

## Biogeography of Cretaceous ammonites – a review of procedures and problems

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With 3 figures

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**Abstract:** Procedures and problems connected with biogeographical work on Cretaceous ammonites are reviewed. Ammonites display distribution patterns similar to those of most other Cretaceous marine invertebrates, although their exceptionally high dispersal potential resulted in weaker biogeographical partitioning than for many other groups. The criteria for distinguishing biogeographical units and relating them to each other can be expressed qualitatively as differences in taxonomic composition and/or phylogenetic relationships but also quantitatively as differences in population structure and/or taxonomic diversity. For sound biogeographical analysis, comparisons of published faunal lists is a much too imprecise method, owing to taxonomic bias, dating inconsistencies, chance dispersal, and because the quantitative components of distribution patterns are concealed. For the study of quantitatively manifested patterns, large sample sets are required, which are rarely available for ammonites. To illustrate the complex interrelationships in biogeographical interpretations of Cretaceous ammonites, the Aptian genus *Australiceras* WHITEHOUSE, 1926, of the Ancyloceratina WIEDMANN, 1966, is selected. Methods of integration of palaeontological, palaeobiogeographical and palaeogeographical data are also considered.

**Zusammenfassung:** Es wird eine Übersicht über verschiedene Verfahren und Probleme in Zusammenhang mit biogeographischer Arbeit an Kreideammoniten gegeben. Die Verbreitungsmuster der Ammoniten sind denen der meisten anderen marinen Wirbellosen der Kreide ähnlich. Allerdings führte ihre außergewöhnlich hohe Ausbreitungsfähigkeit zu weniger ausgeprägten biogeographischen Gliederungen. Die Kriterien für das Unterscheiden und den Vergleich von biogeographischen Einheiten können sowohl qualitativ als auch quantitativ ausgedrückt werden, qualitativ als Unterschiede in der taxonomischen Zusammensetzung und/oder phylogenetischen Verwandtschaft, quantitativ als Unterschiede in der Populationsstruktur und/oder taxonomischen Diversität. Wegen taxonomischer und biostratigraphischer Un-

beständigkeit der Daten, des Fehlens von biogeographisch signifikanten quantitativen Daten sowie der Zufallsausbreitung insbesondere von leeren Gehäusen ist der einfache Vergleich veröffentlichter Faunenlisten eine viel zu unpräzise Methode für solide biogeographische Analysen. Für das Studium von quantitativ definierten Verbreitungsmustern werden große Probenmengen benötigt, welche von Ammoniten selten vorhanden sind. Um die komplizierten Wechselbeziehungen in biogeographischen Interpretationen zu illustrieren, wird die aptische Gattung *Australiceras* WHITEHOUSE, 1926 der Unterordnung Ancyloceratina WIEDMANN, 1966, herangezogen. Zusätzlich werden Methoden zur Integration von paläontologischen, paläobiogeographischen und paläogeographischen Daten diskutiert.

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## Introduction

Study of relationships between biotic–abiotic changes and distribution patterns of ammonites form an important component in palaeogeographical interpretations and reconstructions of the Mesozoic world. This is particularly the case for the Cretaceous, a period characterized by rapidly changing continent–ocean configurations.

A prerequisite for reliable biogeographical work is a sound, consistent and homogeneous taxonomy and a solid biostratigraphical basis. For some groups of Cretaceous ammonites and for some geographical areas this can be claimed to be available but, generally speaking, Cretaceous ammonite taxonomy and biostratigraphy still rest on shaky ground (cf. HANCOCK 1991). As a consequence, opinions about the biogeographical behaviour of ammonites vary considerably, ranging from the belief that, with the advance of science most taxa will eventually be found to be globally distributed, to the opinion that ammonite species have essentially local distributions (largely reflecting the “lumping” and “splitting” approaches of taxonomists). In general terms, the truth lies somewhere between these two extreme opinions; many ammonite taxa indeed show pandemic distributions, but there are also a large number of demonstrably endemic taxa. Biogeographical patterns and the degree of provincialism also varied considerably during the lifespan of the taxa.

Biogeographical distributions of Cretaceous ammonites have been discussed in general terms by, for example, MATSUMOTO (1973, 1987), GORDON (1976), KENNEDY & COBBAN (1976) and WIEDMANN (1988). Specific faunas and/or ages have been dealt with, for example, by WIEDMANN (1973; Jurassic–Cretaceous boundary); KAKABADZE (1971, 1981, 1994), KOTETISHVILI (1988), SACHS et al. (1973), RAWSON (1973, 1981, 1993), and VAŠIČEK & WIEDMANN (1994, early Cretaceous), KLINGER et al. (1984) and KLINGER (1990, late Barremian); HOEDEMAEKER (1990, “Neocomian”), OWEN (1973, 1988, Albian), and FUTAKAMI & OBATA (1988, Turonian–Coniacian collignoniceratids).

A considerable number of regional biogeographical studies of Cretaceous ammonites have also been carried out at the generic and/or specific level. Examples include, for Europe: OWEN (1973, 1979), THIEULOUY (1973, 1977), KLINGER & WIEDMANN (1983), MARCINOWSKI & WIEDMANN (1988), RAWSON (1993, 1994, 1995), for Africa: BERTHOU & REYMENT (1977) and REYMENT (1981), for Asia: GHARE & BADVE (1978), MATSUMOTO (1987) and OBATA & MATSUKAWA (1988), for Greenland: BIRKELUND & HÅKANSSON (1983), for the U.S. Western Interior: KAUFFMAN (1984), for western and Arctic Canada: JELETZKY (1971a, 1971b), and for southern South America–Antarctica: THOMSON (1982) and MACELLARI (1985, 1987). However useful these geographically restricted studies may be, they all suffer from the problem of incompatibility, i.e., they can rarely be compared and synthesized without prior taxonomic and biostratigraphical revision. For some key areas such work has recently been carried out or is in progress (see, for example, references in KENNEDY 1986 and HANCOCK 1991), which is expected to result in a more reliable biogeographical picture than that which is currently available. However, at present it is not possible to synthesize available distributional data on Cretaceous ammonites into a global picture, except, perhaps, at higher systematic levels, where taxonomic inconsistencies are smoothed out. Thus, any reconstruction of biogeographical patterns without prior taxonomic and biostratigraphical revision is bound to be based largely on inadequate data.

We have chosen to focus this review on basic procedures and problems connected with biogeographical work on Cretaceous ammonites, using the genus *Australiceras* WHITEHOUSE, 1926, of the suborder Ancyloceratina WIEDMANN, 1966, to exemplify and illustrate our points. The radiation of Cretaceous Ancyloceratina resulted in the creation of numerous phylogenetic branches, containing a great variety of heteromorph ammonites. Many representatives are characterized by rapid and repeated ontogenetic modifications of shell morphology, resulting in several shell types (KAKABADZE 1987). Among them there are genera (and families), which during their phylogenetic time-span are characterized by changes in the mode of coiling of the shell. This feature may provide an opportunity to analyze – and perhaps correlate – modifications of shell morphology with temporal shifts in biogeographical distribution patterns.

## Biogeographical causes and mechanisms

Biogeographical patterns reflect the combined result of dispersal from centres of origin and vicariance dispersal, i.e., the effects of “traditional” dispersal and those caused by the formation and/or elimination of geographical barriers, chiefly through plate tectonic processes. For Creta-

ceous ammonites the following main factors are thought to determine the biogeographical patterns (see also KENNEDY & COBBAN 1976):

- (a) the appearance and disappearance of dispersal barriers and the nature of such barriers (e.g., physical isolation of basins, climatic changes, existence of warm or cool oceanic currents, upwelling, etc.);
- (b) the distribution potential of the larvae, determined by their longevity and ecological tolerance in combination with prevailing surface currents;
- (c) the basic mode of life of the ammonite (benthic vs. nektonic/planktonic);
- (d) the environmental tolerance of mobile forms, for planktonic forms also influenced by surface currents.

Because of the exceptionally great dispersal potential of many species of ammonites, biogeographical partitioning based on ammonites is prone to be less pronounced than that of less mobile groups. Biogeographical boundaries are therefore likely to reflect only large-scale physical, climatic, and/or biotic environmental changes. Thus, ammonites can be expected to be useful for unravelling *major* dispersal barriers, i.e., the kind of barriers that would have significant bearing on the palaeogeography and overall environmental conditions of the time interval considered.

An important factor in ammonite biogeography is the excellent potential for precise dating of the sequences studied – a prerequisite for reliable biogeographical analysis.

Distribution mechanisms and the resulting patterns of occurrence for fossil marine invertebrates are essentially of five different kinds, viz. (1) pandemic, (2) latitudinally limited, (3) endemic, (4) disjunct, and (5) post-mortem distribution. Examples of all these kinds of patterns can be found in Cretaceous ammonites (cf. KENNEDY & COBBAN 1976).

Genera of Cretaceous Ancyloceratina display a wide range of distribution patterns. Widespread genera (e.g., *Crioceratites*, *Heteroceras*, *Colchidites*, *Tropaeum* and *Australiceras*), although less useful for defining biogeographical boundaries, can help to decipher global migration routes and hence become important in global continent reconstructions. On the other hand, among genera with more restricted distribution patterns (e.g., *Protancyloceras*, *Veveysiceras*, *Manoloviceras*, *Imerites* and *Kutatissites*), there are less environmentally-tolerant and less mobile forms, which can be useful for the definition of minor biogeographical units (provinces, subprovinces, etc.).

The dispersal potential, in combination with the prevailing environmental conditions, determine the resultant geographical ranges of the taxa, which in turn form the bases of the biogeographical units. The criteria for distinguishing biogeographical units and relating them to each other can be expressed not only in the conventional way as differences in (a) taxonomic composition at a given systematic level (usually expressed as presence vs. absence of taxa), including expressions of intraspecific variation, but also as differences

in (b) phylogenetic relationship (expression of the remoteness of common ancestor), (c) population structure (most clearly manifested in the relative abundance of taxa), and (d) taxonomic diversity.

Thus, both qualitative (a and b) and quantitative (c and d) properties in the distribution of ammonites (and most other organisms) are biogeographically significant (see also HENGEVELD 1990, ROSEN 1992). A few examples:

*Qualitative differences:*

- (a) Taxonomic composition: *Taxon X occurs in Provinces A and B but not in Province C (species level or higher). Or, taxon X is more densely ribbed in Provinces A and B than in Province C (intraspecific variation or geographical subspecies, especially if variation is discontinuous or clustered).*
- (b) Phylogenetic relationship: *The taxa in Province A are more closely related to the taxa in Province B than to the taxa in Province C.*

For the definition of a biogeographical unit, as many taxa as possible should be used in conjunction. The units will then be defined by a number of more or less fully overlapping geographical ranges (cf. SMITH 1992).

*Quantitative differences:*

- (c) Population structure: *The relative abundance of taxon X in Province A is different from that in Province B.*
- (d) Taxonomic diversity: *The fauna (that contains taxon X) is more diverse in Province A than in Province B.*

## **Causes of ammonite provinciality**

Changes in biogeographical patterns with time can be ascribed to a variety of factors. Biotic factors cannot normally be discerned in the fossil record, whereas climatic factors may be more evident, particularly where they are manifested as latitudinal gradations. Physical factors in the form of arrangement of continents and oceans can often be double-checked against geophysical evidence – and against evidence from the biogeographical behaviour of other fossil groups – and are therefore more tangible than other factors. During much of the Cretaceous world climate was significantly warmer and ocean temperatures more uniform than during most of the Phanerozoic (FRAKES et al. 1992, see also KAUFFMAN 1979), which contributed to the atypical palaeoceanographical conditions of the time, with widespread shallow epicontinental seas (cf. DULLO et al. 1996). In contrast to the cooler early Cretaceous, climatic factors during the mid- and late Cretaceous appear to have played a less important role for the biogeographical partitioning of ammonites and may have been significant only at the realm level (tropical vs. temperate). We believe that changes in biogeographical patterns in mid- and late Cretaceous times reflect primarily the interaction of transgressions and regressions, oceanic conditions and

changes in plate configuration, i.e. factors that determined the behaviour of physical barriers. Intermittently in the early Cretaceous, distribution patterns of ammonites were clearly also influenced by global climatic changes, especially changes in water temperature (e.g., RAWSON 1973, 1981, KAKABADZE 1981, 1992, KEMPER 1983, 1987, HOEDEMAEKER 1990), although this is evident mainly in the interrealm transitional area and adjacent regions.

The effects of transgressions and regressions on marine invertebrate provincialism are not clearly understood. Most authors seem to adhere to the idea that transgressions facilitate dispersal and therefore should result in decreased provincialism. Thus, widespread rises of sea-level (which often coincide with a global increase in temperature) will promote the exchange of shelf waters, which results in increased contact between faunas, less distinct biogeographical boundaries and ultimately in reduced biogeographical partitioning. Examples are found in the early Cretaceous, during the middle of the late Barremian, when equalization of conditions in the Boreal and Tethyan realms started (KAKABADZE 1992), and during the Aptian, when simultaneously with a global eustatic rise, ammonite provincialism broke down and the previously clear differentiation between the Boreal and Tethyan realms ceased to exist (RAWSON 1994). However, the opposite effect of transgressions has also been recorded. For example, MARCINOWSKI & WIEDMANN (1988) and WIEDMANN (1988) argued that water depth and temperature were the main factors that controlled ammonite distribution, at least in the Mesozoic. Thus, in many cases, transgressions would have caused *increased* provincialism as a result of an increase in ecologically less stable shallow-water areas, as new epicontinental seaways opened up. Prime examples are provided by the Western Interior Seaway across North America, with its endemic mid- and late Cretaceous ammonite faunas, and by the mid-Cretaceous Trans-Saharan Seaway (cf. REYMENT 1988). Similar reasoning can be applied to the interrelation between regressions and changes in ammonite provincialism.

There is no doubt that eustatic sea-level changes exercised considerable influence on the distribution patterns of organisms. The problem of such global changes needs to be addressed in two opposing ways: (1) what are the biogeographical influences of eustasy coinciding with global rise and fall in temperature and (2) what is the magnitude of these influences where eustasy is unrelated to temperature changes?

Transgressions and regressions caused by local or regional tectonic movements also must have influenced marine invertebrate provincialism, although less so in comparison with eustasy.

## Methods and problems of biogeographical analysis

Biogeographical analysis of ammonite taxa is an important tool in reconstructions of palaeogeography and palaeoclimate. However, biogeographical work is complicated by a number of methodological problems.

(1) Lack of data on biogeographically significant parameters other than taxonomic composition.

Most of the published biogeographical work on Cretaceous ammonites consists of analyses of taxonomic similarity, often by applying the well-known Simpson, Jaccard or Dice coefficients (CHEETHAM & HAZEL 1969, FALLAW 1979, RAUP & CRICK 1979) to faunal lists. However, these are only crude instruments that may even be misleading (see also HENGEVELD 1990, HALLAM 1994). For example, if two geographical areas are inhabited by the same taxa, their faunal similarity as expressed by similarity coefficients is total, even if taxa that are abundant in one area should be extremely rare in the other area. Thus, biogeographically significant differences in the relative abundance of taxa do not show up in straightforward comparisons of faunal lists.

(2) Taxonomic inconsistencies.

Comparisons based mainly on taxonomic composition, especially comparisons of faunal lists, are heavily biased by taxonomic inconsistencies. Differences in taxonomic opinion and/or procedure between palaeontologists working in different geographical areas will thus result in distorted biogeographical interpretations. Even if modern taxonomic treatments of the faunas are available, the fact that “one man’s genus is another man’s species” (KENNEDY & WRIGHT 1985) does not form a sound basis for biogeographical work. For example, disjunct distributions may be masked by taxonomic splitting, i.e., geographically separated, monospecific populations may have been ascribed to different taxa. The problem can be diminished by considering only well-established, taxonomically “uncontroversial” taxa. However, because such a procedure would also exclude biogeographically significant taxa, it cannot replace thorough taxonomic evaluation and analyses of the entire faunas.

(3) Chance dispersal.

Occurrences as a result of chance dispersal, e.g., through post-mortem transport of empty ammonite shells, may distort the biogeographical pattern. For example, the find of a single specimen is all that is needed to change the category of a taxon in a faunal list from “absent” to “present”

(4) Age mismatch.

Firm chronostratigraphical control is essential in order to avoid the error of comparing faunas of different ages.

(5) Facies mismatch.

Environmental differences in the rock record are not always readily apparent or taken into due account; in biogeographical analyses this may result in facies mismatch. This is related to the basic problem of how to distinguish locally manifested biofacies from biogeographical units. An example is provided by the distribution of the Tethyan late Cenomanian genus *Neolobites*. Its absence from many otherwise typically Tethyan assemblages may be a result of local ecological conditions (water depth?) rather than of true biogeographical factors.

(6) Incomplete records.

Besides the well-known incompleteness of the fossil record, data based on only one fossil group (e.g. ammonites) are inadequate for general biogeographical conclusions.

(7) Insufficient level of palaeontological knowledge.

Reliable biogeographical interpretations require a fairly advanced level of taxonomic knowledge of the area studied. It would be rash to state that a taxon does not occur in a particular geographical area before the area has been studied in at least some detail.

(8) The effect of small sample sizes.

To obtain a reliable picture of the biogeographical patterns (qualitative and quantitative), large, coeval sample sets (i.e. populations) are required. Unfortunately, for most macrofossils, including ammonites, usually only a handful of specimens are available (rarely derived from a single stratigraphical horizon). In a small sample the most common taxa tend to be over-represented (GRAY & BOUCOT 1976, KOCH 1987), this invariably distorts the quantitatively based biogeographical patterns.

We believe that criteria for distinguishing biogeographical units should be based on differences in both qualitative (taxonomic composition, phylogenetic relationship) and quantitative (relative abundance, taxonomic diversity) parameters in the distribution of organisms. A first step in such studies of Cretaceous ammonites would consist of a reevaluation and classification of genera on the basis of the following distribution patterns: (1) truly Tethyan genera, (2) truly Boreal (North Temperate) genera, (3) genera restricted to the Austral (South Temperate) Realm, (4) cosmopolitan genera, (5) genera that are characteristic of the Tethyan Realm but with some species penetrating into the adjacent areas of the Boreal (North Temperate) Realm, (6) genera that are characteristic of the Tethyan Realm but with some species penetrating into the Austral (South Temperate) Realm, (7) genera that are characteristic of the Boreal (North Temperate) Realm but with some species penetrating into the adjacent area of the Tethyan Realm, (8) genera that are widely distributed in the Austral (South Temperate)



Realm but with some species penetrating into the Tethyan region(s) and (9) genera that show a bipolar distribution.

In such investigations the possibility of post-mortem distribution of empty shells, which will obscure original distribution patterns, needs to be carefully controlled. Biogeographical patterns also need to be analyzed against a background of (a) the sequence-stratigraphic sea-level fluctuation chart (HAQ et al. 1988, see also HALLAM 1992), (b) global climatic changes (BARRON & WASHINGTON 1982), (c) oceanic current data, (d) data on global (or regional) geodynamic changes (e.g., major plate movements and changes in orientation), (e) phylogenetic data (e.g., acmes and principal modifications of shell morphology), and (f) data on the distribution patterns of other fossil groups. Shifts in the distribution of taxa should be traced through the stratigraphical succession in as detailed a way as possible: by zone, by substage, or, for genera, at least by stage.

The various analytical techniques employed in biogeographical work will not be treated here; for a review, the reader is referred to HALLAM (1994).

### Biogeography of *Australiceras* WHITEHOUSE, 1926

To illustrate the complex interrelationships in palaeobiogeographical interpretations, the Aptian genus *Australiceras* WHITEHOUSE, 1926, is selected here for analysis. Three schematic biogeographical maps (Fig. 1) are given for the early Aptian (Bedoulian), i.e., the time of flourishing of the subgenus *A. (Proaustraliceras)* KAKABADZE, 1977, for the middle Aptian (Gargasian), i.e., the time of flourishing of the subgenus *A. (Australiceras)* WHITEHOUSE, 1926, and for the late Aptian (Clansayesian), respectively.

Representatives of the subgenus *A. (Proaustraliceras)*, which are characterized by an ancycloceratoid or aspinoceratoid shell, occur in the lower Aptian of France, England, the Volga region, northern Caucasus, Transcaucasus, northern Koryakia (Siberia) and Japan. There are no reliable records of the subgenus from the southern hemisphere and, accordingly, *A. (Proaustraliceras)* can be considered characteristic of the Tethyan Realm and adjacent marginal areas of the Boreal Realm.

The nominotypical subgenus *A. (Australiceras)* ranges from the lower to upper Aptian. In contrast to *A. (Proaustraliceras)* it is characterized by having a crioceratoid mode of coiling. The tendency towards planispirally coiled shells with contiguous whorls was probably a progressive development, and in mid-Aptian times representatives of this subgenus became widely spread in the seas of both the northern and southern hemispheres. The earliest representatives of the subgenus are known from lower Aptian beds of Zululand (KLINGER & KENNEDY 1977) and Patagonia (AGUIRRE URRETA 1986) and from the uppermost lower Aptian of Australia (DAY 1974). In other regions of both the northern and southern hemisphere

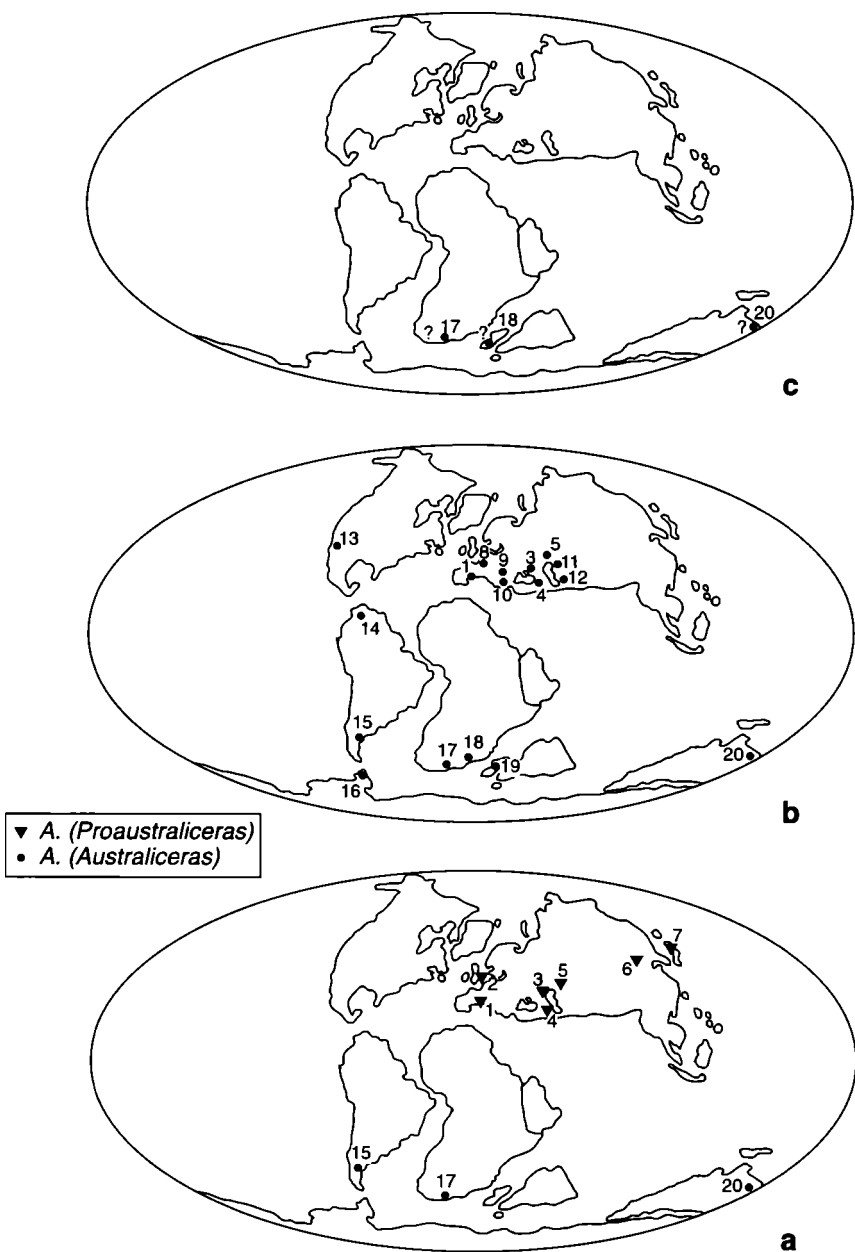


Fig. 1 (Legend see p. 231)

(Fig. 1a), *A. (Australiceras)* appeared later – in the mid-Aptian. On the basis of these data it can be concluded that the subgenus originated in the early Aptian of the “Austral Realm” and in the mid-Aptian (Fig. 1b) spread northwards into the Mediterranean Province via an east African and/or Indian seaway. Open marine connections between the Tethys and eastern Africa and India existed in both Aptian and Barremian times, which facilitated free migration of ammonites (KLINGER & KENNEDY 1977). Then, from the Mediterranean Province, dispersal of *A. (Australiceras)* took place via different seaways: from the western and central Mediterranean (France, Caucasus) further east into Central Asia (Turkmenia, Mangyshlak), as well as towards the north (northern Germany, Volga region); and from the western Mediterranean towards the west (Colombia, California). It is worth noting that the subgenus *A. (Australiceras)* did not penetrate into the high Arctic regions.

In the late Aptian the distribution of *A. (Australiceras)* was reduced to the “Austral Realm” with records only from Australia, Zululand and Madagascar (Fig. 1c). However, their exact chronostratigraphical positions are not clear. No reliable records of the genus are known from the Albian.

Our biogeographical interpretations of the genus *Australiceras* are based on recent, complementary data, which lead to conclusions somewhat different from those presented by KLINGER & KENNEDY (1977, fig. 89) and KAKABADZE (1981, figs. 21, 23). Furthermore, our results are inconsistent with the phylogenetic scheme presented by CASEY (1960, reproduced here as Fig. 2), as follows.

According to WHITEHOUSE (1926), the genus *Australiceras* comprises only crioceratoid forms, although the ancyloceratoid group of “*Ancyloceras*” *gigas* (J. DE C. SOWERBY) should perhaps be included. ANDERSON (1938) and ARKELL et al. (1957) also restricted the genus to crioceratoid forms. However, CASEY (1961, cf. WRIGHT 1996) united three species groups in *Australiceras*, viz. *Australiceras* gr. *gigas* (J. DE C. SOWERBY) with ancyloceratoid shells, *Australiceras* gr. *tuberculatum* (SINZOW) with aspinoceratoid shells, and *Australiceras* gr. *jacki* (ETHERIDGE, JR.) with crioceratoid shells. KAKABADZE (1977) erected the subgenus *A. (Proaustraliceras)* (type species *Hamites gigas* J. DE C. SOWERBY, 1828), early

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**Fig. 1.** Distribution patterns based on occurrences of the genus *Australiceras* WHITEHOUSE in the early (a), middle (b) and late (c) Aptian. 1, south-eastern France; 2, England; 3, northern Caucasus; 4, Transcaucasus; 5, the Volga region; 6, northern Koryakia (Siberia); 7, Japan; 8, northern Germany; 9, Hungary; 10, Bulgaria; 11, Mangyshlak; 12, Turkmenia; 13, California; 14, Colombia; 15, Patagonia; 16, Antarctic Peninsula; 17, Zululand; 18, Mozambique; 19, Madagascar; 20, Australia.

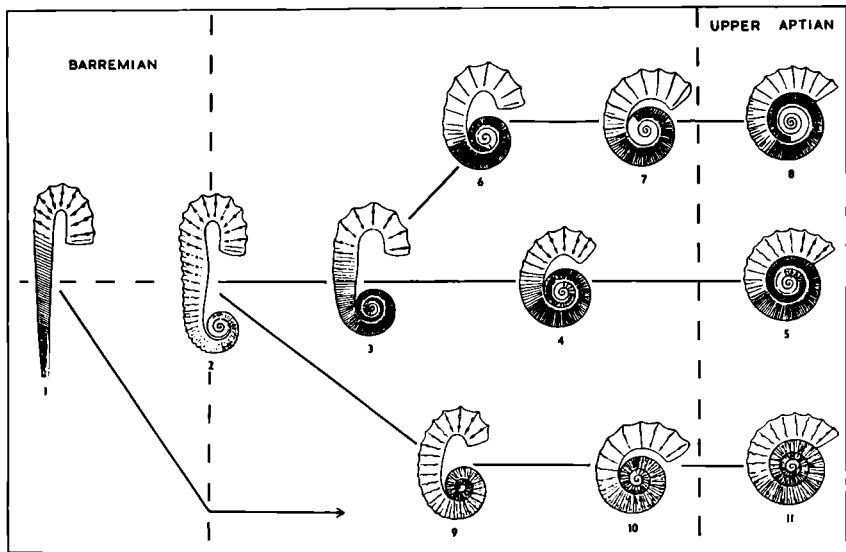
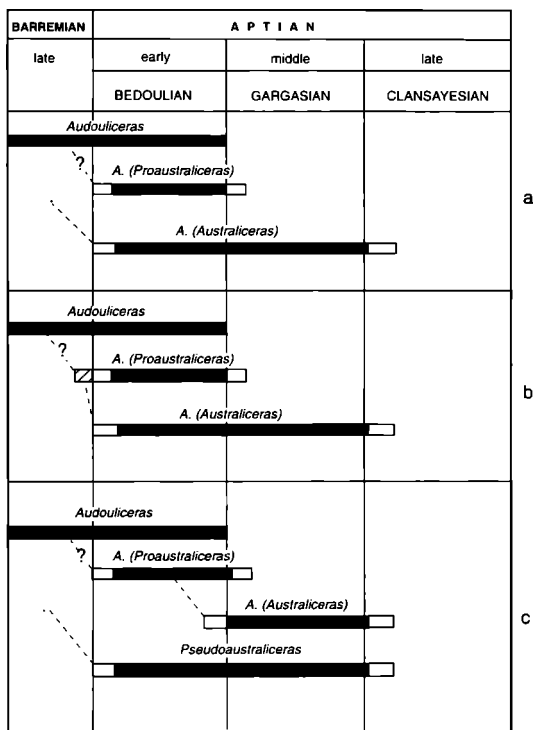


Fig. 2. Suggested lines of evolution in some Ancyloceratidae, according to CASEY (1960, text-fig. 5).

Aptian, with both ancyloceratoid and aspinoceratoid shells, along with *A. (Australiceras)* WHITEHOUSE, 1926 (type species *Crioceras jacki* ETHE- RIDGE, JR., 1880), Aptian, with crioceratoid shells. CASEY (1960, 1961) believed that crioceratoid *A. (Australiceras)* evolved from aspinoceratoid *A. (Proaustraliceras)* in the early mid-Aptian. This conclusion was based on an apparent transition (lineage) from ancyloceratoid through aspinoceratoid to crioceratoid coiling, taking into account overall morphological similarities and stratigraphical distributions.

Complete specimens of *Australiceras* have not been documented, and so the ontogeny of this group is largely unknown. The phylogenetic reconstructions cited above must therefore remain hypothetical. However, biogeographical data can contribute to elucidating the phylogenetic relationships. As noted, representatives of *A. (Proaustraliceras)* are known from the lower Aptian of the northern hemisphere. According to CASEY (1960, 1961), the transition from ancyloceratoid to aspinoceratoid coiling occurs in the lower Aptian, near the boundary between the *Deshayesites deshayesi* and *Tropaeum bowerbanki* zones, with crioceratoid coiling first appearing at the base of the middle Aptian. However, KLINGER & KENNEDY (1977) and AGUIRRE URRETA (1986) reported the earliest crioceratoid forms from the lower Aptian of the "Austral Realm" (Zululand and Patagonia), suggesting



**Fig. 3.** Alternative phylogenetic interpretations for the genus *Australicer* WHITEHOUSE.

that the crioceratoid *A. (Australicer)* originated in the early Aptian in southern high latitudes, from where ancyloceratoid and aspinoceratoid forms have not been recorded (cf. Fig. 1a). This illustrates the problem of reconstructing the phylogenetic and geographic origin of *A. (Australicer)*. At least three alternative phylogenetic interpretations are possible (Fig. 3): (a) If available biogeographical data reflect the true distribution patterns, the genus *Australicer* appears to be polyphyletic (Fig. 3a) and the phylogenetic scheme of CASEY (1960) will need revision. *A. (Proaustralicer)* and *A. (Australicer)* are then better regarded as independent ancyloceratid genera, which originated in the early Aptian in the Tethyan and Austral realms, respectively.

(b) If, on the other hand, the crioceratoid subgenus *A. (Australicer)* evolved from aspinoceratoid *A. (Proaustralicer)* (Fig. 3b), then this must have happened not at the beginning of the mid-Aptian in Europe (CASEY

1961) but in the earliest Aptian, in the "Austral Realm" However, available data do not support this interpretation.

(c) If crioceratoid *Australiceras* did evolve from early Aptian aspinoceratoid forms (e. g. *A. tuberculatum* SINZOW) at the beginning of the mid-Aptian, as suggested by CASEY (1961), then the crioceratoid species of *Australiceras* from the lower Aptian of Zululand and Patagonia would have to be regarded as representatives of different lineages (perhaps belonging to the genus *Pseudoaustraliceras* KAKABADZE, 1981; Fig. 3c here).

To resolve the phylogenetic problems exposed above, a thorough systematic revision of *Australiceras*, *Tropaeum* and related genera of the Ancyloceratidae is needed, taking into account detailed biostratigraphical and biogeographical data. We acknowledge that modifications in the mode of coiling (e. g., aspinoceratoid–crioceratoid) could in some representatives of Ancyloceratidae be regarded as expressions of intrageneric or even intraspecific variation. However, available palaeontological material is inadequate to elucidate this question.

The examples given here illustrate the complexity of palaeobiogeographical investigations. In many cases phylogeny, systematics and biostratigraphy are obscured and/or distorted by the incompleteness of geological and palaeontological data. We believe that only the study of systematically well-known genera and species within a framework of solid data on biostratigraphy, relative abundance, diversity and phylogenetic relationships of species will give clear and reliable indications about directions of dispersal and the geographical origins of taxa.

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