

PALAEOBIOGEOGRAPHY AND MIGRATION IN THE LATE CRETACEOUS BELEMNITE FAMILY BELEMNITELLIDAE

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During the Cenomanian, the lowermost stage of the Upper Cretaceous, belemnites had a tripartite distribution. The family Belemnitellidae Pavlow inhabited the North Temperate Realm, the family Dimitobelidae Whiteaves inhabited the South Temperate Realm, and the family Belemnopseidae Naef inhabited the Tethyan Realm. The latter family became extinct in the Middle Cenomanian, and, consequently, belemnites had a bipolar distribution during the remaining part of the Late Cretaceous.

The belemnitellids, which include nine genera and two subgenera, appeared in the Lower Cenomanian, some way above the base of the substage, and became extinct at the Maastrichtian-Danian boundary. The dimitobelids appeared in the Aptian and disappeared in the lower Maastrichtian.

The belemnitellids were distributed in the North American (NAP) and North European (NEP) palaeobiogeographical Provinces of the North Temperate Realm, in addition to the northern margin of the Tethyan Realm in Europe. The NEP includes the Central European, Central Russian and Baltoscandian Subprovinces. The centre of evolution and dispersal lay in the NEP, which extends from Northern Ireland in the west to the Ural Mountains and beyond in the east.

The belemnitellids invaded the Tethyan Realm at least nine times, first in the Upper Cenomanian and later from the Upper Santonian to the Upper Maastrichtian. Species of five genera and two subgenera occur in this realm, and the majority of these are conspecific with those from the NEP. The belemnitellids immigrated at least six times into the NAP, first in the Middle Turonian and later from the Coniacian to the Upper Maastrichtian. Species of essentially two genera occur in the NAP, and these are endemic, with a few exceptions. More than a score migrations have been recognized within the subprovinces of the NEP.

The palaeobiogeographical distribution and migration patterns of the belemnitellids were to a certain extent controlled by eustatic sea-level changes, cool or warm climatic phases and competition, but the cause of several migration events cannot be satisfactorily explained at present.

A few examples are mentioned below. The genus *Praeactinocamax* invaded NV Europe twice during the Cenomanian coincidentally with rapid rises of sea-level and cool climatic phases: *P. primus* in the Middle Cenomanian and *P. plenus* in the Upper Cenomanian. The latter even invaded the Tethyan Realm. In the Turonian, the belemnitellids retreated northwards in Europe, and entered, via a northern route, the NAP for the first time, probably due to a warming peak in the lowermost Turonian. The parallel evolution of the *Goniotoothis* stock in the Central European Subprovince and the *Goniocamax-Belemnitella* stock in the Central Russian Subprovince during the Middle Coniacian to Early Campanian, a period of about 6-7 million years, was probably due to mutual competition.