

Biogeographical affinities of NW European Barremian ammonite faunas and their palaeogeographical implications

Affinità biogeografiche delle faune ad ammoniti del Barremiano dell'Europa nord occidentale e loro implicazioni paleogeografiche

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IGCP Projects
343: Stratigraphic Correlations Basins of Peritethyan
362: Tethyan and Boreal Cretaceous

ABSTRACT - Closure of the Danish-Polish furrow in latest Hauterivian times led to increased isolation of the NW European basins during the Barremian. For much of the Barremian the ammonite fauna consisted almost exclusively of apparently endemic heteromorph faunas that had evolved from Tethyan-derived Hauterivian ancestors. However, during the mid Barremian desmoceratids appeared briefly. Then in latest Barremian times there was an influx of the normally coiled ammonite *Aconeceras* together with the distinctive late Barremian heteromorph genus *Heteroceras*, recently discovered in the *Aconeceras* beds at Speeton (eastern England). The appearance of these Tethyan forms shows that there was at least intermittent Tethyan influence in NW Europe during the Barremian, probably via a seaway through the North Atlantic. *Aconeceras* may have arrived in the area from the eastern Pacific via a proto-Gulf Stream.

KEY-WORDS - Lower Cretaceous, ammonites, biogeography, palaeogeography, ocean currents.

RIASSUNTO - La chiusura del solco danese-polacco nell'Hauteriviano terminale portò a un crescente isolamento dei bacini dell'Europa nord-occidentale durante il Barremiano. Per gran parte del Barremiano le faune ad ammoniti consistevano quasi esclusivamente di ammoniti eteromorfe apparentemente endemiche, evolute da antenati hauteriviani di origine tetidea. Durante il Barremiano "medio" i desmoceratidi apparvero per un breve periodo. Nel Barremiano superiore, si verificò l'arrivo di *Aconeceras*, ammonite ad avvolgimento normale, insieme al genere eteromorfo *Heteroceras*, scoperto recentemente negli strati ad *Aconeceras* a Speeton (Inghilterra orientale). La comparsa di queste forme dimostra che durante il Barremiano in Europa occidentale ci fu un'influenza tetidea, per lo meno intermittente, probabilmente attraverso il braccio di mare dell'Atlantico settentrionale. Gli *Aconeceras* potrebbero essere dal Pacifico orientale attraverso una proto-corrente del Golfo.

PAROLE-CHIAVE - Cretaceo inferiore, ammoniti, biogeografia, paleogeografia, correnti oceaniche.

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1. - INTRODUCTION

Until the beginning of the Aptian, the Early Cretaceous ammonite faunas of NW Europe (England, the North Sea Basin and North Germany) belonged to the West European Province of the Boreal Realm (RAWSON, 1981; in press). The Berriasian ammonites were exclusively boreal but through Valanginian and Hauterivian times there was a marked Tethyan influence (KEMPER *et alii* 1981). The influx of Tethyan forms took place mainly, though not exclusively, at times of rapid sea level rise (KEMPER *et alii*, 1981; RAWSON, 1993, 1994). Occasionally a Tethyan immigrant gave rise, through allopatric speciation, to major endemic faunas that gave the West European Province a distinctive character (*Platylenticeras*, *Endemoceras*, *Aegocrioceras*). A similarly strong Tethyan influence during the Valanginian and Hauterivian is seen in other fossil groups, such as the belemnites (MUTTERLOSE, 1983), brachiopods (MIDDLEMISS, 1979), foraminifera (MICHAEL, 1974) and nannoflora (MUTTERLOSE, 1992).

The immigrant Tethyan organisms were all forms that lived in western Tethys, from Spain to the Caucasus. There was a direct immigration route from the Carpathians through the Danish-Polish furrow to the NW European basins, and possibly a second route linking the Jura with the Lower Saxony Basin via the Rheinische Senkungszone (MIDDLEMISS, 1976; RAWSON, in press, fig. 1). By the end of the Hauterivian these seaways had apparently closed and NW Europe was no longer open to direct Tethyan influence. Thus the Barremian has been regarded as an interval of increasing endemism among many fossil groups (RAWSON, 1973, 1981; MICHAEL, 1979; MIDDLEMISS, 1979; MUTTERLOSE, 1983, 1992). However, the recent discovery in the Speeton Clay at Speeton (eastern England) of a *Barremites* in the mid Barremian and of several examples of the distinctive Tethyan heteromorph *Heteroceras* in the highest Barremian beds have prompted a reappraisal of the biogeographical relationships and palaeogeographical setting of the Barremian faunas.

2. - COMPOSITION AND BIOSTRATIGRAPHY OF THE NW EUROPEAN FAUNAS

During the Late Hauterivian the West European Province ammonite faunas were dominated by the late perisphinctacean genus *Simbirskites*, but heteromorph ammonites occurred too. Very early in the Barremian *Simbirskites* died out, leaving an almost exclusively heteromorph fauna through the remainder of the Barremian. However, normally coiled ammonites occasionally reappeared alongside the heteromorphs, especially in latest Barremian times when *Aconeceras* invaded the province in significant numbers.

The biostratigraphy of the Barremian ammonites requires further research (RAWSON, this volume). The zonation currently used is:

UPPER BARREMIAN	<i>Parancyloceras bidentatum</i>
	<i>Simancyloceras stolleyi</i>
	<i>Simancyloceras</i>
-- ? --	<i>pingue</i> / <i>"Ancyloceras" innexum</i>
LOWER BARREMIAN	<i>Paracrioceras denckmanni</i>
	<i>Paracrioceras elegans</i>
	<i>"Hoplocrioceras" fissicostatum</i>
	<i>"Hoplocrioceras" rarocinctum</i>
	<i>Simbirskites (Craspedodiscus) variabilis</i>

3. - BIOGEOGRAPHICAL AFFINITIES OF THE NW EUROPEAN FAUNAS

The simbirskitid ammonites of the earliest Barremian are typical Boreal perisphinctaceans. The heteromorphs are of Tethyan origin but their exact relationships are difficult to determine. KOENEN's (1902) monograph of the German faunas is still the most complete review available. KEMPER (1973), IMMEL (1978) and IMMEL & MUTTERLOSE (1980) added further information. SPATH (1924) listed the English fauna and RAWSON (1975) and RAWSON & MUTTERLOSE (1983) have reviewed English Lower Barremian occurrences. These various works indicate that by the beginning of the Barremian the heteromorphs of the West European Province had diverged considerably from their mid-Hauterivian Tethyan ancestors.

Unfortunately it is difficult to compare these "boreal" forms with the classic Tethyan faunas of SE France, monographed by SARKAR (1955) and THOMEL (1964). A plethora of species names has been proposed from both areas, but there is hardly a name in common between the two. This excessive monographic "splitting" of both the German and French faunas helps to obscure their true taxonomic relationships, as does the fragmentary preservation of many specimens in a group that shows considerable morphological change during ontogeny. In France only the early to intermediate growth stages are usually preserved, while it is often the mid to later stages that are best preserved in NW Europe.

Because of these taxonomic problems the biogeographical affinities of the Barremian heteromorphs of the West European Province are difficult to interpret. While Tethyan species definitely occurred there during the Hauterivian (KEMPER *et alii*, 1981), the Barremian faunas may have diverged from those of Tethys in response to the increasing geographical isolation of the NW European basins (RAWSON 1973; in press). However, the divergence may have been slight for there are some interesting parallels in the development of faunas in the two areas. For example, for the Lower Barremian KEMPER *et alii* (1981, p. 261) recognised close similarities between *Crioceratites (Paracrioceras) spathi* (Boreal) and *"Emericiceras"* of the *thiollierei* group (Tethyan), *C. (P.) strombecki* (B) and the *"E." emerici* group (T), and *C. (P.) fissicostatum* (B) and the *"Binelliceras" binelli* group (T).

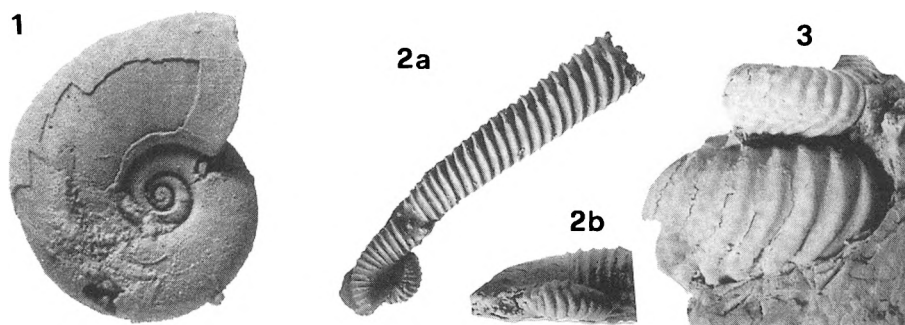


Fig 1-3 - Ammonites from the *Parancyloceras bidentatum* Zone (Upper Barremian); Upper B Beds, Speeton Clay Formation, Speeton, North Yorkshire, UK. All specimens are in the author's collection at University College London. 1): *Aconeceras* sp.(nucleus), x 7 (actual diameter 6 mm); 2): *Heteroceras* sp. - 2a lateral view of a slightly distorted specimen, x 1.5 - 2b distorted earliest whorls of the same specimen, showing the characteristic curvature of the ribs over the venter at the helical stage, x 2.7; 3): *Heteroceras* sp., helical earliest whorls, x 5.

- Ammoniti della zona *Parancyloceras bidentatum* (Barremiano superiore): "Upper B Beds" della formazione Speeton Clay, Speeton, Yorkshire settentrionale, Gran Bretagna. Tutti gli esemplari appartengono alla collezione dell'autore, University-College di Londra. 1): *Aconeceras* sp. (nucleo). x 7 (diametro effettivo 6 mm); 2): visione laterale di un esemplare di *Heteroceras* sp. - 2a leggermente distorto, x 1.5 - 2b spirali iniziali distorte dello stesso esemplare, con la caratteristica curvatura delle coste sull'area ventrale nello stadio ad avvolgimento elicoidale, x 2.7; 3): *Heteroceras* sp., spirali elicoidali iniziali, x 5.

The new discoveries at Speeton coupled with a re-evaluation of some of the North German faunas suggest that whatever the uncertainties in interpreting the systematics and biogeographical relationships of many of the heteromorphs, NW Europe must have retained at least intermittent connection with "Tethyan" areas. There appear to have been two main intervals when such connection occurred.

The first was at about the middle of the Barremian (*elegans-denckmanni* zones), when desmoceratid ammonites appeared in NW Europe. In North Germany they appear to be quite common (e.g. Lange collection, Hamburg). KOENEN (1902) recorded his "*Desmoceras*" (= *Callizoniceras*) *plicatum* from the *elegans* and *denckmanni* zones, while his "*Desmoceras*" (= *Callizoniceras*) *hoyeri* occurs in the upper *denckmanni* to lower *pingue* zones, according to KEMPER (1976, table 8; KOENEN originally recorded it from the top of the Barremian). The horizon is also represented in England, where Mr J. C. DOYLE has recently collected a single *Barremites* from bed LB1B (probably basal *elegans* Zone) at Speeton. This supplements an earlier record of desmoceratids from unknown horizons in the Speeton Barremian, based on two small specimens collected in the last century by J. W. JUDD (British Geological Survey, nos. 30973 and 30974). These were recorded by SPATH (1924, p. 78) as "*Pseudosaynella plana* (PHILLIPS, non MANTELL)" but reidentified by CASEY (1954, p. 268) as true desmoceratids, "belonging to the Barremian group of *Barremites strettostoma*".

It is at about mid Barremian times that "Boreal" crioceratitids may have spread into western Tethys. *Crioceratites* (*Paracrioceras*) of the *elegans* group are recorded from Morocco (ROCH, 1930; IMMEI. &

MUTTERLOSE, 1980) and *C. (P.) denckmanni* (KOENEN) from the Caucasus (KAKABADZE, 1981, pl. 2, fig. 1). The specimens certainly look very similar to the NW European forms and indicate the possibility of southward as well as northward migration at that time.

A second, more clearly defined invasion of Tethyan ammonites occurred in NW Europe very late in the Barremian. The oppeliid genus *Aconeceras* suddenly appears in the highest Barremian beds of both Speeton and north Germany (KOENEN, 1902, 1908). In the Hildesheim area it is sufficiently common that its horizon was referred to as the *Oppelia nisoides* beds (e.g. at Hoheneggelsen: BRANDES collection, Hamburg). German published records (e.g. STOLLEY, 1908; KEMPER, 1976, table 8) indicate that *Aconeceras* first appears at the base of the *stolleyi* Zone. However, new collecting at Speeton suggests that in eastern England it first appears higher in the sequence, at the base of the *bidentatum* Zone (though ammonites are very rare in the immediately underlying beds). It is common at several levels in that zone, though easily overlooked as often only the earliest whorls, up to 2 mm diameter, are preserved (Fig. 1).

More remarkable is the recent (1992) discovery at Speeton of the distinctive heteromorph *Heteroceras*, which first appears with the first *Aconeceras* at the base of the *bidentatum* Zone. *Heteroceras* has an initial helical spiral followed by a straight or curved shaft and a recurved crozier. Both small and very large forms are known, but at Speeton only the helix and fragments of shaft of a diminutive form of the *H. elegans* ROUCHADZE - *H. baylei* REYNES group have been found (author's collection). The material will be described in full in a revision of the Speeton Late Barremian heteromorphs

(RAWSON, in preparation), but two specimens are illustrated here (Figs 2-3). *Heteroceras* is of latest Barremian age and achieved a remarkably wide distribution, from Japan and South Africa, through western Tethys to Colombia, Patagonia and Canada (AGUIRRE URRETA & KLINGER, 1986, p. 322).

This sudden spread of "Tethyan" *Heteroceras* and common *Aconeceras* in the latest Barremian may indicate another rapid sea level rise, not previously documented in NW Europe. This could link with a similar event recently recognised at about the base of the *giraudi* Zone of SE France (ARNAUD-VANNEAU & ARNAUD, 1990).

4. - PALAEOGEOGRAPHICAL IMPLICATIONS

While the exact biogeographical affinity of the NW European Barremian heteromorphs remains a matter of debate, the appearance of desmoceratids in the mid Barremian and of *Aconeceras* together with *Heteroceras* very late in the Barremian points firmly at intermittent Tethyan connection. This is also indicated by Tethyan elements in the dinocysts (MUTTERLOSE & HARDING, 1987) and possibly the nannoplankton.

The position of the connection is problematic. The Danish-Polish furrow had apparently closed by the end

of the Hauterivian, severing connections between NW Europe and the Carpathian area. However, some of the sandstones within the furrow show limited evidence of marine conditions (glauconite, agglutinated foraminifera), so it is possible that there were brief spillovers of Tethyan waters into NW Europe during the Barremian. On the other hand, if this were the migration route then there should be records of the appropriate ammonites in the Barremian of adjacent parts of western Tethys, from the Caucasus, through the Carpathians to SE France. While desmoceratids and *Heteroceras* certainly occur in those areas, *Aconeceras* is not recorded (e.g. DRUSHCHITS & KUDRYAVTSEVA, 1960; BRESKOVSKI, 1975; AVRAM, 1983) and thus appears to have reached NW Europe by another route.

The most likely alternative route by which Barremian Tethyan ammonites would have reached NW Europe was through the North Atlantic (Fig. 4), where a connection from western Tethys to East Greenland was first inferred to explain Valanginian faunal links between the two areas (DONOVAN, 1957; AGER, 1971; RAWSON, 1973). This has also been suggested as the route by which "boreal" crioceratitids migrated to Morocco (IMMEL & MUTTERLOSE, 1980) and Tethyan microflora reached the North German Basin (MUTTERLOSE & HARDING, 1987) during the Barremian. It could easily explain the appearance of desmoceratids

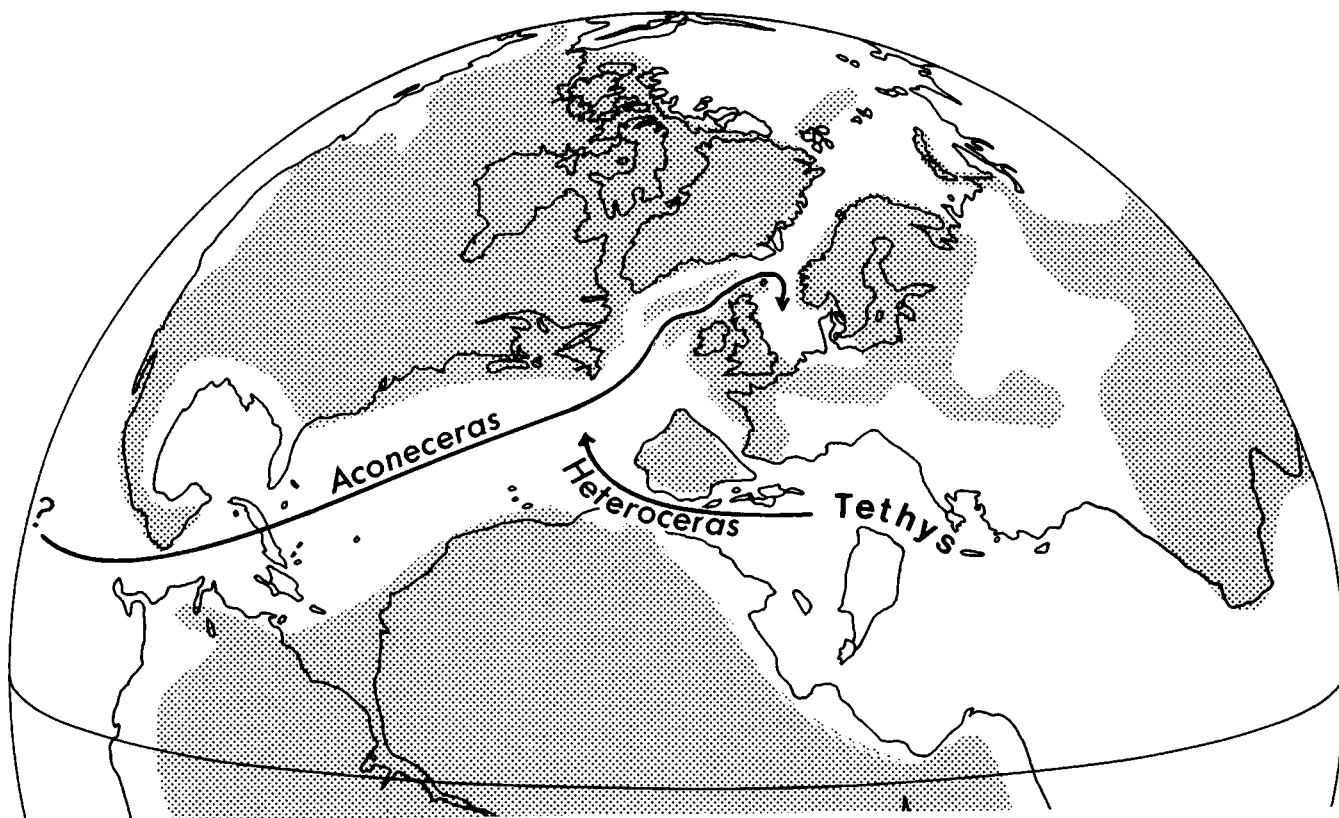


Fig. 4 - Late Barremian palaeogeography and possible migration routes.
- Paleogeografia del Barremiano superiore e probabili vie di migrazione.

and *Heteroceras* in the West European Province. However, the ultimate origin of *Aconeceras* is more problematic. Both CASEY (1954) and RAWSON (1981) thought that the Opeletiidae may have been open ocean dwellers, the latter author suggesting that they possibly lived in the Pacific area. In that case *Aconeceras* may have migrated from the eastern Pacific, through the central Atlantic and to the west of the British Isles - following a proto-Gulf Stream (AGER, 1971). Recent reconstructions of mid Cretaceous surface ocean currents (BARRON & PETERSON, 1989) support this interpretation, though they represent a slightly later time interval and a slightly higher sea level. Such a route could also explain the earlier (Late Hauterivian) curiously disjunct distribution of a forerunner of *Aconeceras*, *Protaconeceras* - known mainly from a thin horizon in the gottschei Zone at Speeton and from Patagonia, Argentina.

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