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Fossil water lily fruits with seeds *Nymphaea* subgenus *Lotos*, from the Oligocene of Armissan/Narbonne (France)

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Abstract

Based on specimens from a historical collection from the classical Oligocene locality Armissan (Southern France) fossil fruits of Nymphaeaceae are described that can be affiliated to the Nymphaeaceae genus *Nymphaea* subgenus *Lotos* with confidence. Such findings were first described in 1865 by Saporta from Armissan as an extinct genus, *Anoectomeria*. However, in the absence of preserved seeds, and due to a misinterpretation of the organisation of the fruits, the fossils could only be affiliated to Nymphaeaceae in general. The identification of the historical specimens with preserved seeds allows a new interpretation of such fossils and, hence their identification as fruits of the subgenus *Lotos*. Especially the characteristic mode of fruit dehiscence, which leads to typical stigmatic discs in extant as well as in fossil specimens, confirms this affiliation. In this study, the flowers/fruits described by Saporta (rhizome, leaves and isolated seeds were also included in his taxa) are revised to *Nymphaea* (subgenus *Lotos*) *brongniartii*. Comparable Paleogene fossils from other localities are also discussed. Based on *N. (L.) brongniartii* the minimal geological age of the subgenus *Lotos* can be determined as Late Oligocene. By interpretation of the comparable Paleogene fossils as belonging to subgenus *Lotos* the minimal geological age of this taxon would even be Middle Eocene. The Late Oligocene minimal geological age of *Lotos* is in agreement with phylogenetic trees based on molecular data and allows a better calibration of molecular phylogenetic trees of Nymphaeaceae.

Key words: *Anoectomeria*, Armissan, *Lotos*, Nymphaeaceae, Oligocene

Zusammenfassung

Nach Exemplaren einer historischen Aufsammlung von der klassischen Oligozän-Fundstelle Armissan (Südfrankreich) werden fossile Nymphaeaceen-Früchte mit Samen beschrieben, die eindeutig der rezenten Nymphaeaceen Gattung *Nymphaea* Untergattung *Lotos* zuzuordnen sind. Derartige Funde wurden zuerst 1865 von Saporta ebenfalls von Armissan als *Anoectomeria brongniartii*, *A. nana* und *A. media* beschrieben, und konnten aber wegen des Fehlens von Samen und der Fehldeutung des Fruchtaufbaus nur dieser Kunstgattung und allgemein den Nymphaeaceae zugeordnet werden. Die Auffindung der historischen Exemplare, die anders als die von Saporta beschriebenen, Samen aufweisen und die damit mögliche Neuinterpretation dieser fossilen Früchte erlaubt eine eindeutige Zuordnung zur Untergattung *Lotos*. Besonders die sehr charakteristische Fruchtdehiscenz, die rezent wie fossil zu isolierten Scheiben aus verwachsenen Griffelnarben führt, erlaubt nur diese Zuordnung. Die Blüten bzw. Früchte der Saporta-Taxa (Rhizome, Blätter und isolierte Samen wurden von ihm auch jeweils in die Taxa mit einbezogen) werden hier zu *Nymphaea* (subgenus *Lotos*) *brongniartii* revidiert. Vergleichbare paläogene Funde von anderen Lokalitäten werden diskutiert. Mit *Nymphaea (Lotos) brongniartii* kann das minimale geologische Alter der Untergattung *Lotos* als Oberoligozän bestimmt werden. Mit der Zuordnung vergleichbarer paläogener Funde zu *Lotos* wäre das minimale geologische Alter sogar Mitteleozän. Das Oberoligozäne minimale geologische Alter von *Lotos* ist mit den aus molekularen Daten erstellten Stammbäumen vereinbar und ermöglicht eine bessere Kalibrierung molekularer Stammbäume der Nymphaeaceae.

Schlüsselwörter: *Anoectomeria*, Armissan, *Lotos*, Nymphaeaceae, Oligozän

1. Introduction

The family of water lilies, Nymphaeaceae, is one of the basal angiosperm families (APG III, 2009). They include six modern genera which are globally

distributed. Together with Cabombaceae (two extant genera *Brasenia* and *Cabomba*) the Nymphaeaceae form the order Nymphaeales (Les et al. 1999). Assessments of the phylogeny of extant angiosperm taxa based on multiple genes indicate that the Nym-

phaeales represent a monophyletic group that diverged early from other angiosperms (Les et al. 1999; Borsch et al. 2008, 2011). The family Nymphaeaceae is composed of three subfamilies, i.e. the Nupharoideae, with the single genus *Nuphar*; Barclayoideae, with the single genus *Barclaya*; and Nymphaeoidae, which includes the four genera *Euryale*, *Nymphaea*, *Ondinea*, and *Victoria* (Les & Schneider 1995; Takhtajan 1997; Les et al. 1999). Flowers of Nymphaeaceae are characterized by their large size, high numbers of floral organs, flattened petal like stamens, and a syncarpous gynoeceum.

There is a wealth of old fossil evidence of the evolutionary history of Nymphaeaceae. For example, *Monetianthus mirus* is a fruit from the Lower Cretaceous of Portugal which is interpreted as a Nymphaeales (Friis et al. 2009). Nymphaeaceae leaves from the Cretaceous of Europe (Portugal) (*Nymphaeites choffatii*) were first described by Saporta (1894) and confirmed later (Coiffard et al. 2007). From the Lower Cretaceous of the Brazilian Crato Formation inflorescences with leaves (*Pluricarpellatia peltata*) were found to belong to Nymphaeaceae (Mohr et al. 2008). *Jaguariba wiersemana* is an Early Cretaceous Nymphaeaceae complete plant from Crato Formation (Coiffard et al. 2013). Takahashi et al. (2007) reported the seeds of *Symphaenale futabensis* (Nymphaeales) from the Late Cretaceous (early Santonian) Tamayama Formation (Futaba Group) of northeastern Honshu. From the Maastrichtian of Canada the pollen taxa *Zonosulcites scollardensis* and *Z. parvus* were affiliated to *Nymphaea zanzibarensis* (Muller 1981). Small Nymphaeaceae fruits from the Turonian (Upper Cretaceous) of New Jersey are related to extant *Victoria* and were named *Microvictoria svitkoana* (Gandolfo et al. 2004) although the affinities to Nymphaeaceae were later challenged because of fundamental differences in floral arrangement (Endress 2008).

Numerous occurrences of Nymphaeaceae, mostly represented by seeds, are known from the Cenozoic. Collinson (1980) reviewed the Cenozoic record of nymphaeaceous seeds from Britain. Other records include Caspary (1856, 1866, 1891), Lancucka-Srodniowa (1956), Kirchheimer (1957), Miki (1960), Szafer (1961), Chandler (1961, 1963), Dorofeev (1963a, 1963b 1970, 1971, 1972, 1973, 1974), Nikitin (1965, 1976), Mai (1988, 1995), Friis (1979, 1985, 2001), Negru (1972), and Velichkevich & Zastawniak (2003, 2008).

The oldest record for the genus *Nymphaea* is based on seeds from the Upper Eocene or Lower Oligocene of England *Nymphaea liminis* (Collinson 1980). Remarkably, there are Late Eocene seeds from Europe that must be assigned to the subgenus *Lotos* of the genus *Nymphaea* (Löhne 2006, 2008; Mai 1995).

Seeds of Nymphaeaceae were reported from the Middle Eocene Allenby Formation of Princeton, British Columbia (Cevallos-Ferriz et al. 1989) and a stig-

matic disc of *Nuphar* from the Eocene of Washington Republic (Wehr & Manchester 1996) and Eocene of Oregon (Meyer & Manchester 1997). Fossil nymphaeaceous fruits from the Eocene of Messel (Germany) comparable to extant *Barclaya* have been mentioned (Schaarschmidt 1988) and the corresponding seeds were illustrated and described as "Nymphaeales unnamed seeds" (Collinson et al. 2012). Dispersed pollen of Nymphaeaceae is known from the Middle Eocene of Stolzenbach, Germany (Hesse & Zetter 2005).

Although seeds of this family are relatively common in the fossil record, fruits and especially complete ones are among the rarest nymphaeaceous fossils. In this work we describe fossil Nymphaeaceae fruits with seeds from the Oligocene of France, which we demonstrate to be affiliated to the genus *Nymphaea* subgenus *Lotos*. Other occurrences of Cenozoic fruits of *Nymphaea* are also discussed.

2. Material and Methods

The fossils described in this paper are housed at the Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany, under accession numbers BSGP 1888 XI 80 (Fig. 1), 1888 XI 78, 1888 XI 79 (Fig. 2), 1888 XI 77 (Fig. 3), and the Muséum national d'Histoire Naturelle Paris (MNHN) under accession numbers 11100, 11113, 11098, and 12754.

For morphological interpretation we used the standard literature for Nymphaeaceae, including Caspary (1856, 1866, 1891), Conard (1905), Lotzy (1911), Goebel (1933), Troll (1933), Li (1955), Heslop-Harrison (1955), Corner (1976), Wiersema (1987), Moseley (1961, 1965, 1993), Schneider & Williamson (1993), Yamada et al. (2004), Schneider et al. (2003), Soltis et al. (2003). Material from the Herbarium Munich and the Botanical Garden Munich Nymphenburg was also used.

Abbreviations used in text and captions:

(BSPG) = Bayerische Staatsammlung für Paläontologie und Geologie München

(UI) = Geologisches Institut der Universität Innsbruck, Österreich

(M) = Botanische Staatsammlung München

(MNHN) = Muséum national d'Histoire Naturelle Paris

(NKMB) = Naturkunde Museum Berlin

3. Results

Order Nymphaeales Dumortier, 1829
Family Nymphaeaceae Salisbury, 1805

Genus *Nymphaea* Linnaeus, 1753
Section *Symphytopleura* Caspary, 1865/6
Subgenus *Lotos* Conard, 1905

Nymphaea brongniartii (Caspary, 1856) Saporta,
1865b emend.
(Fig. 4a, lectotype)

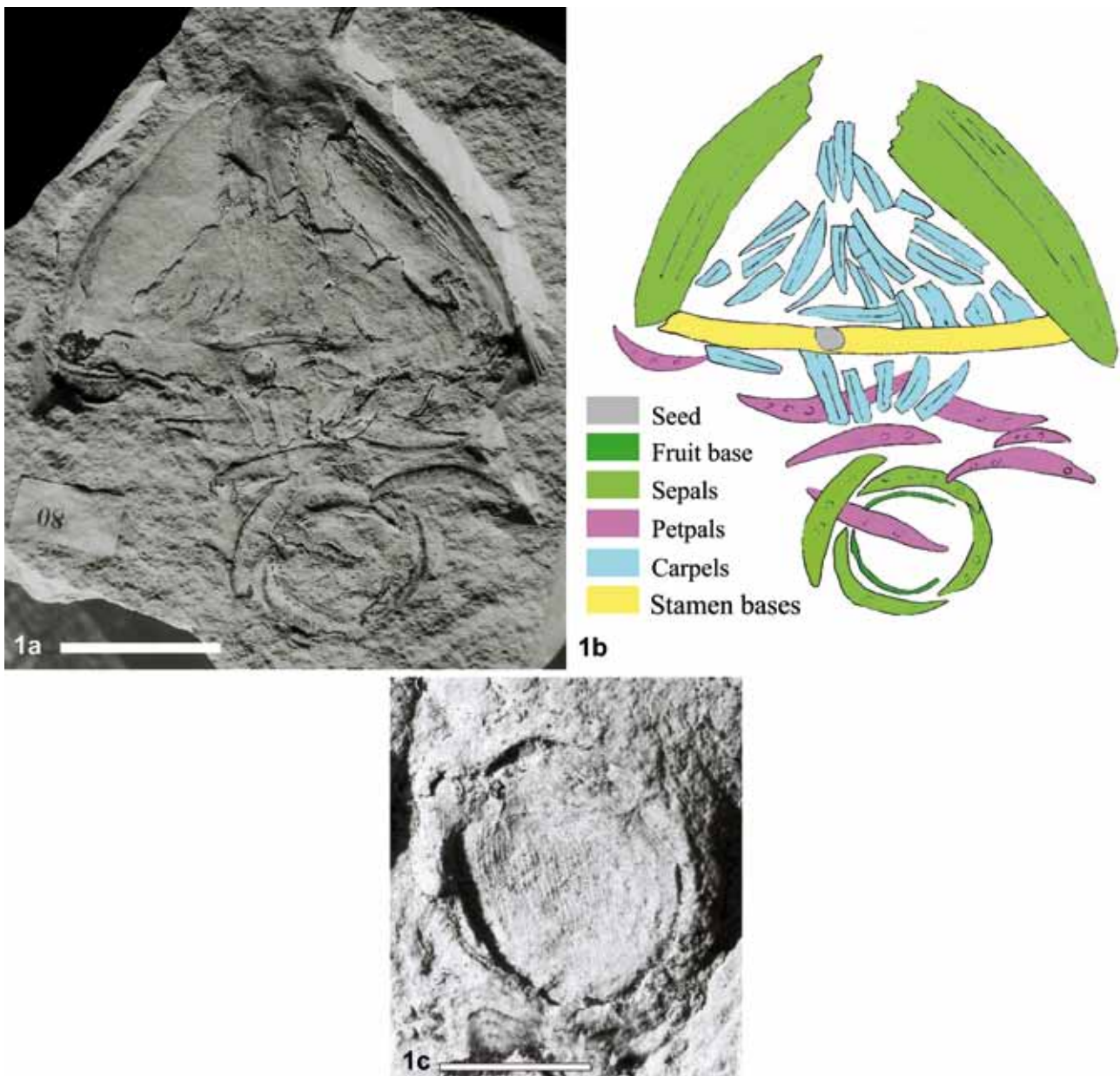


Figure 1: (a) *Nymphaea (Lotos) brongniartii*, dehiscent fossil fruit with seed from the Upper Oligocene of Armissan (BSGP 1888 XI 80); scale bar = 1 cm; (b) Diagrammatic representation of Fig. 1a; scale bar = 1 cm; (c) Detail showing seed; scale bar = 0.5 cm.

v 1849 *Nymphaea arethusae* Brongniart – pp. 84 & 119, 74, pl. 6, fig. 9, seed (NMHN Paris 3014), Armissan, Chattium.

1856 *Nymphaeites brongniartii* Caspary – pp. 203, 204, pl. 13, Armissan, Chattium.

1859 *Nymphaeites brongniartii* Caspary – Heer: Teil 3, pp. 195, pl. 155, fig. 20 a,b,c, seeds and rhizomes, Oron, Lausanne/Switzerland, Oligocene.

* v 1865b *Anoectomeria brongniartii* (Caspary, 1856) Saporta: Stigmata: pp. 161, 162, pl. 10, fig. 3, A, A', B, C, (NMHN Paris, 11100, 11113, 11098, 12754). Seeds: pp. 161–174, pl. 10, fig. 5, 5 A (NMHN, Paris, 11108.1, 11108.2)

* v cf. 1889 *Anoectomeria nana* Saporta: Stigma: pp. 13, 14, pl. 2, fig. 3 (NMHN 13960). Seeds (NMHN 16277, NMHN 14760, NMHN 12735), Saint-Jean-de-Garguier/ Manosque, Rupelium

* v 1891 *Anoectomeria media* Saporta: Stigma: pp. 15, 16, pl. 3, fig. 2 (NMHN, Paris, 12735), Bois-d'Asson/ Manosque (France), Rupelium

Locus typicus: Armissan/Narbonne (France), former owner of quarry Deveze and Cie (Zittel diaries, 1888, H. Mayr, personal commun. 2004).

Stratum typicum: Chattium, (Lavocat 1955; Schmidt-Kittler 1971; Nel 1987; Mai 1995). Saporta referred to the stratum as „couches á dalles“ (Zittel diaries, 1888, H. Mayr, personal commun. 2004; Doncieux 1903).

Lectotypus: NMHN, Paris 11100 (Fig. 4a; originally figured in Saporta 1865b: p. 161, pl. 10, fig 3 A), *hic designatus*

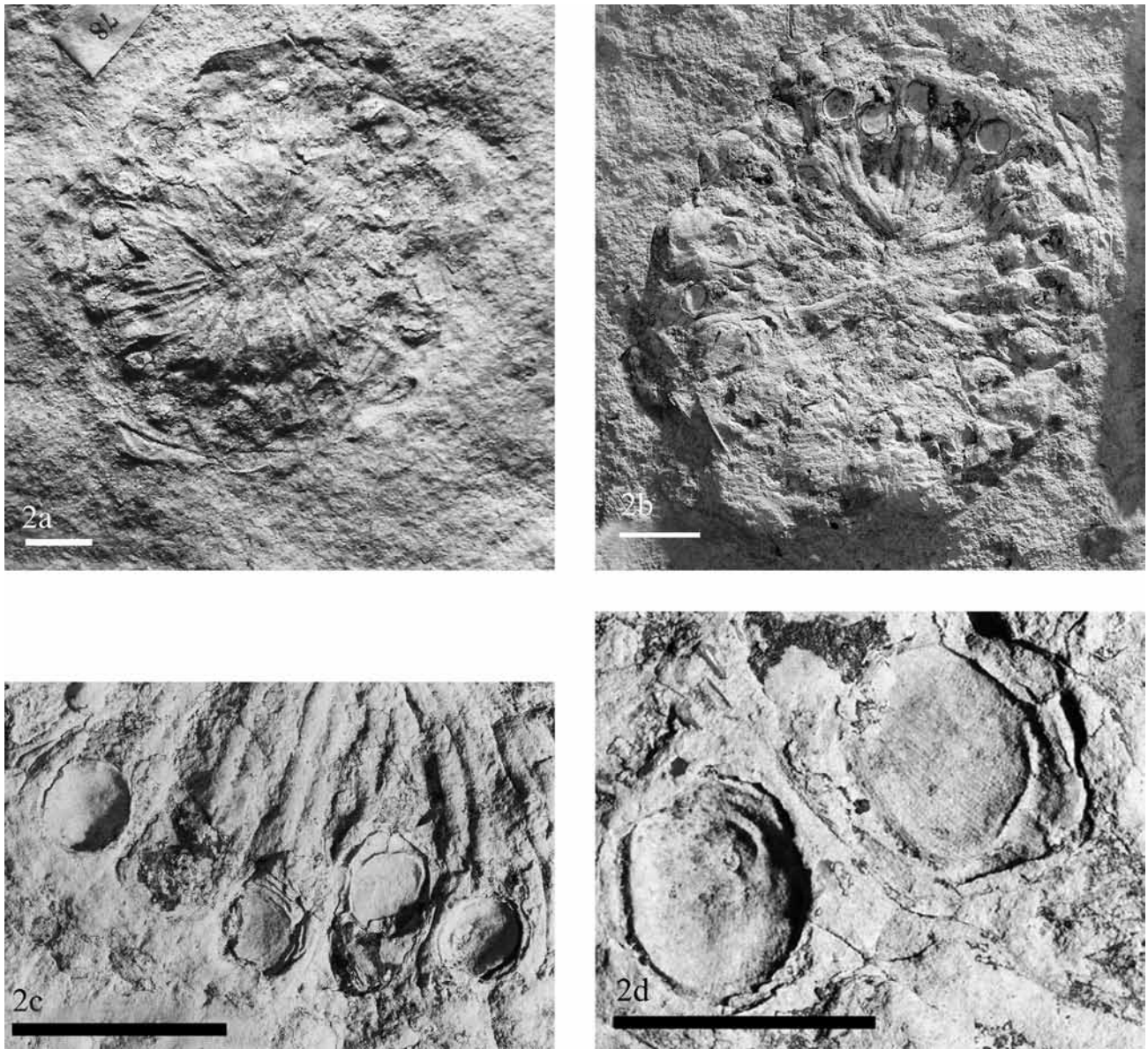


Figure 2: (a) *Nymphaea (Lotos) brongniartii*, dehiscent fossil fruit with stigmatic disc and many seeds from the Upper Oligocene of Armissan (BSGP 1888 XI 78 and 1888 XI 79); scale bar = 1 cm; (b) Counterpart of specimen illustrated in Fig. 2a; scale bar = 1 cm; (c) Detail showing seeds; scale bar = 1 cm; (d) Seed with operculum; scale bar = 0.5 cm.

Syntypes: NMHN, Paris 11113 (Fig. 4b), 11098 (Fig. 4c), and 12754 (Fig. 4d)

Paralectotypes: BSGP 1888 XI 80 (Fig. 1), 1888 XI 78, 1888 XI 79 (Fig. 2), and 1888 XI 77 (Fig. 3)

3.1 Description of new specimens

The base of the fruit (Fig. 1a) is preserved as a ring (receptacle) (Fig. 1b) directly surrounded by four 18 mm sickle-shaped sepal bases (scars of attachment sites) in tetramerous arrangement. In the centre of the ring remains of the peduncle with six major air canals are faintly recognizable. The sickle-shaped sepal bases each show a number of vascular bundles pos-

sibly with air channels. The largest and outermost sepal base at the lower right side likely represents the medial sepal of the flower. The 15–20 mm wide bases of the petals are also sickle-shaped, possess vascular bundles, and have been dislodged during dehiscence of the fruit: one is positioned at the fruit base, while the others are scattered. A fused band (ca. 80 mm long) composed of seven rows of approx. 180 sickle-shaped stamen scars, each ca. 3.5 mm long and 0.6 mm wide is preserved adjacent to the scattered petal bases. The successive rows of staminal bases are shifted against each other, indicating a spiral arrangement of stamens. A single oval seed (3.8 x 2.5 mm) is preserved on top of the band of stamen bases. The surface of this seed consists of a system of longitudinal ridges with putative

scars of hairs between the two poles formed by the operculum and chalaza. The ridges are overlain by a system of transverse striations (caused by undulating cell walls in extant *Nymphaea lotus*). A bulge representing the raphe is slightly visible at one side of the seed (left side in Fig. 1c). Scattered across the sediment surface are 25–30 carpels, each up to 22 mm long and lacking appendages (Fig. 1b). These carpels are linear and wedge-shaped and have a prominent longitudinal rib. The dehiscent carpels together with the band/ring of staminal bases represent the former stigmatic disc (indehiscent form visible in Fig. 2). Two sepals of 40 mm length are preserved (Fig. 1b) and show a strong longitudinal venation. Their bases are truncate.

The second specimen (Fig. 2a,b) represents a complete stigmatic disc (45 mm wide) viewed from the ventral side. In the centre an area (8 mm in diameter) occurs that represents the axis of the fruit. About 30 wedge-shaped stigmata or remains of carpels (up to 22 mm long) are radially arranged around the central axis. Each has a longitudinal groove in the positive sediment surface (Fig. 2a). The stigmata are connate in the central area of the stigmatic disc; at the outer area the stigmata are not fused. The outermost parts of the stigmatic disc/carpel remain contain seeds (seeds described in detail below). At one side the outermost ring of sickle-shaped staminal bases is partially preserved.

The third specimen (Fig. 3) represents another dehiscent fruit. From the base of the fruit a ring (receptacle) (Fig. 3b), with residue of organic material within, is preserved. Around this ring four sepal bases are arranged. Petal bases are preserved, some in their original position around the sepal bases, some scattered on the sediment plane. A band (68 mm long) composed of seven parallel rows of sickle-shaped bases of staminal bases is positioned in vicinity to the fruit base. Attached to this band are unidentifiable remains of tissue (probably staminal or petal remains) or mucilage from the fruit. Several operculi from seeds (1 mm in diameter) are scattered across the sediment plane (Fig. 3b). Between the base of the fruit and the band of staminal bases about 14 carpels (20–25 mm) are preserved. Close to one carpel a putative seed arillus is seen (identifiable by its surface structure).

The seeds (Fig. 2a–e) have a height of 3,8–4,1 mm and width of 2,5–3 mm. The anatropous seeds with an ovoid to elongate shape show apically a circular operculum. In the middle of the operculum is the micropyle which is formed by a ring of small teeth. Lateral to the micropyle the hilum is visible as a bulge. The circular operculum is slightly lifted. Outside the circular operculum paired stripes radiate all over the seed towards the other pole of the seed with the pointed chalaza. There are approximately 20–25 paired longitudinal stripes on the visible half of the seed. The border of the operculum is with less visible cells, next to this there is a lifted ring. Outside of this the radiating

longitudinal stripes become more prominent. Along one meridian from the operculum towards the chalaza there is a furrow which represents the raphe. On the raphe ridge the longitudinal stripes are less differentiated. The outer cells of the stripes have an undulating border and are arranged at about the same positions in parallel longitudinal stripes, resulting in an overall crosswise structure. The longitudinal cells are most prominent in their middle; towards the operculum and chalaza pole they become flat. On top of the longitudinal stripes, especially where the paired stripes meet at their ends, papillae are found. The specimens BSPG 1888 XI 78 and 1888 XI 79 show seeds with lost operculi. The cross section of a seed testa preserved in calcite analyzed by SEM shows two integuments (bitegmic), the inner one being thinner (5 µm) than the outer one (35 µm). On the outer integument papillae occur. Such papillae are the bases of hairs in extant *Nymphaea lotus* seeds, but hairs have not been observed and were not expected to be present in the fossil seeds. The outer integument is sclerenchymatous and has a rectangular columnar structure. A rarely preserved sack-shaped arillus (Fig. 3a,b) shows a reticulate structure.

3.2 Description by Saporta

The description of the fossil fruit genus *Anoectomeria brongniartii* (Caspary, 1856) by Saporta (1865b) was based on four specimens, but no holotype was designated. We have therefore designated NMHN, Paris 11100 (Saporta 1865b: pl. 10, fig 3A; refigured here in Fig. 4a) as the lectotype. Other specimens included in Saporta's contribution include NMHN, Paris 11113 (Saporta 1865b: pl. 10, fig 3B; this paper: Fig 4b), 11098 (Saporta 1865b: pl. 10, fig 3C; this paper: Fig. 4c), and 12754 (Saporta 1865b: pl. 10, fig. B'; this paper: Fig. 4d).

Saporta (1865b) gives a detailed description of the fruits, and affiliates them to *Nymphaeites brongniartii*, a taxon introduced by Caspary (1856) for rhizomes from Armissan/Narbonne (France), and also refers to isolated seeds (NMHN, Paris 3014) and rhizomes from Armissan described by Brongniart in 1849 as *Nymphaea arethusae* Brongniart, 1849. However, *Nymphaea arethusae* does not only refer to the specimens from Armissan, but also to material from Longjumeau. Grambast (1962) later re-described the fossils from Longjumeau as *Nymphaea arethusae* (Brongniart, 1822a; Brongniart, 1822b, 1828), and separated them from the fossils from Armissan. Saporta also mentions the description of seeds and rhizomes by Heer (1859) from the Oligocene of Oron, Lausanne/Switzerland as *Nymphaeites brongniartii* Caspary, 1856.

In Saporta's interpretation the fruit is a dehiscent capsule constructed of ellipsoid components. Based on this interpretation he established the new genus *Anoectomeria* for such fossil fruits. Based on

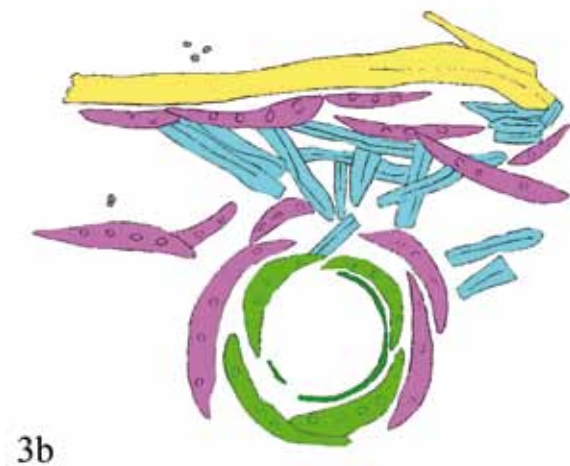
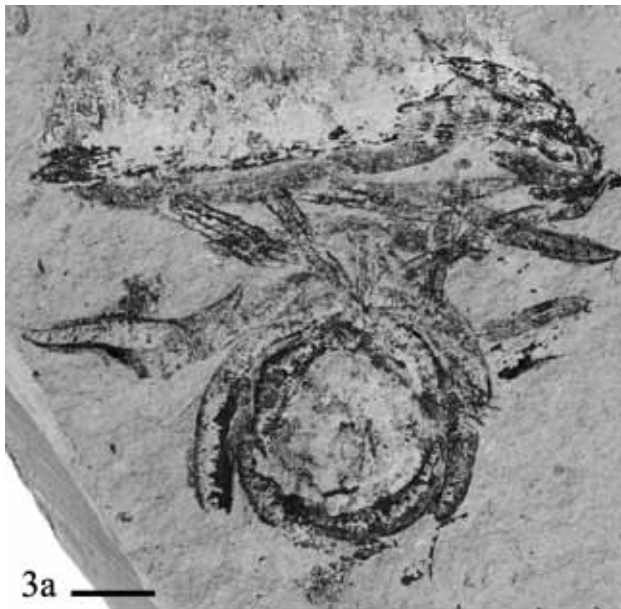


Figure 3: (a) *Nymphaea (Lotos) brongniartii*, dehiscent fossil fruit with seed operculi from the Upper Oligocene of Armissan (BSGP 1888 XI 77); scale bar = 1 cm; (b) Identification of parts (see Fig. 1b for legend); scale bar = 1 cm.

associated seeds (*Nymphaea arethusae* Brongniart, 1849), which do not occur within his fossil fruits, but which come from the same sediments as the fruits, he assigned the genus to the Nymphaeaceae. Many later authors have criticised this interpretation and the new genus *Anoectomeria*, regarding the fossils as belonging to *Nymphaea* (Schimper 1874; Fritel 1927; Kirchheimer 1957; Grambast 1962; Collinson 1980; Mai 1988; Borsch 2000; Borsch et al. 2008; Dorofeev 1974). However, none of these latter scholars re-described the fossils. What was interpreted by Saporta as ellipsoidal parts of the fruit with seeds is interpreted here (and by other authors) as bases of sepals and petals with air channels.

In 1888, Zittel acquired a collection from Armissan for the Bayerische Staatssammlung für Paläontologie und Geologie in Munich, Germany. This collection contains several interesting specimens of water lily reproductive organs, showing characteri-

stic seeds within *Nymphaea brongniartii* fruits. These specimens now allow for a reinterpretation of the fossils as fruits of *Nymphaea* subgenus *Lotos*.

3.3 Emendation of *Nymphaea brongniartii*

The diagnosis and emendation rely on Saporta's specimens of *Anoectomeria brongniartii* (Caspary, 1856) Saporta, 1865b, *A. nana* Saporta, 1889 and *A. media* Saporta, 1891 (both viewed as synonyms), as well as the specimens from the Munich collection with seeds preserved *in situ* (Figs 1–3).

Emended Diagnosis: Herbaceous, pedunculus with 5–7 major air channels; dome shaped floral base, whorled-trimerous; 4 sepals (evident by scars), sepal venation evident; maximal 12 petals (number evident by scars, only single petals preserved); transition from petals to stamina with a gap, numerous stamens (> 100), sickle-shape bases of stamens arranged in seven concentric fused rows, base of stamens petaloid, stamens apical tapering and not slit; 30–32 carpels, carpels linear and with longitudinal furrow, placentation laminar-diffuse, ascidiate, fused for at least 50% forming a stigmatic disc; seeds anatropous, more than one seed per carpel, carpel consisting mainly of stigma, continuous stigmatic surface, carpellary appendages not recognizable; fruit fleshy, aril present, seed shape ovoid, testa of the seeds with longitudinal ridges and putative scars of hairs, testa cells regular and with digitate cell walls, operculum present and cup-shaped, hilum in close vicinity to operculum, raphe present.

3.4 Reconstruction of *Nymphaeae brongniartii*

The swimming flower is alternate to whorled (helicocyclic) in its organization. Five whorls can be recognized, representing sepals (one whorl), petals (two whorls), stamens (one whorl, separated from the stamens whorl by a gap along the flower axis) and carpels (one whorl). There are four sepals and approximately twelve petals. In the opened flower petals and sepals are oriented more or less perpendicular to the floral axis, thus producing a flower with a diameter of 6–8 cm. Like in extant flowers the thecae of the stamens was positioned above the pistil. Like in extant taxa such as *Nymphaea (Lotos) lotus* var. *lotus* L. (Fig. 5a,b) dehiscence led to the separation of a ring formed by adhering stamen bases to which stamens are often still attached.

4. Discussion

4.1 Systematic affiliation

The presence of air channels in the peduncle is

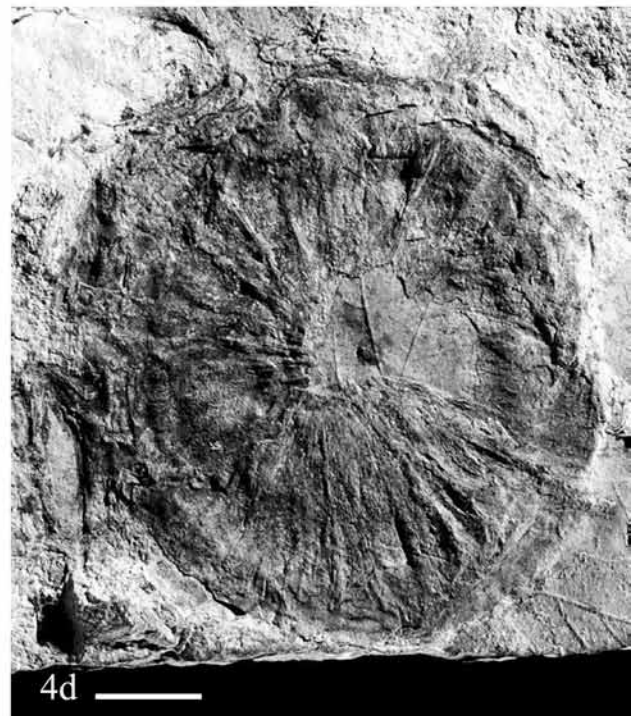
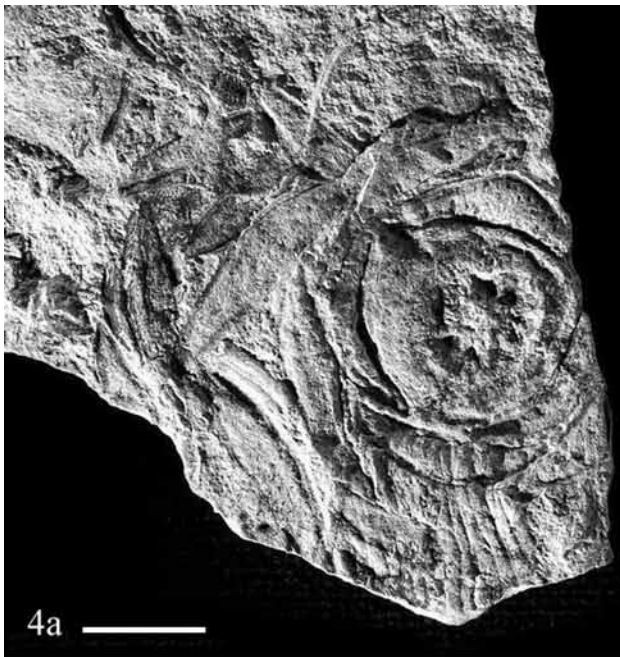


Figure 4: (a–d) Specimens of *Nymphaea (Lotos) brongniartii*; (a) Lectotype (NMHN, Paris 11100) and (b–d) syntypes from Armissan (Aude), Narbonne (France), Chattium; formerly *Anoectomeria brongniartii* (Caspary, 1856) Saporta, 1865; scale bars = 1 cm.

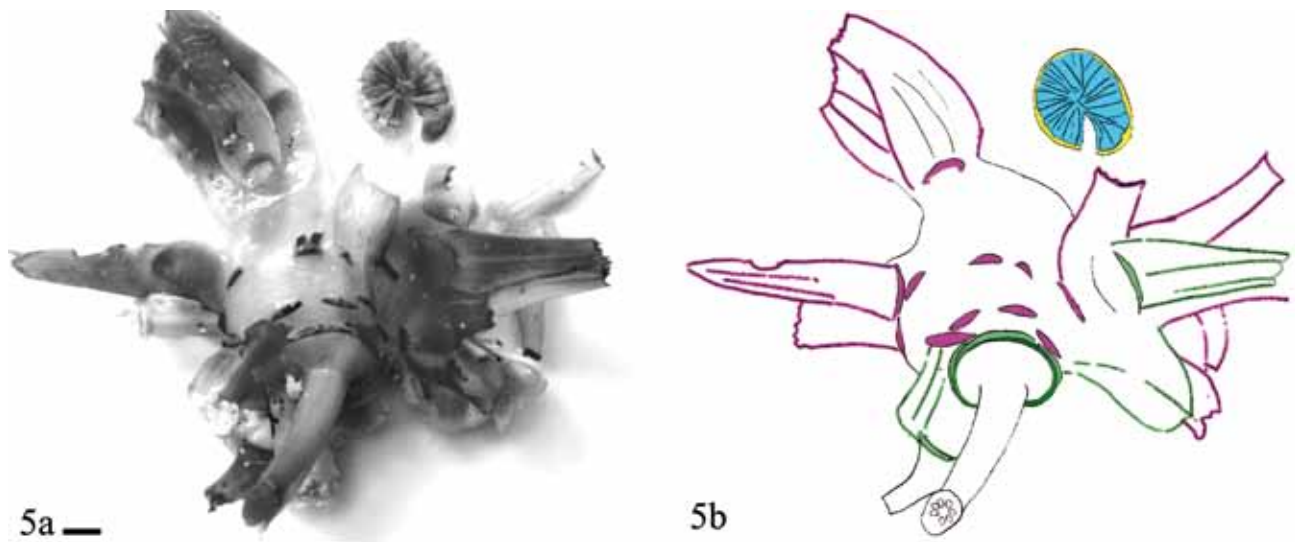


Figure 5: (a) Extant dehisced fruit of *Nymphaea (Lotos) lotus* var. *lotus* from the Botanischer Garten München Nymphenburg; (b) Line drawing of the fruit in Fig. 5a; scale bars = 1 cm.

characteristic of water plants like Nymphaeaceae (Wiersema 1987). A number of four sepals in hypogynous position is characteristic for the genus *Nymphaea* (Ito 1987). Among Nymphaeaceae seeds showing an irregular dehiscence during germination around the operculum is a characteristic of the genus *Nymphaea* (Weberbauer 1894; Dorofeev 1974). Reinvestigation of all morphological characters (according to Borsch et al. 2008) also observable in fossils confirmed the expected apomorphies for the *Nymphaea* genus group comprising *Victoria*, *Euryale*, *Brachyceras*, *Anecephya*, *Lotos*, *Hydrocallis*. These features include: “arillus present”, “perianth organ number 15–32”, and “dome-shaped floral base distinctly exceeding the carpels”. “Testa with hairs” is an apomorphy for the subgenera *Lotos*, *Hydrocallis*, *Brachyceras*, and *Anecephya*. Furthermore, almost complete fusion of the carpels in the fossils indicates that the fossil fruits belong to *Symphytoleura* (eusyncarpous, fused more than 50%: *Lotos*, *Hydrocallis*), and not to *Leptopleura* (eusyncarpous, but fused less than 50%: *Brachyceras*, *Anecephya*). This is also supported by presence of the apomorphic character “linear shape of carpellary appendages” in subgenus *Lotos*. Conversely, *Hydrocallis* shows “strongly clavate carpellary appendages”. A transition from petals to stamens with a gap is typical for the subgenera *Lotos* and *Anecephya* (Conard 1905; Tuzson 1909). In addition, the presence of five to seven major air channels in the peduncle, the seed surface structure, and the venation of sepals are also characteristics of subgenus *Lotos*, but not *Hydrocallis* (Wiersema 1987). A ring-shaped receptacle is a mechanically supporting structure that occurs in all taxa of *Nymphaea* subgenus *Lotos* that produce flowers rising above the water level (Conard 1905). An apomorphy and a most characteristic trait of flowers of the subgenus *Lotos* is a stigmatic disc formed by 30–32 carpels that are fused at least for



Figure 6: *Nymphaeites saxonica* Friedrich from the Upper Eocene of Bornstedt (Germany); NKMB; scale bar = 1 cm.

half of their length (Borsch et al. 2008). Consequently, all the fossil nymphaeaceous fructifications can be assigned to subgenus *Lotos* with confidence.

4.2 Geological age of *Nymphaea* subgenus *Lotos*

The specimens of *Nymphaeae brongniartii* from the BSPG Munich collection that formed the basis for

the emendation of *Nymphaea* subgenus *Lotos* (see above) represent the best preserved fruits and contain also seeds available to date. The fossils come from the Upper Oligocene (28.4–23.0 Myr, Gradstein et al. 2004) of Armissan (Basin of Narbonne), France. The specimens have mainly been collected from the bituminous limestone “La Clape”, which represents a freshwater deposit. The fine-grained sediment allows a good preservation of delicate structures of plants. The sediments have been dated as Late Oligocene based on mammal (*Anthracotheium hippoideum* Nolet Urne, *Pseudosciurus suevicum* Lavocat), reptile (*Lazarussuchus inexpectatus* Hecht) and insect (*Sapho armissani* Nel) fossils (Lavocat 1955; Schmidt-Kittler 1971; Hecht 1992; Ducreux 1985; Nel 1987; Mai 1995).

From other localities nymphaeaceous fruits are known that also undoubtedly belong to the subgenus *Lotos*. Although preservation is in some cases not optimal, these fruits are all characterized by the presence of a receptacle consisting of fused linear carpels with longitudinal furrows surrounded by sickle-shaped bases of stamens arranged in concentric fused rows. The oldest fruits showing this suite of characters are *Nymphaeites palaeolobioides* (Engelhardt) Kirchheimer from the Middle Eocene of Messel (Engelhardt 1922; Kirchheimer 1957) and *Nymphaeites saxonica* Friedrich from the Upper Eocene of Bornstedt (both Germany) (Friedrich 1883; Kirchheimer 1957) (Fig. 6). *Nymphaea polyrrhiza* (Saporta, 1865a) from the Oligocene of Saint Zacherie (France) seems to belong to genus *Nymphaea* but not to subgenus *Lotos* because a stigmatic disc is lacking. Putative fossil members of subgenus *Lotos* include *Nymphaea haeringiana* (Unger) Butzmann, Fischer

et Rieber, 2009 (formerly *Palaeolobium haeringianum*) from Bad Häring, Duxer Köpfl (both Austria) and Socka (Slovenia) (Unger 1851), and *Nymphaea brongniartii* (formerly *Anoectomeria media* and *A. nana*, see above) from Manosque (Ducreux et al. 1985) (Fig. 7a,b). In conclusion, the subgenus *Lotos* has a minimal geological age of Oligocene based on the evidence presented above, but might even be Middle Eocene in age.

Compelling fossil evidence for the occurrence of members of *Nymphaea* subgenus *Lotos* cannot be found among isolated fossil seed occurrences. Seeds of the genus *Nymphaea*, including those of subgenus *Lotos*, are characterized by undulating epidermal cell walls and by the organisation of the operculum with micropyle and hilum (Cevallos-Feriz and Stockey 1989: fig. 17). Seeds displaying this set of characters have been discovered from many fossil localities, and have been described as *Palaeonymphaea* (Eocene, Chandler 1961), *Dusembaya* (Oligocene, Dorofeev 1973), *Sabrenia* (Oligocene, Collinson 1980), *Allenbya collinsonae* (Eocene, Cevallos-Feriz and Stockey 1989), *Nymphaea liminis* (Eocene, Collinson 1980) and simply ‘nymphaeaceous seeds’ (Eocene of Messel, Collinson et al. 2012). However, similar seeds occur and are produced in fruits of a number of extant Nymphaeaceae (Weberbauer 1894; Collinson 1980), and thus do not allow for positive identification of *Nymphaea* subgenus *Lotos* in the fossil record.

4.3 Correlation with molecular phylogenetic analysis

Assignment of fossil nymphaeaceous fruits con-

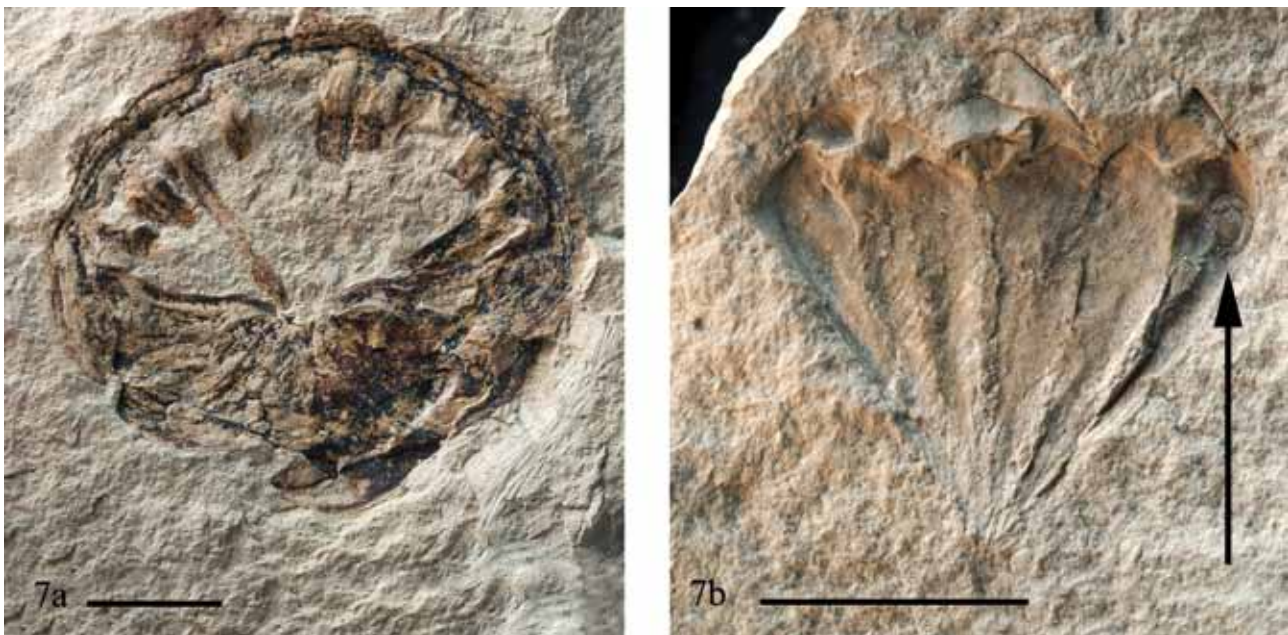


Figure 7: (a&b) *Nymphaea (Lotos) brongniartii*; (a) specimen formerly known as *Anoectomeria media* Saporta (NMHN, Paris 12735, Bois-d’Asson, Manosque, France, Rupelium) and (b) specimen formerly known as *Anoectomeria nana* Saporta (NMHN, Paris 16277, Saint-Jean-de-Garguier/ Manosque, France, Rupelium); a seed preserved in one carpel is also visible; scale bars = 1 cm.

taining seeds from well-dated localities to *Nymphaea* and, more specifically, to the subgenus *Lotos* allows correlation of paleontological data with the Nymphaeaceae phylogenetic tree based on morphological characters and its dating of divergence times by chloroplast DNA sequence analysis (Borsch et al. 2008, 2011; Löhne et al. 2006, 2008). The Eocene *Nymphaea saxonica* and the Early Oligocene *Nymphaeae brongniartii* show almost completely fused carpels and carpellary appendages of linear shape, and thus can be recognized as belonging to the subgenus *Lotos*. As a result, the origin of subgenus *Lotos* and its divergence from *Hydrocallis* (strongly clavate carpellary appendages) (divergence point “10”, Löhne et al. 2008) and, in consequence, the previous divergences within the genus *Nymphaea* (divergence points “5”, “6”, and “8”) must be dated back to the Late Eocene (approx. 40 myr). This is within the given time span for the basal divergence of the genus *Nymphaea* at 25,4 ± 14,3 myr (point “5”), but much older than the calculated divergence time for subgenus *Lotos* at 11,3 ± 7,8 myr (Miocene to Pliocene). Similar results were obtained by Yoo et al. (2005) and Biswal et al. (2012).

5. Conclusions

Well preserved fossil nymphaeaceous fruits from a historical collection from the Upper Oligocene of Armissan, France, have been recognized as belonging to *Nymphaea* subgenus *Lotos*. Moreover, other fossil nymphaeaceous fruits, previously assigned to *Anoectomeria brongniartii*, *A. nana*, and *A. media*, have been revised and transferred to *Nymphaea (Lotos) brongniartii*. Based on the fossils, a minimal geological age of Oligocene is proposed for the subgenus *Lotos*. The clade formed by the palaeotropical/neotropical sister-subgenera *Lotos* and *Hydrocallis* is defined by morphological characteristics and is strongly supported by molecular phylogenetic analyses (Löhne et al. 2008). The fossil fruits described in this study come from a palaeotropical European locality and are clearly identifiable as subgenus *Lotos*. The Oligocene age of the fossils falls within the expected time interval for the origin of this clade. This identification is in good agreement with the extant occurrences of subgenus *Lotos* in Europe, Asia and Africa, and of subgenus *Hydrocallis* in South America.

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