

SHORT COMMUNICATION

FOSSIL MASTIXIOID (CORNACEAE)
ALIVE IN EASTERN ASIA¹

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ABSTRACT

The tree species *Diplopanax stachyanthus*, wrongly placed in the Araliaceae, belongs in fact to the mastixioid subfamily of Cornaceae. Fruit features make it congeneric with *Mastixicarpum*, part of a woody-fruited complex known heretofore from Tertiary fossils.

WHEN A GROUP of organisms known just from fossils turns out to have survivors, the finding attracts wide attention. Among animals the famed example is a fish, the coelacanth. Among higher plants the one example has been *Metasequoia*, found alive in the 1940s. We report the discovery of a living woody-fruited mastixioid, member of a plant group thought to have expired some 4 million years ago.

No fossils are more prominent in lignite beds of Europe than mastixioid fruits. Collectors of the 19th century called them palm fruits, acorns, or *Annona* seeds. By the early 1930s, however, British paleobotanists had trained their lenses on internal structure and had made correct comparison with fruits of *Mastixia*, a genus of trees now confined to Southeast Asia and islands of the western Pacific. The 19 living species of *Mastixia* have fruits that are much alike, but related fruits from fossil beds are diverse—so diverse that fossil species have been added to *Mastixia* and fossil genera established near *Mastixia*, to make taxonomic sense of the diversity. Species of *Mastixia*, extant and extinct, with species of related fossil genera, comprise subfamily Mastixioideae of the dogwood family, Cornaceae.

Following the British lead, German paleobotanist Franz Kirchheimer searched the rich fossil fruit collections of the European mainland with mastixioids in mind and found kinds not represented in the British record (Kirch-

heimer, 1957, for review). Fifteen genera of mastixioid fruit remains came into print eventually, but current taxonomic views reduce the worldwide list to eight fossil genera, 33 fossil species. Mastixioids are relatively few in North America, and the record ends in the early Tertiary. The European record, however, reaches from uppermost Cretaceous to late Miocene, roughly from 65 million to 7 million years ago. Some of these fruits are superbly preserved, and in some places they abound; Poland's Turów mine alone has yielded 2,400 fruits in five mastixioid genera. Though *Mastixia*-like leaves and pollen grains occur as fossils, they lack the diversity that makes mastixioid fruits important for inferring past climatic changes. Mastixioid flora is the European term for the subtropical to paratropical broad-leaved evergreen vegetation that once covered much of the northern hemisphere.

Mastixioid fruits are stone fruits; as the fruit grows, its inner cell layers turn into a woody housing for a chamber that contains a single seed. Some of the ancient mastixioids had multiple seed chambers in their stones, and the various kinds differed with regard to the hardness of the fruit's outer layers. Fossils indicate that the Mastixioideae evolved in two main lines: a single-genus line (*Mastixia* itself) having fruits with soft outer cell layers, and a several-genus line having fruits with hard outer layers. For convenience we call the latter group woody-fruited, even though the outer tissue was more leathery than woody in some species. Tooth marks and gnawed holes in fossil and modern stones show that mastixioid fruits can be moved about, and often destroyed, by rodents. The fleshy outer layers of *Mastixia*'s fruits give it the advantage of nondestructive bird dispersal, and that may be the reason for *Mastixia*'s survival into modern times.

It was long supposed that *Mastixia*'s woody-

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Fig. 1. *Diplopanax stachyanthus* by A. Tangerini from herbarium specimens. Flowers $\times 3$; branches, fruits $\times \frac{1}{2}$.

fruited relatives had died out in the late Miocene. The duration of supposed extinction dropped to 4 million years with the finding, viewed as startling at the time (see Czeccott and Skirgiełło, 1975, p. 54), of two fruits in the Pliocene of western Asia. Now we know that the line is not extinct. A woody-fruited species lives in eastern Asia.

This living fossil has been in the literature of botany for decades but not as a mastixioid. Qin Renchang (R. C. Ching) found the species—one tree with flowers and no fruits—during a

Chinese collecting expedition to Guangxi in 1928. As Qin was an expert on ferns, he sent pressed specimens of the discovery to Handel-Mazzetti, an Austrian whose own explorations had made him the authority on China's flowering plants. The Austrian saw that the flowers were diplostemonous, but otherwise resemblance seemed to be with the araliaceous *Dendropanax* and its relatives. So he named the new plant *Diplopanax stachyanthus* and put it in Araliaceae (Handel-Mazzetti, 1933).

In time collectors brought in more pressed

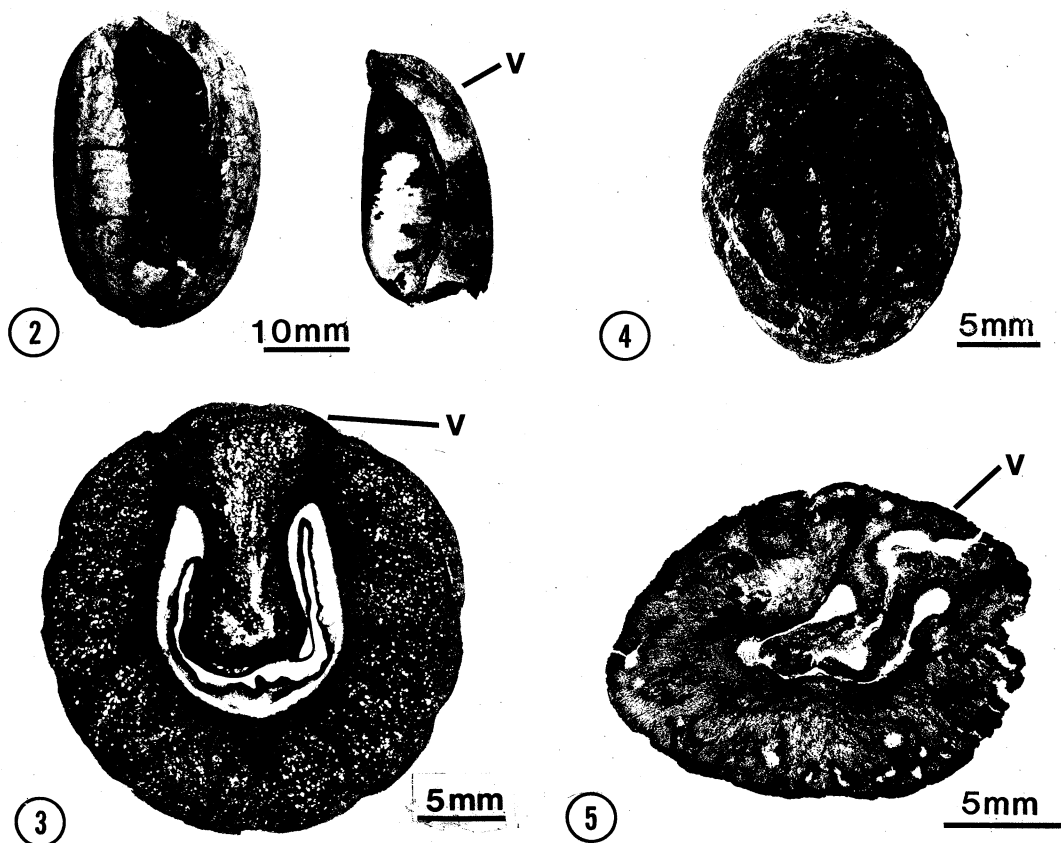


Fig. 2-5. Fruit stones from living *Diplopanax* (2, 3) and from Miocene. 2. Uncut. Cracks result from boiling, drying to free valve (V). 3. Cross section, valve in place. 4. *Mastixicarpum limnophilum*. Examples can be twice linear size of this one. Valve of intact stone is invisible. 5. Same, cross section.

specimens of *Diplopanax*, including some with fruits. The genus still has just one modern species, but its known range has broadened to include sites in Hunan, Guangdong, Yunnan, and Vietnam. Though the fruits, when cut across, were found to be unlike the fruits of other araliads, the family assignment was not questioned until 1978, when He Jing and Zeng Cangjiang published their treatment of Araliaceae in *Flora Reipublicae Popularis Sinicae*. He and Zeng described in brief the internal similarity of *Diplopanax* fruits to *Mastixia* fruits and to one of the fossil mastixioids. A later, posthumous note by Zeng (1983) repeated the comparison and pressed the point more strongly.

Zeng's note might easily have been ignored because it lacked supporting pictures and it garbled information. Zeng had not looked at fossils but at figures in an outdated paleobotanical source, and he compared *Diplopanax* with the wrong fossil genus. Nevertheless, oth-

ers did read the note, and some saw the truth of its main point, that *Diplopanax* had been incorrectly placed (Mabberley, 1987; A. L. Takhtajan, personal communication). We are the first to make a side-by-side comparison of *Diplopanax* fruits with fossil fruits.

Our preparations (Nye, Dean, and Hinds, 1972, for methods) leave no doubt that *Diplopanax* is mastixioid. Its fruit-stones, like those of all mastixioids, have an intrusive germination valve (Fig. 1-3), and along the midvein of a *Diplopanax* leaf are one-celled, two-armed hairs, a rare kind found also in *Mastixia*. Hooked petals are yet another sign that *Diplopanax* and *Mastixia* share common ancestry, but the fruits are so special that added evidence is hardly needed. In structural details a *Diplopanax* fruit agrees more with some mastixioids than others. There is always just one seed chamber. The inner zone of thick-walled, fiber-like cells is so tightly joined to the outer zone of thinner-walled, less elongate cells that the

two cannot be torn apart. The valve contains an undivided column of relatively thin-walled cells or a long undivided cavity caused by the disruption of such cells. Absence of a longitudinal septum in the valve unites *Diplopanax* with *Mastixicarpum* (see Knobloch and Mai, 1986, p. 106). We leave nomenclature and much else for a later, longer article.

Of the four *Mastixicarpum* species, *M. limnophilum* (Fig. 4, 5) best matches *Diplopanax* fruits in size (see Gregor, 1978, pp. 60, 64), but the two are not identical. The *Diplopanax* valve has a narrower, less triangular cross-sectional form than the valve of *M. limnophilum*, and the outer layers of *M. limnophilum* contain lacunae that are lacking in our specimens of *Diplopanax*. The fossil's empty spaces may have formed where thinner-walled cells broke down after burial.

We must emphasize that we could not survey the full range of variation in the modern species or the fossils. We sliced three examples of *Mastixicarpum limnophilum*—all that were in the U.S. national collections—and seven liquid-preserved fruits of *Diplopanax*. The wet fruits were from just one tree (we studied dried herbarium specimens from several places), and the fossils were from one Miocene collecting site, Wiesa in the German Democratic Republic. *M. limnophilum* occurs at other Miocene localities in both German republics as well as in Poland and Czechoslovakia, and the Pliocene mastixioid (see Mai, 1981, p. 537) is close to or conspecific with *M. limnophilum*. Published pictures suggest that some of these fossils, being less compressed than ours, will eventually be more informative than ours.

The discovery that *Diplopanax* is a live *Mastixicarpum* provides a means of matching mastixioid fruit features with floral features and structure with function. *Diplopanax* grows in

wet mountain forests, not in the swampy lowlands favored by extinct mastixioids. Still, observations of *Diplopanax*'s dispersers, predators, and pollinators will be clues to what went on within those ancient swamps. Moreover, *Diplopanax* traits provide a test of evolutionary inferences that have been made without considering *Diplopanax* (Eyde, 1988). *Diplopanax*'s double set of stamens, for example, makes it almost certain that diplostemony preceded haplostemony in the mastixioids. And the two-armed hairs shared by *Diplopanax*, *Mastixia*, and *Cornus* accord with the view that *Cornus* and Mastixioideae are sister groups.

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