquelia yenbaiensis N.B.Hung, J. Huang & S.F. Li sp. nov.	21.9	13.6	Elliptical	Rounded	Rounded	Pitted, ridged	Reticulate	Sharp and thin	5	Circular, occasionally ovoid or elliptic and organized in longitudinal lines	0.2–1.0	10–14	8–10	110–120	This study
M. assamica (Griff.) Mast. ex B.D.Jacks.	13.5	8.9	Elliptical	Acute	Rounded	Pitted, ridged, rugose	Reticulate	Large, rounded	3	Circular and organized in longitudinal lines	1–2	3–4	3–4	ca. 12	Del Rio et al., 2020
M. caudata King	17	12.2	Elliptical	Acute	Rounded	Pitted, ridged	Reticulate	Sharp and thin	3	Circular and organized in longitudinal lines	0.4–1.2	8–9	ca. 6	ca. 44–48	Del Rio et al., 2020
M. celebica Blume	8	7.8	Ovoid	Acute	Rounded	Pitted, ridged	Reticulate	Rounded and thin to large	3	Circular and organized in longitudinal lines	0.4–0.9	3–5	4	ca. 17–19	Del Rio et al., 2020
M. reticulata Merr.	18.2	10.8	Ovoid	Acute	Rounded	Pitted, ridged	Reticulate	Rounded and thin to large	5	N/a	N/a	N/a	N/a	N/a	Pelser et al., 2011 onwards

the Phytocreneae might have originated in the Americas. Abundant fossil species of this tribe from the Paleocene and Eocene of North America and Europe (e.g., Reid and Chandler, 1933; Manchester, 1994; Rankin et al., 2008; Stull et al., 2011, 2012, 2016) indicate that the Phytocreneae initially diversified in America and expanded to Europe during the early-middle Eocene. This expansion may have involved migration across the North Atlantic Land Bridge (Tiffney, 1985) before the late Eocene climatic deterioration (Zachos et al., 2008). Meanwhile, endocarp fossils of *Manchesteria* from the Eocene of southern Australia (Rozefelds et al., 2021) provide additional evidence that the Phytocreneae were broadly distributed during the globally warm Eocene (Zachos et al., 2008). The occurrence of the Phytocreneae in Australia during the Eocene is hypothesized to mean that Antarctica functioned as a conduit for biotic exchange between South America and Australasia during the early Paleogene (Rozefelds et al., 2021; Poore et al., 2023) possibly before the onset of global cooling. Younger Phytocreneae are also known from the Oligocene of Peru (Stull et al., 2012) and Egypt (Stull et al., 2020b). The fossil record of the Phytocreneae from the early Oligocene of Egypt suggests the migration of the Phytocreneae from North America and/or Europe to Africa occurring between the middle Eocene and early Oligocene (Stull et al., 2020b) probably responding to the global cooling during the late Paleogene (Zachos et al., 2008). Here, we document *Miquelia* from the late Miocene of northern Vietnam, indicating that the Phytocreneae lineages migrated to tropical Asia and have been present in the tropical forests of Indo-Malesia at least since the late Miocene. Our fossil finding further supports the hypothesis that the range contraction of the Phytocreneae during the late Paleogene cooling and the modern geographic ranges of the tribe likely reflect trends of migration of thermophilic plants in response to Cenozoic global climate changes (Rozefelds et al., 2021; Poore et al., 2023). More fossil records will help to better understand the evolutionary history of the Phytocreneae in this region.

Molecular studies placed *Miquelia* as a sister group of *Phytocrene* (Stull et al., 2015). Fossil records of *Phytocrene* include two reliable endocarps, *P. punctilinearis* Collinson, Manchester et Wilde from the middle Eocene of Germany (Collinson et al., 2012) and *P. densipunctata* Stull, Moore et Manchester from the late Eocene of southeastern North America (Stull et al., 2011). This suggests that *Phytocrene* likely originated in the Northern Hemisphere at least during the Eocene. Although the fossil of *Miquelia* has not yet been discovered in high latitude regions, such as North America or Europe, this does not rule out a potential Northern Hemisphere origin for *Miquelia*, similar to *Phytocrene* (Stull et al., 2011). If this hypothesis is true, the presence of *M. yenbaiensis* in northern Vietnam, as well as the extant distribution of the genus, could indicate a floristic connection among America, Europe, and Indo-Malesia. This is supported by another fossil record of Icacinaceae, specifically *Iodes elliptica* C. Del Rio & J. Huang from the Oligocene of southern China (Del Rio et al., 2022), as well as the notable taxonomic similarities found in the early Cenozoic floras of North America (Manchester, 1999) and Europe (Reid and Chandler, 1933; Collinson et al., 2012) when compared to the modern flora of Indo-Malesia. Further paleobotanical work with the discovery of older records of *Miquelia* will be necessary to determine the biogeographical history of the genus in more detail.

4.3. Paleoecological implications

Modern species of *Miquelia* are typically woody climbers growing primarily in the tropical forests of Southeast Asia and India (Potgieter and Duno, 2016) (https://powo.science.kew.org/) (Fig. 1). They thrive in a variety of habitats, ranging from lowland rainforests to mountainous regions. These species are well-adapted to the wet tropical biome and often contribute to the forest undergrowth. The preference of the genus for humid, tropical environments suggests that regions where *Miquelia* fossils are found likely experienced similar climates in the past. As climbers, these species often rely on larger trees for support, creating a complex network of interactions within the forest canopy (Schnitzer and Bongers, 2002). The current endocarp fossil obtained from the lacustrine sediment in the Yen Bai Basin suggests a comparable growth environment for *M. yenbaiensis* in the Red River valley during the late Miocene. This contributes to our understanding of tropical forest evolution and stability in Southeast Asia.

The climatic tolerance inferred for extant *Miquelia* is consistent with a warm climate with a mean annual temperature of 21.8–26.6 °C, a minimum temperature of the coldest month of 9.8–21.0 °C, and a maximum temperature of the warmest month of 30.1–37.7 °C (Table 2). The mean annual precipitation is high, ranging from 1230.0 to 3502.5 mm (Table 2). It might be biased to utilize the climatic tolerance of modern plants to reconstruct past climate due to the existence of outliers and ambiguous resolution (Utescher et al., 2014); nevertheless, recent preliminary floristic and physiognomic analyses of the Yen Bai megafossil assemblage, collected from another outcrop in the same formation in the Yen Bai Basin, indicate that the Yen Bai flora likely occurred in tropical conditions (Nguyen et al., 2024). This is consistent with the climatic tolerance of extant *Miquelia*. Quantitative paleoclimate reconstruction for this fossil assemblage, using the Climate-Leaf Analysis Multivariate Program and the Coexistence Approach, indicates a modern-like warm and humid tropical monsoon climate with mean annual temperatures ranging from 18.5 °C to 23.0 °C and mean annual precipitations from 1183.1 mm to 2078.5 mm (Nguyen et al., 2024). In addition, the warm climatic preference of *M. yenbaiensis* is also evidenced by the historical distribution of the Phytocreneae lineages. Numerous fossil occurrences of the Phytocreneae from the Paleogene of North America and Europe, as documented by various studies (e.g., Reid and Chandler, 1933; Manchester, 1994; Rankin et al., 2008; Stull et al., 2011, 2012, 2016; Collinson et al., 2012), indicate their prevalence within mid-latitude forests during the early Paleogene warm period (Stull et al., 2012). Similarly, the younger occurrence of this tribe from the Oligocene of Egypt (Stull et al., 2020b) indicates the migration of this group to tropical regions of Africa during the middle-late Eocene or the early Oligocene. These provide evidence that fossil lineages of the Phytocreneae might preferentially grow in warm climatic conditions. Collectively, these data confirm our climatic assertions based on the modern occurrences of *Miquelia*.

The discovery of *M. yenbaiensis* provides valuable evidence for the long-term stability and continuity of tropical ecosystems in the region. As a liana species, *M. yenbaiensis* added structural complexity to the multi-stratified forest in the Yen Bai area during the late Miocene. For instance, abundant other fossil taxa have been discovered in the same fossil-bearing outcrop, comprising over 30 morphotypes such as *Bauhinia, Boehmeria, Dalbergia, Equisetum, Homalium, Lagerstroemia, Litsea, Machilus, Mangifera, Mezoneuron, Parashorea, Pongamia, Xylosma, Trigonostemon*, and *Typha* (Nguyen, 2024). These floristic components represent a mixed tropical evergreen and deciduous broadleaved lowland forest (Nguyen, 2024). Therefore, the occurrence of *M. yenbaiensis*, in combination with other plants, indicates a tropical forest ecosystem with multiple strata around the Yen Bai Basin during the late Miocene, similar to the modern vegetation structure in northern Vietnam nowadays.

MAT, mean annual temperature; WMT, temperature at the warmest month; CMT, temperature at the coldest month; MAP, mean annual precipitation; WMP, precipitation or the wettest month; DMP, precipitation at the driest month.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 2
Range of climatic parameters of extant *Miquelia*.

MAT (°C)	WMT (°C)	CMT (°C)	MAP (mm)	WMP (mm)	DMP (mm)
21.8–26.6	30.1–37.7	9.8–21.0	1230–3502.5	251.6–1232.5	3.5–151

Data availability

The data that has been used is confidential.

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Appendix A

Voucher information for specimens illustrated in this study with the following information: Genus name and specific epithet Authorship of the species name, voucher = collector's name + collection number, year of collection, country of collection, and number of the barcode, URL link of the page of the specimen on the official institution website

Miquelia caudata King., Mohd, Shah & Sidek 1168, 1965, Malaysia, L.2289517 (dir. Obs.), (https://data.biodiversitydata.nl/naturalis/specimen/L.2289517).

Miquelia reticulata Merr., Pelser P.B. & Barcelona, 2018, Philippines, DOL131136 (dig. Img.) (http://phytoimages.siu.edu/imgs/pelserpb/r/Icacinaceae_Miquelia_reticulata_131136.html).

Phytocrene hirsuta Blume., O. Beccari HB.2497/98, 1874, Sulawesi, L. 2,289,339 (dir. Obs.), (https://data.biodiversitydata.nl/naturalis/specimen/L.2289338).

Phytocrene oblonga Wall., sn, s.d, s.loc, P (dir. Obs.)

Pyrenacantha thomsoniana (Bail.) Byng & Utteridge., M. Le Testu 1038, 1907, Gabon, MNHN-P-P04494723 (dir. Obs.) (http://coldb.mnhn.fr/catalognumber/mnhn/p/p04494723).

Pyrenacantha soyauxii (Engl.) Byng & Utteridge., R.P. Klaine 1469, 1899, Gabon, MNHN-P-P04494736 (dir. Obs.) (http://coldb.mnhn.fr/catalognumber/mnhn/p/p04494736).

Stachyanthus zenkeri Engl., Carvalho 3626, 1988, Equatorial Guinea, MNHN-P-P05030978 (dir. Obs.), (http://coldb.mnhn.fr/catalognumber/mnhn/p/p05030978).

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