

## Pollen from a *Hedyosmum*-like staminate structure (Chloranthaceae) from the Early Cretaceous of the western Portuguese Basin: morphology, ultrastructure, and evolution

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Since Couper compared the Barremian reticulate-columellate monosulcate dispersed pollen genus *Clavatipollenites* with extant *Ascarina* in the Chloranthaceae, this near-basal family has emerged as one of the most important groups of Early Cretaceous angiosperms. The chloranthaceous affinities of several dispersed pollen types have been confirmed by studies of *in situ* pollen. One is *Asteropollis*, first described by Hedlund and Norris from the middle Albian of Oklahoma, which is like *Clavatipollenites* in exine structure but differs in having a four- to six-armed sulcus, as in the extant genus *Hedyosmum*. Similar grains with a three-armed sulcus (trichotomosulcate) have been variously assigned to *Clavatipollenites*, *Asteropollis*, or *Jusinghipollis*. Both *Asteropollis* and similar trichotomosulcate pollen have been associated with *Hedyosmum*-like female flowers (*Hedyflora*) from the Early Cretaceous of Portugal. However, corresponding male structures are known only as isolated stamens with *in situ* pollen, or immature inflorescences containing no pollen.

Here we describe pollen from a well-preserved spike of flowers that consist of a single stamen with no subtending bract, as in *Hedyosmum*, from the Catefica mesofossil flora (late Aptian–early Albian) in the Estremadura region, western Portugal. This pollen is only half the size of living *Hedyosmum* pollen and middle Albian *Asteropollis*. The aperture is often poorly delimited under SEM (cryptoaperturate) but most often a sulcus with three arms. The exine is reticulate-columellate, with nanoverrucate suprategular sculpture. The non-apertural nexine consists of a thick foot layer and a thin but continuous endexine, which is thicker and lamellated under the aperture; total nexine thickness is less than in most extant Chloranthaceae. Phylogenetic relationships of the fossil were examined using a morphological data set for extant basal angiosperms and fossils, with extant taxa arranged as found in molecular analyses. Despite some uncertainty due to similarities between the Catefica fossil and the staminate structures of *Ceratophyllum*, these analyses are most consistent with a position of the fossil on the stem lineage of *Hedyosmum*.

These results show that extinct relatives of *Hedyosmum* were more diverse in pollen size and aperture condition than the extant genus and suggest an evolutionary sequence from an ancestral simple sulcus (as in *Clavatipollenites*), through a three-armed sulcus, to the four- to six-armed sulcus of *Hedyosmum*. Dispersed trichotomosulcate pollen has been compared with *Ascarina*, which produces occasional trichotomosulcate grains, but much of it may have been produced by relatives of *Hedyosmum*. A sulcus with more than three arms may have originated as variation within a trichotomosulcate species, but its appearance may be stratigraphically useful as an Indicator of Albian age.



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