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The Gnetales: past and present

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Abstract

The present issue of GRANA is devoted to pollen morphology and diversity of the Gnetales in time and space. Three papers address fossil pollen and two papers concern pollen of the extant genus *Ephedra*. Together, the papers of the issue contribute new information relevant for the understanding of the fossil and evolutionary history of the Gnetales, pollination biology in the group and implications for ephedroid pollen as indicators of palaeoclimate.

Keywords: *Ephedra*, *Ephedripites*, *Gnetaceaepollenites*, palaeoclimate, pollen, pollination

Scientific progress is motivated by knowledge gaps; or as the physicist Paul Dirac put it: ‘In science one tries to tell people, in such a way as to be understood by everyone, something that no one ever knew before’ (Dirac 1970, p. 22). The gymnosperms of the Gnetales have fascinated botanists because of their peculiar morphology, which often has been considered difficult to understand in comparison with that of other seed plants. They share many similarities with the angiosperms, but are, nevertheless, hard to associate with them with certainty; something that prompted Thompson (1916, p. 135) to call the Gnetales ‘the lure and despair of the morphologist’. Now, a 100 years later, the question of whether the similarities between the Gnetales and the angiosperms are homologous or analogous is still not answered. This gap in knowledge, frustrating and compelling as it is, continues to inspire scientists to study the Gnetales, decade after decade.

The evolutionary history of the group was for a long time very poorly known. When Crane (1996) reviewed the topic, few gnetalean megafossils and mesofossils were known. Since then, an extensive gnetalean diversity has been discovered from almost all current continents (e.g. Krassilov & Bugdaeva 1982, 2000; Crane & Upchurch 1987; Krassilov et al. 1998; Rydin et al. 2003, 2006; Dilcher et al. 2005; Yang et al. 2005; Wang & Zheng 2010; Friis

et al. 2013, 2014), albeit almost exclusively from a relatively short time period in the mid Early Cretaceous. This temporal restrictedness of the megafossil and mesofossil record is surprising since palaeo-palynology strongly indicates the presence of the group throughout the Mesozoic (Friis et al. 2011), perhaps even earlier (Wilson 1962; Wang 2004). The fossil record after the Early Cretaceous is, as currently known, completely devoid of megafossil and mesofossil evidence of the Gnetales, and the microfossil record is, therefore, particularly valuable and important to study as being the only evident testament of the group’s fate from the late Albian and henceforth.

The present issue is devoted to the palynology of the Gnetales. Two papers study ephedroid pollen from Cenozoic assemblages of Brazil (Garcia et al. 2016) and Tibet (Han et al. 2016). Garcia et al. (2016) review the spatial and temporal occurrence and diversity of fossil ephedroids in Cenozoic sediments and make important contributions to questions about ephedroid ecology and climatic tolerance through time in the Brazilian area. An interesting point is that fossil ephedroids may, in fact, be poor indicators of a dry palaeo-climate if the plants that produced the pollen grew as does an extant species of the area (*Ephedra tweedieana* Fisch. et C.A.Mey.), in well-drained soils (e.g. sand dunes)

that provide a dry habitat also with high annual precipitation (Garcia et al. 2016). Garcia et al. (2016) further discuss whether the low occurrence of ephedroid grains (less than 1% in Cenozoic sediments of Brazil according to their literature review) reflects a very low abundance of ephedroid plants in the vegetation. An alternative hypothesis is that ephedroid plants were common in the vegetation, but insect-pollinated, thus with low dispersal ability of the pollen (Garcia et al. 2016). Comparison with pollen of living species, with a known pollination syndrome, may help clarify such questions.

Han et al. (2016) describe the ephedroid pollen flora of the Eocene of Tibet, review the taxonomy and make comparisons with composition in earlier and later strata of the area. They find that sediments of the Cretaceous contain a higher ephedroid diversity than Eocene sediments. Some of the Cretaceous diversity (e.g. *Gnetaceaepollenites*) went extinct by the Cretaceous–Paleogene (K–Pg) boundary; other common ephedroid elements of the Cretaceous remain in the Cenozoic but in much lesser abundance (e.g. *Ephedripites* subgen. *Ephedripites*; i.e. the ancestral ephedroid pollen type of Bolinder et al. 2016). In the Eocene, *Ephedripites* subgen. *Distachyapites* (i.e. the derived ephedroid pollen type of Bolinder et al. 2016) increases strongly and largely replaces the ancestral pollen type in the Tibetan sediments. Han et al. (2016) further conclude that the significant drop in ephedroid diversity in modern China, compared to that found in Cretaceous and Paleogene sediments, is explained by climate change. The onset of seasonal monsoons in the Eocene (Licht et al. 2014) increased aridification and may have favoured wind pollination, as reflected in the increased occurrence of the probably wind-borne grains of *Ephedripites* subgen. *Distachyapites* (see also Bolinder et al. 2016). Later cooling and further aridification in the early Oligocene appear to have put an end to the ephedroid-rich steppe vegetation of the Tibetan area (Han et al. 2016). These evolutionary and ecological conclusions are largely in agreement with interpretations made from ephedroids in Brazilian sediments (Garcia et al. 2016), and studies of pollen of extant *Ephedra* (Bolinder et al. 2016; Luz 2016), although the correlation between ephedroid pollen and a dry paleoclimate may be more complex than previously thought.

To fully understand the fossil pollen record, better knowledge of the pollen of living descendants is needed and two papers of the present issue study pollen of extant *Ephedra* (Bolinder et al. 2016; Luz 2016). Luz (2016) focuses on *Ephedra tweedieana*, a South American species that occurs in the xerophytic Pampas and Restinga areas of southern Brazil,

Argentina and Uruguay (Luz 2016). Palynological studies have indicated that the distribution of the species has shrunk during the last 5000 years (Leal & Lorscheitter 2007) and it is now considered vulnerable in Brazil, probably due to climate change (Luz 2016). Luz (2016) studies pollen morphology of *Ephedra tweedieana* and discusses it in comparison with classical palynological concepts (Steeves & Barghoorn 1959) and the pollen morphology of other extant *Ephedra* species from South America. The author concludes that pollen of the studied South American species is similar, which prevents assignment of fossil and historical palynomorphs from the area to any particular extant species. The conclusion is largely in agreement with results in Bolinder et al. (2016), who study pollen morphology in the genus *Ephedra*. *Ephedra* species inhabiting a certain geographical area are often (but not always) closely related (Rydin & Korall 2009) and have similar pollen morphology, which means that fossil pollen from the area rarely can be assigned to a particular extant species of the same area. Bolinder et al. (2016) find, however, that pollen of *Ephedra* can be divided into two distinct types, an ancestral type and a derived type (i.e. *Ephedripites* subgen. *Ephedripites* and *Ephedripites* subgen. *Distachyapites* of Han et al. 2016, respectively). Grains of the ancestral type are found throughout the Mesozoic, perhaps even from the latest Palaeozoic (e.g. Wang 2004) and they are also present in early diverging lineages of the living clade (Bolinder et al. 2016). The derived pollen type is never found among species of the early diverging lineages of extant *Ephedra*, but is the prevailing type in the remaining extant genus. In the fossil record, the derived pollen type appears much later than the ancestral type. The earliest record of the derived type is probably from the Turonian (Raritan Formation; Steeves & Barghoorn 1959), but it remains very rare throughout Cretaceous strata. It increases strongly in abundance during the early Paleogene however, and from the Eocene and onwards, the derived pollen type dominates over the ancestral type (Bolinder et al. 2016; Garcia et al. 2016; Han et al. 2016).

In the Cretaceous, the gnetalean diversity was clearly greater than it is today. One probable example of this is the presence of elaterate grains, studied in the fifth paper of this issue (Pramparo et al. 2016). Pollen of the Elaterate Complex is diverse and abundant during a short period in the Cretaceous (early Albian to Cenomanian; Friis et al. 2011). They disappear from the fossil record soon after, and are therefore stratigraphically valuable (Jardiné 1967; Pramparo et al. 2016). Although the systematic position(s) of this pollen assemblage is uncertain, it was probably produced by plants of the Gnetales or related extinct groups (Friis et al. 2011; Pramparo

et al. 2016). As far as known, they have no close relatives among living plants. The study by Pramparo et al. (2016) comprises a revision of the elaterate genera, which is important because very little is known about these elusive palynomorphs. Pramparo et al. (2016) also describe a new palynomorph that documents further variation among elaterates and shows that this pollen type occurred outside of the equatorial region, from which elaterates (as most gnetalean pollen of the Cretaceous) have otherwise been discovered.

Outlook and future perspectives

The findings described in the present issue have several interesting implications and one of them is that it, for the first time, is possible to conduct dating analyses with a fossil calibration point within the group of living species of *Ephedra* (Bolinder et al. 2016). The extant clade is much older than previously estimated, probably around 120 Ma (Aptian) according to preliminary analyses (confidence interval of c. 130–110 Ma, using a Bayesian framework and Random Local Clocks; Thureborn and Rydin, work in progress). Among other interesting implications is ephedroid pollen as indicators of paleoclimate. The results of the papers of the present issue provide a basis for further studies of this area. Additional work on the Eocene–Oligocene transition and the Neogene by C. Hoorn will contribute to a better understanding of the response of steppe vegetation to climate change. Ongoing work by Bolinder et al. investigates abundance of the ancestral and derived ephedroid pollen types in time and space, in correlation with climate and palaeo-climate. While it appears probable from preliminary analyses that ephedroid pollen from the Cenozoic indicates a dry (palaeo)-environment (but see Garcia et al. 2016), the correlation with temperature is less obvious. It would also be interesting to further study the correlation between climate and ephedroids in earlier geological times. Their presence in exclusively dry environments appears less clear for the Cretaceous than for the Cenozoic.

The papers of the present issue also have implications for a better understanding of pollination biology among living and fossil members of the Gnetales. Ephedroid pollen is often thought of as wind-borne, and the derived pollen type has indeed several features that indicate adaptation to anemophily (Bolinder et al. 2015; with the tradeoff that they germinate more slowly than the ancestral type, see Bolinder et al. 2016). However, the ancestral pollination syndrome in the Gnetales is probably entomophily. *Welwitschia* is insect-pollinated (Pearson 1907) as are investigated species of *Gnetum* (Kato

et al. 1995). In *Ephedra*, most extant species are wind-pollinated, but the ancestral-most lineage is insect-pollinated (Bolinder et al. 2015; Rydin & Bolinder 2015). Therefore, it is very interesting that the complexity of elaterate pollen indicates that they were produced by entomophilous plants (Friis et al. 2011). It has recently been shown that pollen wall ultrastructure differs between entomophilous species and at least some anemophilous species of the Gnetales, such that wind-borne pollen often has a much more spacious pollen wall than has insect-borne pollen (Bolinder et al. 2015). Future studies of the ultrastructure of gnetalean palynomorphs, including the elaterates, would therefore be highly interesting.

For the future, it would also be relevant to study pollen morphology of *Gnetum* more in depth. A few studies have provided valuable information (e.g. Yao et al. 2004; Tekleva & Krassilov 2009), but additional analyses of potential variation in an evolutionary perspective would be highly interesting. Recent studies have shown that one of very few reports of nectar among gymnosperms (in *Gnetum cuspidatum* Blume) appears incorrect (Jørgensen & Rydin 2015). Insect-pollinated species of the Gnetales use their sweet pollination drops to attract insects, and as far as currently known, there is a correlation (in the Gnetales) between bisexuality in male plants and insect pollination. This opens up for interesting possibilities of a shift to wind-pollination also in *Gnetum* as in *Ephedra*. African species of *Gnetum* stand out as different from other members of the genus in two ways. They have unisexual male plants (Pearson 1912), and *Gnetum africanum* Welw. has a more spacious pollen wall than other studied species of *Gnetum* with only a few large granules (Tekleva & Krassilov 2009, fig. 2.1), which sharply contrasts with the dense granular layer filled with small granules in other studied species (see e.g. Yao et al. 2004). There are therefore gross morphological as well as ultrastructural indications that African species of *Gnetum* may have shifted to wind pollination. Field experimentation and additional knowledge of pollen morphology and ultrastructure in *Gnetum* would help answer the question.

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No potential conflict of interest was reported by the authors.

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