Paläont. Z.	55	3/4	185–190	Stuttgart, Dezember 1981

Euodia costata (CHANDLER) TIFFNEY, (Rutaceae) from the Eocene of Southern England

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With 4 figures in the text

Kurzfassung: Samen von *Phellodendron costatum* CHANDLER aus eozänen Sedimenten von Hordle, Hants (Süd-England) werden mit solchen der Gattung *Euodia* FORSTER in Verbindung gebracht und die Art neu kombiniert (beide Gattungen gehören zu den Rutaceen). Rezente *Euodia*-Arten finden sich in tropisch bis warm-temperierten Gebieten von China und Indo-Malesian, südwärts bis Australien und westwärts bis Madagaskar.

Euodia costata ist eine eigenständige fossile Art, ähnelt aber stark den sommer- und immergrünen Formen der sog. »Nördlichen Gruppe« der Gattung (China, Japan, Indien) mit meist glatten bis leicht retikulaten Samen. Eine sichere fossile Art der Gattung wurde aus dem Oligozän des Brandon Lignite (Vermont, USA) beschrieben – *Euodia lignita* TIFFNEY, während *Euodia nitida* (NIKITIN MAI) (West-Sibirien und DDR) als problematisch angesehen wird. Die Verbreitung der fossilen Arten von *Euodia* stützt die WOLFEsche Hypothese eines floristischen Austausches über den Nord-Atlantik hinweg zur Zeit des Palaeogen.

Abstract: Seeds describe as *Phellodendron costatum* by CHANDLER from Eocene sediments at Hordle, Hants, southern England are reassigned to *Euodia*, also in the Rutaceae.

I. Introduction

In her 1925–1926 publication on the Upper Eocene flora of Hordle, Hants, CHANDLER described a new species of *Phellodendron* RUPRECHT (Rutaceae), *P. costatum*. Subsequent work by the same author (CHANDLER, 1961a, 1961b, 1962, 1963) revealed that the species was present in four other floras, and that its morphology was consistent over a range of about 13 million years (from latest Paleocene through latest Eocene). Doubts were voiced as to its identity, however. KIRCHHEIMER (1957) suggested that the seed was improperly assigned and that it belonged to the Toddalieae within the Rutaceae, while TRALAU (1963) noted that its morphology was at odds with that characteristic of the seeds of *Phellodendron*. The present author had the opportunity to examine both the published accounts of fossil seeds of the Rutaceae as well as seeds of living representatives of all the genera of the family in the process of identifying rutaceous seeds from the Brandon Lignite (TIFFNEY, 1980a). As a result of this survey it became clear that the earlier suspicions were well grounded, and that the fossils described as *Phellodendron costatum* were more similar to modern seeds of *Euodia* than to those of *Phellodendron*.

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0031-0220/81/0055-0185 $ 1.50

II. Systematics

Euodia costata (Chandler) Tiffney, comb. nov.

Fig. 1 – 4

Phellodendron costatum Chandler, The Upper Eocene Flora of Hordle, Hants: 28, pl. 4, figs. 6a – c. 1925–1926.
Phellodendron costatum Chandler, Bulletin of the British Museum (Natural History) Geology 5: 125. 1961.
Phellodendron costatum Chandler, Lower Tertiary Floras of Southern England, I: 75, pl. 7, figs. 10, 11. 1961.
Phellodendron costatum Chandler, Lower Tertiary Floras of Southern England, II: 73, pl. 10, fig. 1. 1962.
Phellodendron costatum Chandler, Lower Tertiary Floras of Southern England, III: 92, pl. 14, figs. 24 – 28. 1963.

Diagnosis: Seeds 3.0 – 3.5 mm long, 1.8 – 2.25 mm in diameter; ellipsoidal, with prominent apical knob and elongate ventral hilar scar flanked by hilar margins; outer integument bipartite with outer layer missing, the testal surface marked by clear longitudinal ribs; the outer layer of the two to three cell thick inner integument of equiaxial cells with spiral thickenings.

Type: British Museum (Natural History) number V 20062.

Material: Nine seeds presently known.

Provenance: The seeds come from four localities in Paleogene sediments from southern England. They range from the Late Paleocene Reading beds through the Late Eocene Lower Headon sediments at Hordle, a period of some 13 million years.

Description: The seeds of *Euodia costata* are semi-anatropous and range from 3.0 to 3.5 mm in length and 1.8 to 2.25 mm in diameter. Their overall form is subovoid to ellipsoid, the ventral (hilar) margin being almost straight, while the dorsal margin is convex, curving up to meet the ventral at the base and apex of the seed (Fig. 1). None of the seeds collected to date possess any flattened faces. A small knob, formed by a local zone of constriction, occurs at the apex of most of the specimens. The crustaceous layer of the outer integument is absent, and is presumed to have been eroded away, exposing the outer face of the inner portion of the outer integument. The narrow hilar scar traverses the full length of the ventral face, and is flanked on either side by lighter colored hilar margins (Fig. 2). The hilar scar terminates apically in a small depression on the apical knob which holds the micropyle, and basally in the entrance to the raphal canal. The short raphe passes around the base of the seed, and enters the seed cavity via the large basal chalaza.

The testal surface is traversed by approximately 24 clear longitudinal (apex to base) ribs, which are linked by numerous weaker latitudinal ribs, the whole forming a reticulum. The exterior is further marked by very fine striations spaced 16 to 30 µm apart, presumably formed by eroded cells of the outer face of the inner layer of the outer integument. In section, the sclerotesta is 200 – 300 µm thick and is formed of six to nine layers of isodiametric to elongate cells ran-

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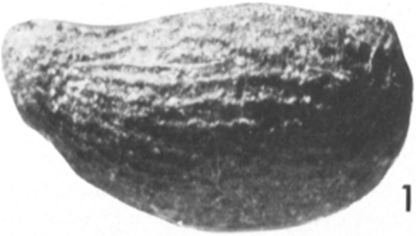
Fig. 1–4.
1.: Lateral view of *Euodia costata.* The longitudinal ridges run from the apical knob (left) to the base (right), the relatively straight ventral margin is uppermost. BM(NH) specimen V43373. × 14.
2: Ventral view of *E. costata.* The hilum is flanked by the two raised hilar margins. The sunken micropyle (left) lies at the apical end of the hilum, the sunken raphal pore at the basal end (right). BM(NH) specimen V43373. × 14.
3: Cross section of the testa of *E. costata,* formed by the inner layer of the outer integument. BM(NH) specimen V40506. Scale bar: 100 µm.
4: Inner integument of *E. costata.* The annular/spiral thickenings of the outermost cell layer of the inner integument are visible as lineations within each cell. BM(NH) specimen V40506. Scale bar: 100 µm.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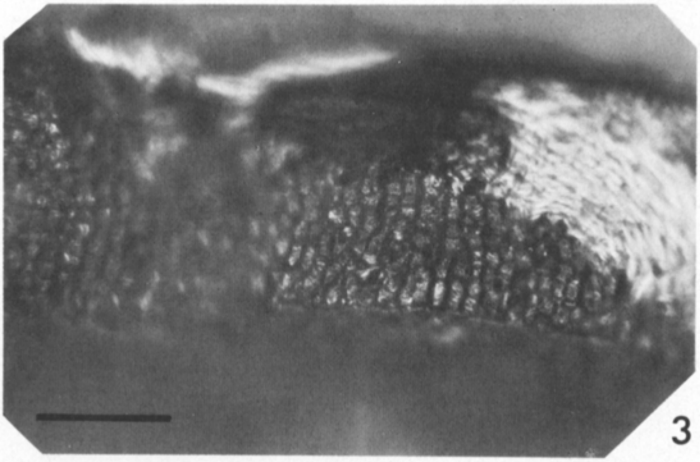
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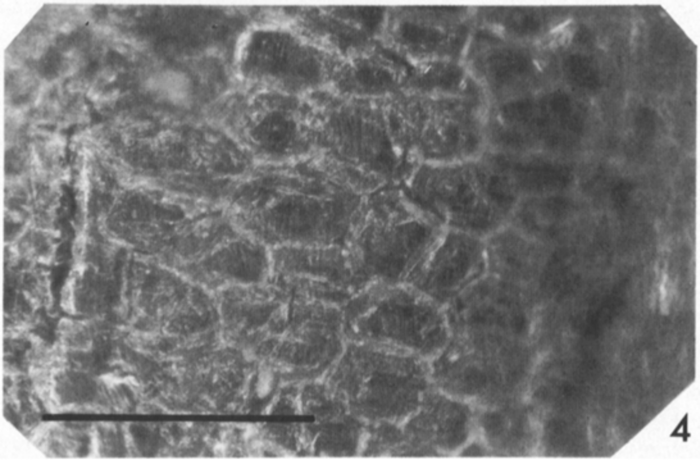
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ging from 15 to 35 µm in length and 15 – 20 µm in diameter (Fig. 3). The inner integument is formed of two to three layers of isodiametric cells, 25 – 40 µm in diameter. The outermost layer of these cells possesses spiral or annular wall thickenings (Fig. 4). Some seeds display a tendency to split along the medial plane of symmetry, suggesting the manner of dehiscence. The foregoing is based both on CHANDLER's published descriptions and on direct observation on four of the nine specimens.

Assignment: CHANDLER's assignment of these fossils to *Phellodendron* was not without good reason. It is likely that she had not seen herbarium specimens of *Euodia*, and she assumed that the morphology of the fossil could be linked to that of modern seeds of *Pellodendron* through the Pliocene species *P. elegans* (REID & REID, 1915). However, with material of both genera to hand, the seeds of the two may easily be separated. The seeds of *Phellodendron* are larger than those of *Euodia*, and lack the apical knob, longitudinal ridges and deep micropylar pit of the latter. While both genera possess long narrow hilar scars, hilar margins are found only in *Euodia*. Both *Phellodendron* and *Euodia* possess multi- (usually five) locular fruits. In *Phellodendron* the locules each bear one seed which is laterally flattened by mutual interlocular pressure within the drupe. By contrast, the locules in *Euodia* are considerably more spacious, and as a result, the seeds are smoothly rounded and lack signs of flattening. As the other previously described species of fossil seeds of *Phellodendron* (KIRCHHEIMER, 1957; TIFFNEY, 1980a) conform to the characters of the seeds of the modern species of the genus, it is appropriate to consider that the rounded shape, apical knob, hilar margins, sunken micropyle and surficial testal ribbing of *P. costatum* do not mark it as an aberrant species of *Phellodendron*, but as a good species of *Euodia*.

III. Discussion

The modern genus *Euodia* is restricted to the tropical through warm temperate climes of the Old World, occurring from central China south to Australia and west to the eastern shores of India and Madagascar (see TIFFNEY, 1980a). It includes some 45 (LI, 1963; WILLIS, 1973) to 100 (MAI, 1970a) species of trees and shrubs, the majority of which are evergreen, although many of the north and central Chinese species are deciduous (WANG, 1961). The genus may be tentatively subdivided into two groups based on seed morphology: a southerly group from Malaysia, Indonesia and the Philippines which is characterized by angular, rugose, irregularly shaped seeds, and a northerly group from China, Japan and India which is characterized by smooth to lightly reticulated, spherical to ellipsoidal seeds (TIFFNEY, 1980a).

Euodia costata is most similar to the seeds of the northern group of modern species, but its exact combination of characteristics is not found in the seeds of any single modern taxon. Various degrees and strengths of testal reticulation are exhibited by *Euodia bodinieri* DODE, *E. colorata* DUNN, *E. glauca* MIQ., *E. hirsutifolia* HAYATA, *E. meliifolia* BENTHAM and *E. officinalis* DODE, the latter possessing the most strongly developed sculpture. *Euodia daniellii* HEMSLEY ex FORBES & HEMSLEY has a wide-margined hilum similar to that of the fossil, but none of the modern species examined have an apical knob as pronounced as that of *E. costata*. The age and morphology of this fossil set it apart as a distinct species.

The floristic affinities and presumed ecological habitat of *E. costata* as inferred from the most similar group of modern species are in relatively good accord with the assumed subtropical to tropical climate and vegetation of the Eocene of southern England. While several of the smooth, round-seeded Chinese species of the present day are deciduous, others are evergreen (WANG, 1961). It must be borne in mind that the physiological selection during the Tertiary has been for greater adaptation to cooler and more seasonal climates, and thus the appearance of some deciduous members of *Euodia* would be in keeping with the forces which were selecting for the evolution of the mixed mesophytic forests during this time (WOLFE, 1977).

Euodia seeds have been described from the fossil record on two previous occasions. *Euodia (Evodia) nitida* (NIKITIN) MAI was published by MAI (1970a, 1970b), but a detailed examination of its morphology does not support the identification (TIFFNEY, 1980a), for which reason it is here considered as *Carpolithus nitidus* NIKITIN. TIFFNEY (1980a) described *Euodia lignita* from the (?) Oligocene Brandon Lignite of Vermont (USA). This species is similar to *E. costata* in being most closely allied to the northern group of euodias based on seed morphology, but differs in possessing a less pronounced apical knob, a reduced intensity of testal sculpturing and a larger average size. Thus, while similar in hilar configuration and overall shape, the two do not overlap in the finer aspects of morphology and are justifiably treated as separate species.

The recognition of *Euodia costata* in the European Paleogene is of particular interest in that it provides evidence of yet another element of the modern flora of east Asia in the Paleogene of both North America and Europe. This supports WOLFE's (1975) hypothesis that a widespread warm-temperate to subtropical or "boreotropical" flora existed in the northern hemisphere during the Paleogene. This hypothesis explains the "Asa Gray" pattern of distribution of temperate and tropical floristic elements in the modern day, and is in keeping with available paleoclimatic data (WOLFE, 1978). The Paleogene distribution of *Euodia* is of further interest in that the occurrence of two reasonably similar species of fossil seeds on opposite sides of the North Atlantic adds credence to the hypothesis (TIFFNEY, 1980b) that the Paleogene North Atlantic land connection which was of importance to animals (McKENNA, 1975) was of equal importance in explaining the distribution of plants. Given the presence of the genus in the Paleogene of England, it is a bit puzzling that *Euodia* has yet to be recognized in the diverse fruit and seed floras of the European Miocene.

Acknowledgements

I wish to thank Dr. M. COLLINSON, British Museum (Natural History) for her assistance, the Keeper of Palaeontology of the British Museum (Natural History) for permission to study specimens in his care, and Dr. HANS-JOACHIM GREGOR, Munich, for assistance in the preparation of the abstract. Research partially supported by NSF Grant DEB 7905082.

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Eingang des Manuskripts bei der Schriftleitung am 20.12.1980.