Plate Tectonics, Sea Level Changes, Climate — and the Relationship to Ammonite Evolution, Provincialism, and Mode of Life

(Plattentektonik, Meeresspiegelschwankungen, Klima — und die Beziehung zu Evolution, Provinzialismus und Lebensweise der Ammoniten)

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With 16 Text Figures

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Abstract: An attempt is made to elucidate to what extent plate tectonic processes affected ammonite life, especially during the Cretaceous. In most cases, ammonite evolution is unrelated to plate tectonic events. The geodynamic processes which are most important for ammonite diversification and decline are sea level schanges, and possibly fluctuations in temperature. A combination of both might have been the cause firstly of biotic crises of ammonites at the system boundaries and secondly of their final extinction.

Kurzfassung: Es wird versucht aufzuhellen, inwieweit die Prozesse der Plattentektonik — insbesondere während der Kreide — Evolution und Lebensweise der Ammoniten beeinträchtigten. Wie sich herausstellt, läßt sich im allgemeinen keine Beziehung zwischen beiden Vorgängen herstellen. Wichtigster geodynamischer Prozeß für die Entwicklung der Ammoniten — in positiver wie negativer Hinsicht — dürften die Meeresspiegelschwankungen gewesen sein; auch Temperaturschwankungen haben vermutlich eine Rolle gespielt. Die Kombination beider Prozesse dürfte für die Krisen der Ammoniten-Evolution an den Systemgrenzen und schließlich für ihr endgültiges Aussterben verantwortlich zu machen sein.

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1. Introduction

Can geodynamic and evolutionary processes really be related? Knowing much more today about plate tectonics and the formation of oceanic basins and continental margins — where evolution mainly took place — and about the magnitude of sea level and climatic changes than we did 15 years ago, it may be desirable to pose this question again and reconsider both previous and new results in the light of our increasing knowledge.

There is no question that plate tectonic processes may have affected and continue to affect organic evolution — in this case that of nectonic organisms — to varying degrees. Rifting and spreading processes can weaken provincialism through the opening of seaways. The extent of spreading may be related to sea level changes which mainly affect the continental margins and thus all the shelf habitats. The development of active continental margins may lead to the establishment and evolution of particular ecosystems. The collision of continents may close seaways and create provincialism. But can these purely theoretical considerations be supported by real evidence, and does this evidence contribute to our understanding of ammonite life habitats? Here I attempt to answer these questions with some selected examples, mainly from our own investigations in the late Mesozoic, during which some plate tectonic mechanisms are especially obvious.

2. Plate tectonics

2.1 Rifting

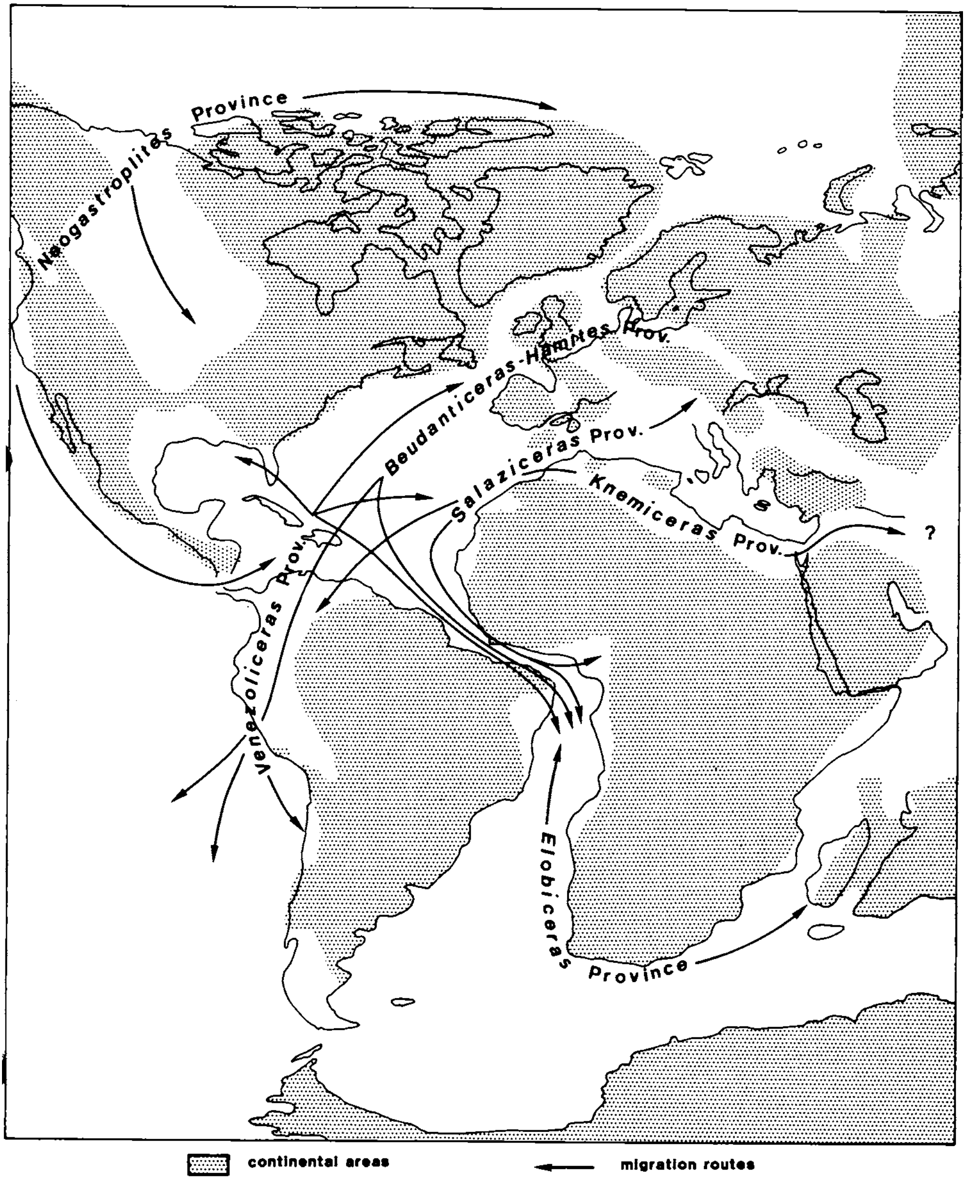
No positive example can be given — at least from the late Mesozoic — that rifting processes are related with ammonite evolution. Early redbed, evaporitic, and euxinic stages of rifting did not at all affect ammonite life. But thereafter, when normal shallow marine conditions had generally been established, ammonite migrations were naturally facilitated: (1) into the Lusitanian-Grand Banks section of the North Atlantic during the Sinemurian (Mouterde et al. 1972, Exton & Gradstein 1984), (2) into the Biscay basin during the Sinemurian at first (Dahm 1967, Schaaf 1986), and again (3) during the Aptian (Rat 1959, Wiedmann 1965, Wiedmann & Boess 1984), after renewal of the Biscay rifting or (4) into the Benue aulacogene during the Middle Albian (Reyment 1956).

However, nothing quantitatively nor qualitatively exciting happened during these times in ammonite evolution.

2.2 Continental break-up, plate motion, and spreading

The final break-up of the Gondwana Plate at what is now the Romanche Fracture Zone was caused by continuing spreading of the North and South Atlantic; there we have a good example of ammonite evolution influenced by the opening of the mid-Atlantic seaway (Text Figs. 1, 2). In contrast to previous observations (Reyment 1969, Reyment & Tait 1972) and in accordance with the discovery of ammonites in the DSDP cores from the Angola Basin and the Walfish Ridge (Wiedmann & Neugebauer 1978; and Text Fig. 2), we know:

a) that the mid-Atlantic seaway started to open during the Middle(?) Albian;
b) that European and Mediterranean species were able to invade the South Atlantic basins (Text Fig. 2A-C: *Hamites, Beudanticeras, Salaziceras*);
c) that, as a consequence, endemism and pronounced provincialism in these areas as well as in the separated South African faunal province (Text Fig. 2D: *Elobiceras*) weakened and finally disappeared, allowing the establishment of a late Albian Cosmopolitan Realm; and



Text Fig. 1. Late Albian paleogeography around the opening Atlantic, ammonite provinces and migration routes. Paleogeography adopted from Barron et al. 1981, Smith et al. 1981, Ziegler 1982, Kauffman 1984 and own observations.

d) that all of these genera were probably shallow marine forms which had not drifted *post-mortem* into near-shore environments where they are generally detected; they must have lived in inner shelf environments since they had to cross the very shallow, young central Atlantic. The area around the Romanche Facture Zone subsided much later to greater depths, i.e., during the Turonian.

These observations were confirmed by benthic (and planktonic) assemblages of foraminifera (Guerin 1981, Moullade & Guerin 1982). The first evidence for an Albian opening of the Central Atlantic came, however, from the ammonites discovered in DSDP cores of Sites 363 and 364, and from the presence of members of northern faunal provinces in the young South Atlantic (Text Fig. 2).

A similar example for defining migration routes is the poorly preserved but interesting ammonite fauna from Curaçao (Wiedmann 1979). These "ammonites" — preserved are only the cavities where the ammonite shells previously has been — occur in the pelagic intercalations in the pillow lavas and hyaloclastites of the Curaçao Lava Formation (Beets 1972). Despite the poor preservation (Text Fig. 3) they enabled us to date with precision the oceanic basement of the Lesser Antilles with the result of a late Middle Albian age. Moreover, they allow recognition of members of the European faunal province (*Beudanticeras*), and of Atlantic provenance (*Dipoloceras*). In addition, representatives of a *Gastroplites-Grycia* Province, forerunners of the late Albian *Neogastroplites* Province in Text Fig. 1, are found. The *Gastroplites-Grycia* Province is located on the Pacific margin of North America. A migration route from the NE Pacific to the Caribbean can be concluded.

Direction of migration routes can be supported by slight age differences and decreasing abundance.

Another interesting example of faunal evidence for plate motion is known from the Lower Cretaceous of Sardinia. Only in one region of the island is a complete and macropaleontologically well represented Lower Cretaceous sequence known; this is the area of Orosei near Dorgali, eastern Sardinia (Wiedmann & Dieni 1968). Here nearly all Lower Cretaceous stages can be dated by their ammonite content, except the Barremian (op. cit., text fig. 2); this stage was first identified in western Sardinia by the presence of the larger foraminifera genus *Valserina* (Cherchi & Schroeder 1973). The most interesting portion of the sequence is the condensed Upper Albian,

Text Fig. 2. Members of different faunal provinces in the Middle-Upper Albian South Atlantic.

North Temperate European Province:

A. *Hamites tenuis* Sow., NMB J 28118.
Middle-Upper Albian, DSDP Site 364-37-2, Angola Basin. 2.5 × .

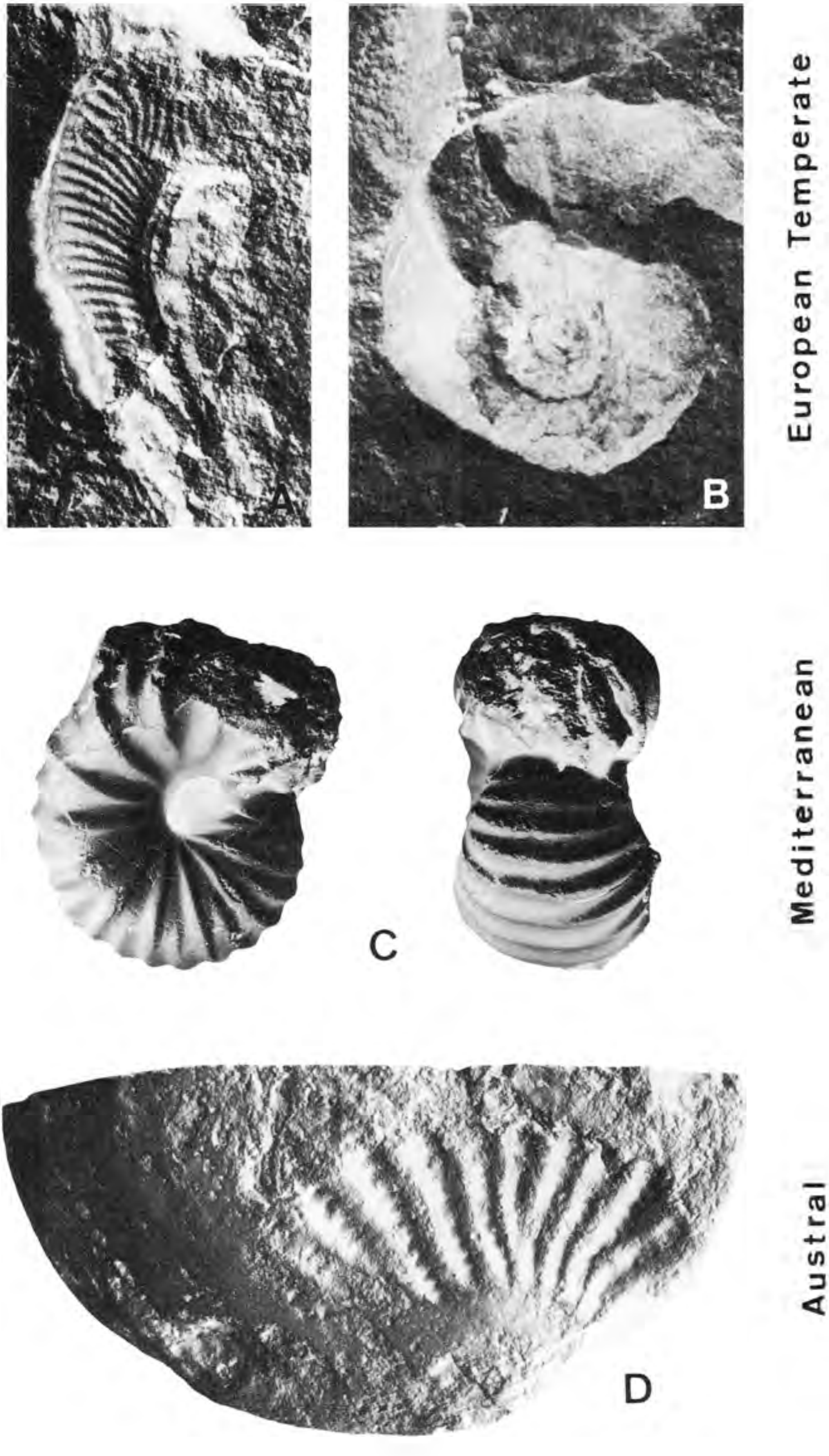
B. *Puzosia quenstedti* (Par. & Bon.), NMB J 28121.
Upper Albian, DSDP Site 364-29-2, Angola Basin. 2/1.

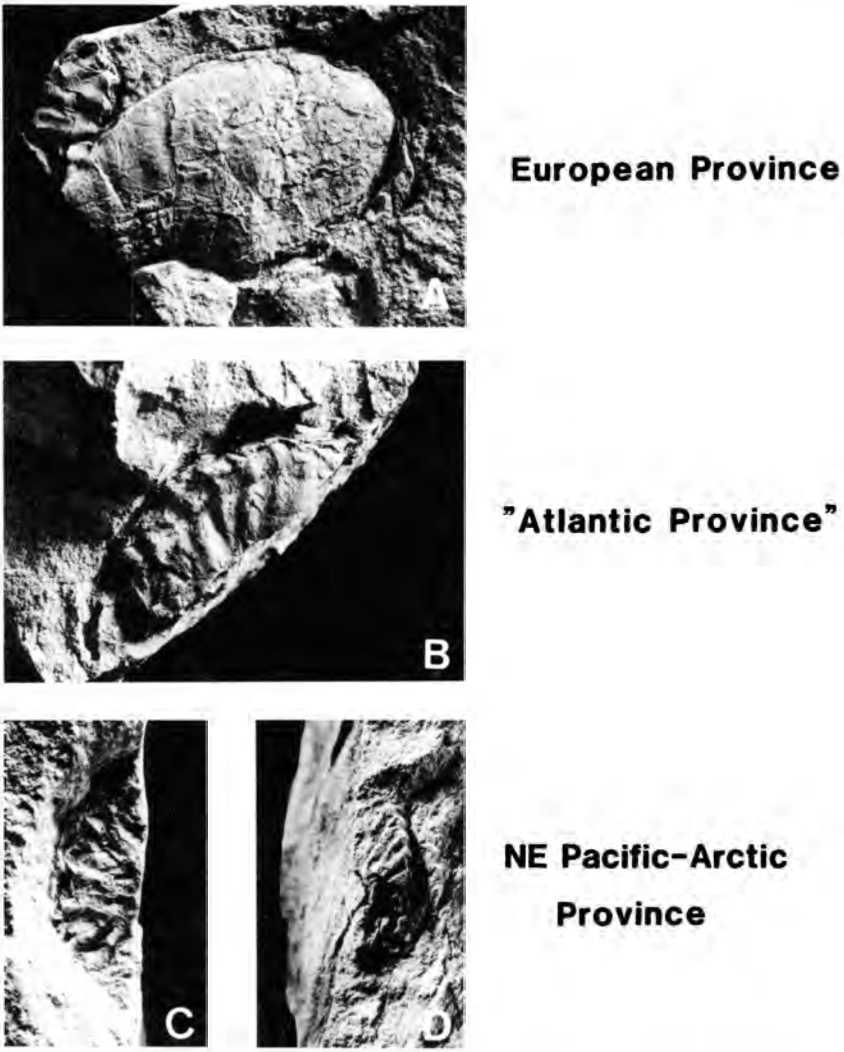
Mediterranean Province:

C. *Salaziceras* cf. *salazacense* (Héb. & Mun.-Ch.), GPIT 1649/1.
Late Albian, Tarfaya (Morocco). 1/1.
The genus is known from France, Hungary, Tunisia, Morocco, Nigeria and South Africa (see Klinger & Wiedmann 1983, fig. 1).

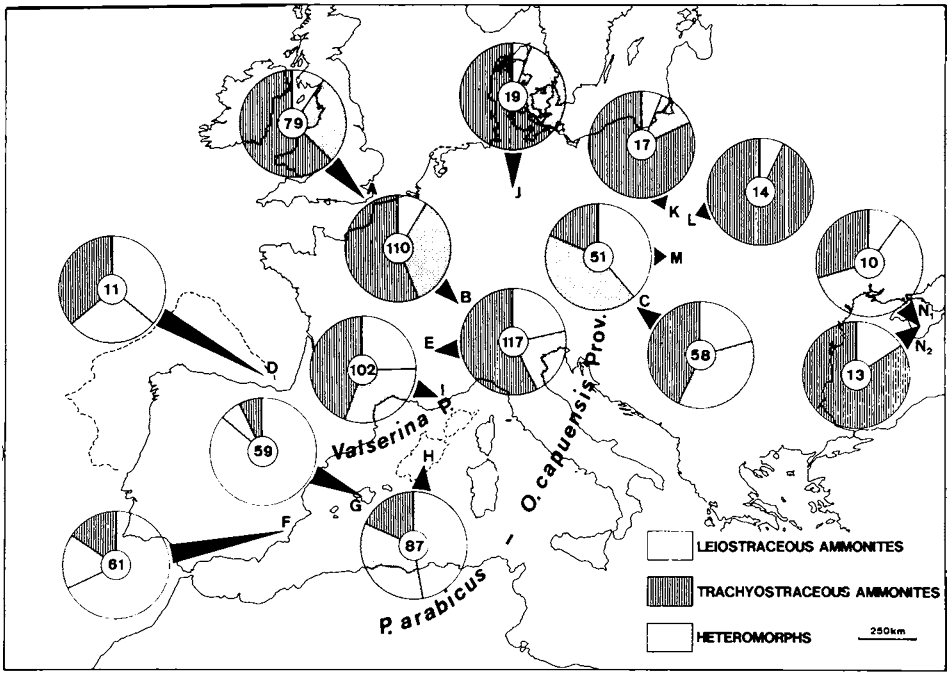
Austral Province:

D. *Elobiceras elobiense* (Choffat). GPIT 1649/2.
Upper Albian, DSDP Site 364-35-2, Angola Basin. 2/1.
Typical member of South Atlantic Upper Albian endemics, extending from Madagascar to Angola, Nigeria and Morocco.


A
B
European Temperate
C
Mediterranean
D
Austral



Text Fig. 3. Members of different faunal provinces in the late Middle Albian Curaçao Lava Formation, Curaçao (see Wiedmann 1978).
North Temperate European Province:
A. *Beudanticeras* sp., USNM coll., 2/1.
Atlantic Province:
B. *Dipoloceras* sp., USNM coll., 2/1.
NE Pacific-Arctic Province:
C. *Gastroplites* sp., USNM coll., 2/1.
D. *Beudanticeras (Grycia)* sp., USNM coll., 2/1.



Text Fig. 4. Ammonite eco-morphotypes of the European Middle-Upper Albian (see Marcinowski & Wiedmann 1985). The number of species counted is given in the center of each spectrogram. Albian positions of the Iberian Plate and the Cor-Sardinian Microplate, before rotation, are indicated by dotted lines.

Localities considered:

A. Folkestone, SE England (Dispar Zone)
B. Sainte Croix, Switzerland (Dispar Zone)
C. Bakony Mountains, Hungary (Dispar Zone)
D. Basco-Cantabric Ranges, N Spain (Dispar Zone)
E. Salazac, Gard, S France (Dispar Zone)
F. Subbetic of Caravaca, Murcia, S Spain (Upper Albian)
G. Mallorca (Upper Albian)
H. Orosei, Sardinia (Dispar Zone)
I. Escragnolles, SE France (condensed Dentatus through Dispar zones)
J. Salzgitter, N Germany (Upper Albian)
K. Mt. Chelmowa, Poland (Auritus through Inflatum zones)
L. Annopol-on-Vistula, Poland (condensed Dentatus through Inflatum zones)
M. Wielka Rówień, Tatra Mts., Poland (condensed Mammillatum through Inflatum zones)
N1. Crimea Highland, Soviet Union (Inflatum Zone)
N2. Same locality (Inflatum through Dispar zones).

in which a comparatively rich ammonite association accumulated. Despite the position of Sardinia in the center of the western Mediterranean, only 20% of the ammonite species there are also known from the nearby Balearic Islands. An equal number of Upper Albian endemics (17%) was registered, but most of the species (63%) surprisingly show relation to species of the northern Hoplitid Province.

Grouping the European Upper Albian and especially the Vraconian ammonite species in the three main "ecomorphotypes" (Text Fig. 4), i.e., the smooth leiostraceous, sculptured trachyostraceous, and uncoiled heteromorph species, the Sardinian spectrum has much more in common with those of the northern epicontinental seas (northern Spain, southeastern France, Switzerland, Hungary, England, and the Polish Carpathians) than with those of the Mediterranean basins (Balearic Islands and Spanish Subbetic area), where leiostraceous species generally prevail.

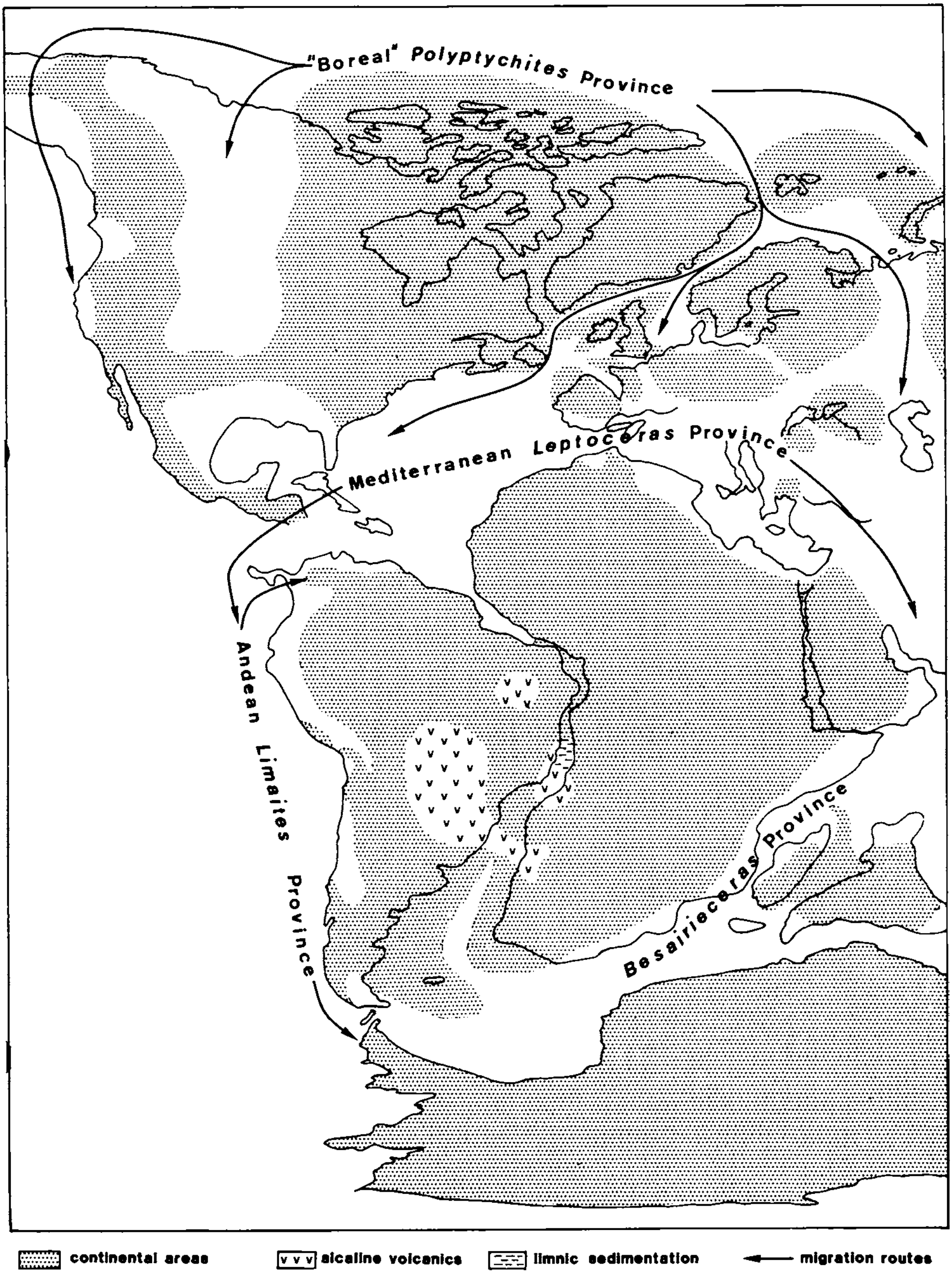
A northern relationship is also shown by the larger foraminifera of the western Sardinian Barremian studied by Cherchi & Schroeder (1973). The authors were able to demonstrate that these forms do not belong to the true Mediterranean contemporaneous *Paleodictyoconus arabicus* - *Orbitolinopsis capuensis* Province, which covers a large area between North Africa, Italy, and Yugoslavia, but have to be attributed to the more northern *Valserina* Province of the Pyrenees and southern France (Schroeder et al. 1974). Both macro- and micropaleontological observations thus pointed to a more northern position of Sardinia during the Lower Cretaceous. Paleomagnetic research carried out by Alvarez (1972, 1976) and Westphal et al. (1976) supported this idea and indicated a counterclockwise rotation of the Cor-Sardinian Microplate from its original position near the present coastline of southern France. The discontinuous Lower Cretaceous faunal pattern in the western Mediterranean thus cannot be related to faunal but to plate migration.

It is worth mentioning that in these cases foraminifera and ammonite provincialism was used for reconstructing both plate motion and the opening of seaways, sometimes against current opinions and long before confirmation of paleomagnetic research. Also in the case it has to be concluded that, aside from facilitating migration and replacement of endemic by cosmopolitan species, these types of plate motion did not affect ammonite evolution substantially.

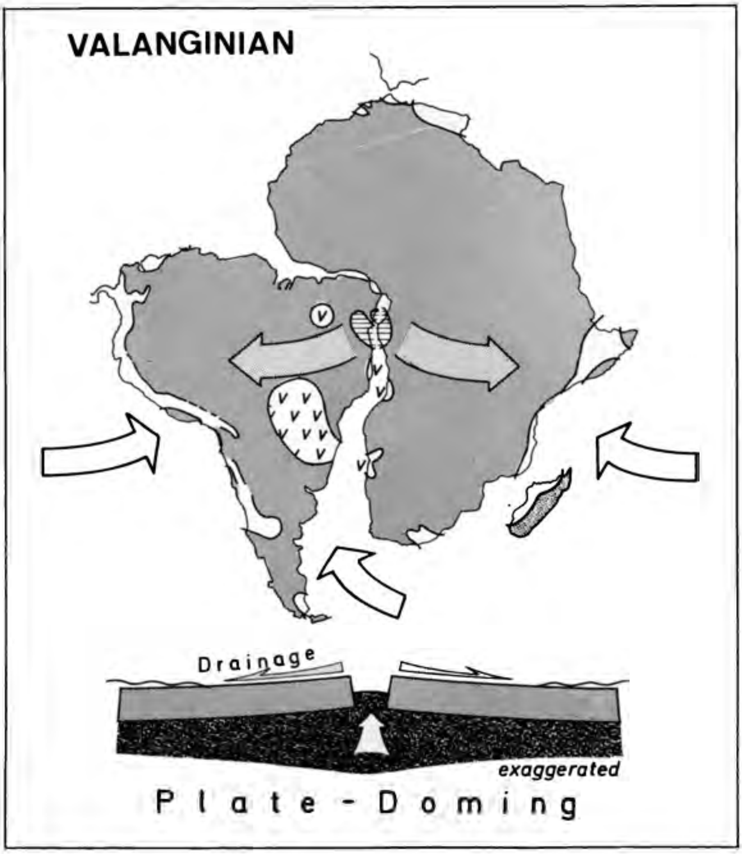
We have to admit that the picture of ammonite provincialism changes continuously due to new discoveries. Good examples are the recently increasing informations on the distribution of the previously endemic *Salaziceras* and *Heteroceras/Colchidites* as demonstrated by Klinger & Wiedmann (1983, figs. 1, 2), or the discovery of the Indo-Pacific *Utaturiceras* and *Yubariceras* in northern Germany (Wiedmann & Schneider 1979) and the Alpine Gosau beds, respectively (Wiedmann in Herm et al. 1979).

2.3 Plate tilting and shelf-sea development

Break-up of the southern megaplate and early rifting of the South Atlantic were initiated by extrusion of thick alcaline volcanics, followed by continental to limnic sedimentation in the northern, and first marine invasion in the southernmost South Atlantic (Text Fig. 5). It is interesting to note that following a period of widespread continental sedimentation along the Andean Trough, we have a new marine sedimentary cycle and increase of subsidence beginning in the latest Jurassic and continuing through the Lower Cretaceous. Similar conditions are known for the eastern margin of the African Plate, where similar enlarged shelf basins developed (Text Fig. 5). It can be assumed that the South Atlantic rifting was preceeded by central doming resulting in plate tilting which is documented in the subsiding outer plate margins (Text Fig. 6). We can, moreover, observe that the young South American



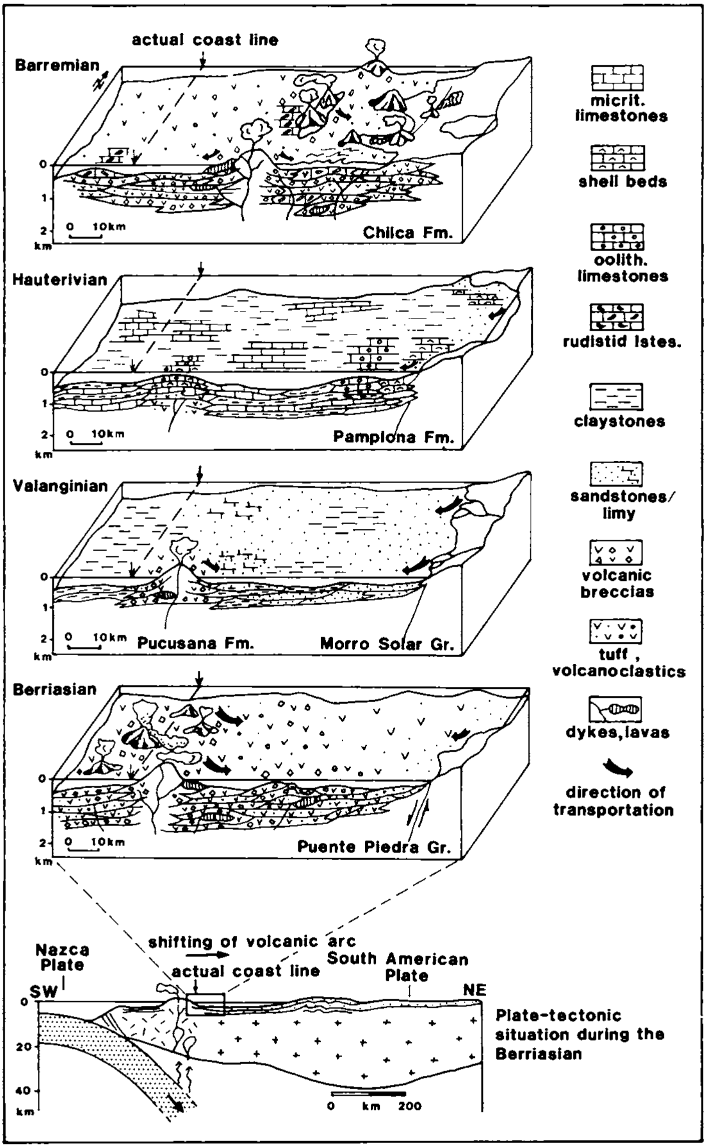
Text Fig. 5. The Valanginian Atlantic, break-off of South America and Africa, early rifting of South Atlantic with alcaline volcanics and limnic sedimentation in the north and marine ingression in the south. Notice the time-equivalent subsidence at the outer plate margins (see also Text Fig. 6). Paleogeography mainly from Barron et al. 1981, Smith et al. 1981, Dercourt et al. 1985, and own observations.



Text Fig. 6. Presumed plate-tilting of the South American and African plates in consequence of central doming and rifting at the Jurassic-Cretaceous boundary (see also Text Fig. 5).

plate tilted as a whole not only towards the west, but also towards the north. The age of the late Jurassic-early Cretaceous Andean transgression becomes younger from south to north (Oxfordian in the Neuquen Basin and Central Chile, Berriasian in the Coastal Cordillera of Peru, and Albian in Ecuador and Columbia (Wiedmann 1980), just as the opening of the South Atlantic proceeded from the Cape Basin into the Angola Basin and, finally, towards the equator (Ponte & Asmus 1978).

At the same time the late Jurassic — early Cretaceous Andean Faunal Province (Text Fig. 5), which was characterized by a high degree of endemism (Gerth 1921, 1925, Leanza 1980, Leanza & Wiedmann 1980), disappeared. In the course of the Lower Cretaceous, the largely endemic ammonite faunas (e.g., the Valanginian *Limaites* Province) were increasingly substituted by Mediterranean and cosmopolitan species. Finally, the Albian opening of seaways towards the northeast gave access to the cosmopolitan douvilleiceratids, dipoloceratids, and mortoniceratids. Again, no new evolutionary lines developed.



Text Fig. 7. Evolution of the Peruvian active continental margin near Lima during the early Cretaceous (from Wiedmann et al., in prep.).

The rate of subsidence of the Andean margin was very low in the beginning; the presence of rudistid limestones, for example, is evidence for nearshore and inner-shelf environments (Text Fig. 7).

2.4 Island arcs; trenches, and active continental margins

At the same late Jurassic to early Cretaceous time, development of an active continental margin proceeded in the Andean Realm with island arcs and smaller lagoons and with an increasing amount of volcanics and volcanoclastics being deposited (Text Fig. 7). It is evident from our knowledge of the coastal cordilleras of Chile, Peru, and Columbia, that these restricted environments did not favour organic evolution of any kind. Microbiotas seem to be virtually absent in these deposits, and macrofaunas are not abundant vertically nor horizontally. However, a diagenetic overprint cannot be totally exluded.

One exception to the rare macrofaunas is the comparatively ammonite-rich Plattenkalk deposited in an restricted lagoonal environment of the Puente Puedra Formation near Lima, Peru (Rivera 1951, Wiedmann 1980, Wiedmann et al. in prep.). The fauna of Berriasian age is 90% cosmpolitan (surprisingly high), and only 10% endemic (Text Fig. 8).

No extensive investigations have been made of biotas in active margin zones.

2.5 Passive margin evolution

The study of Atlantic-type continental margins and related coastal basins was found to be particularly significant (Text Fig. 9):

a) we are able to detect some analogous stages of formation of oceanic basins and continental shelves independent of geologic time, but governed by large-scale crustal and tectonic events;

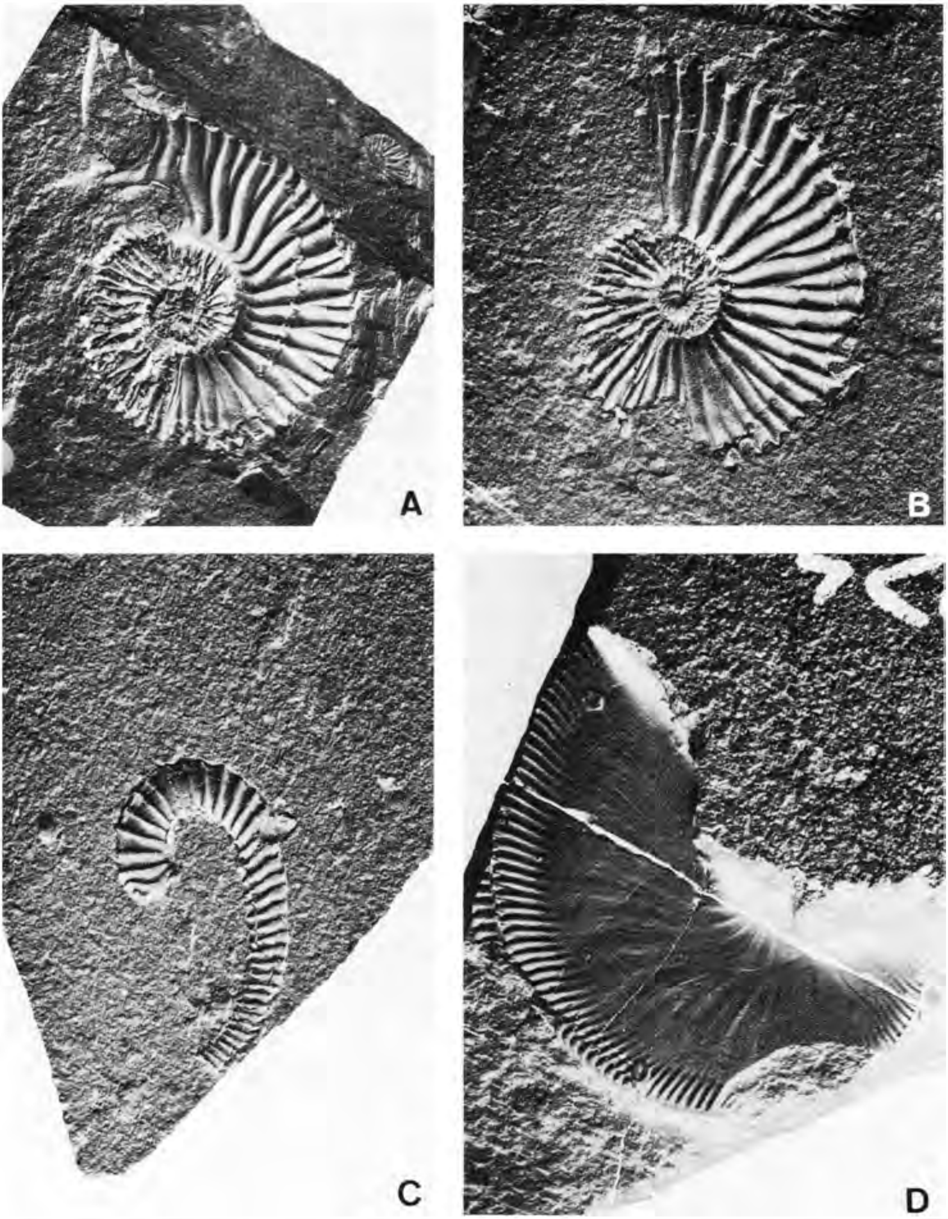
b) in spite of the results obtained from deep sea drilling, only the coastal basins permit the exact recognition of sea level changes; from here we can try to link these changes with possibly related spreading events;

c) finally, much of our knowledge of fossil life comes from shelf deposits, not accidentally, but because this is the main area for biotic evolution in the marine realm.

Therefore it is reasonable to assume that our knowledge of the evolution of fossil life and biotas will increase as we learn more about the evolution of the continental shelf areas.

Main episodes in the formation of oceanic basins and continental shelves — such as the euxinic black shale phase, the formation of delta cones, the construction of carbonate ramps and platforms, or the subsequent episode of pelagisation, — have their own characteristic biotas, and we can follow their appearance, evolution and disappearance. Comparable sequences can be observed at any passive margin, unrelated to the age of its development. It can, thus, be assumed, that these episodes in the development of oceanic basins and continental margins are governed by one and the same geodynamic process, a process which is not yet clearly understood. It is not surprising to find some of these episodes superimposed or maybe controlled by large-scale tectonic events, and these in turn related with "global" sea level changes (Jansa & Wiedmann 1982, Wiedmann 1982).

An example of this is the development of the late Jurassic carbonate platforms which formed the shelves around the North Atlantic (Text Fig. 9) and became partly destroyed and drowned by distensive "Late Cimmerian" tectonics and subsequent



Text Fig. 8. Selected ammonites from the Berriasian Puente Piedra Formation of Puente Inga, near Lima, Peru (see Text Fig. 7).

Cosmopolitan forms:

A. *Berriasella limensis* (Lisson). GPIT 1649/3. 1/1.

B. *Berriasella*(?) cf. *tenuicostata* Burckh. GPIT 1649/4. 2/1.

C. *Protancyloceras* cf. *steinmanni* Riv. GPIT 1949/5. 2/1.

Endemic species:

D. *Limaites peruanus* (Lisson). GPIT 1649/6. 2/1.

subsidence (Wiedmann et al. 1982a). Most of the pre-existing biotas disappeared at the same time. It is noteworthy that these tectonics affected the shelf as well as the deep basins and can be related to spreading activity, which may also be the case for the immediately following Valanginian transgression. Similar processes can be observed in the younger Biscay Ocean in exactly the same way but at a later time (Wiedmann 1982, text fig. 10): The Urgo-Aptian carbonate platforms — mostly island platforms on top of tilted blocks — were destroyed by both Albian "Austrian" tectonics and increasing subsidence in the late Albian; this event and the following mid-Cretaceous transgression on the Iberian Plate are related not only to the first spreading activity in the young Biscay Ocean, but presumably to a global spreading event in late Albian-early Cenomanian time (Sheridan 1986).

There is no question that the development of carbonate platforms and continental shelves favoured cephalopod life, but it is still hard to determine the controlling factors (changing water depth, temperature, salinity, etc.) from the fossil record.

3. Global and local sea level changes

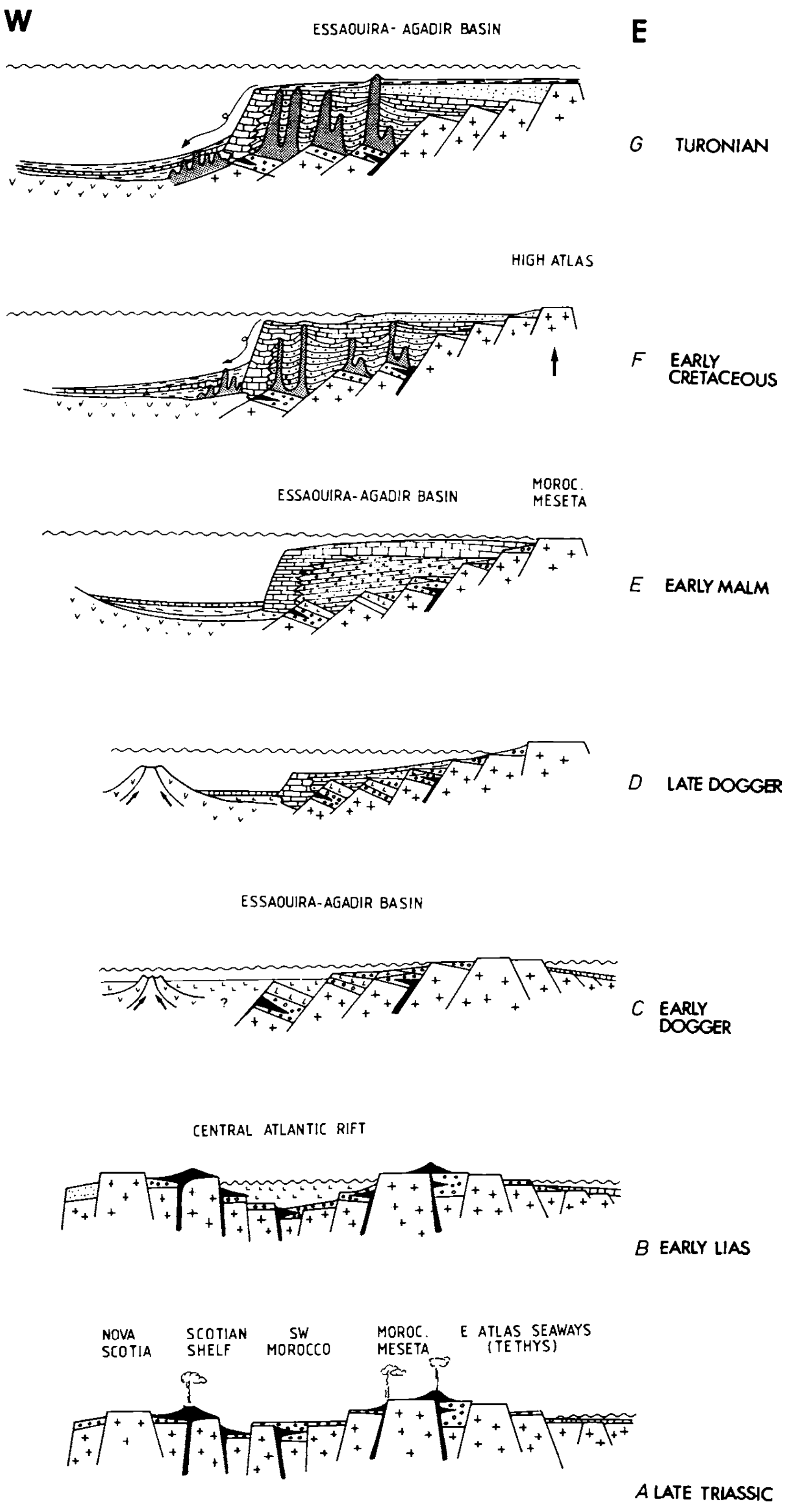
Continental margins and marginal basins are not only the places where sea level changes can best be detected, but they are also the places where local fluctuations can be separated from global ones (Text Fig. 10). Sea level changes are the processes which most affect organic evolution, at least in shelf and continental seas.

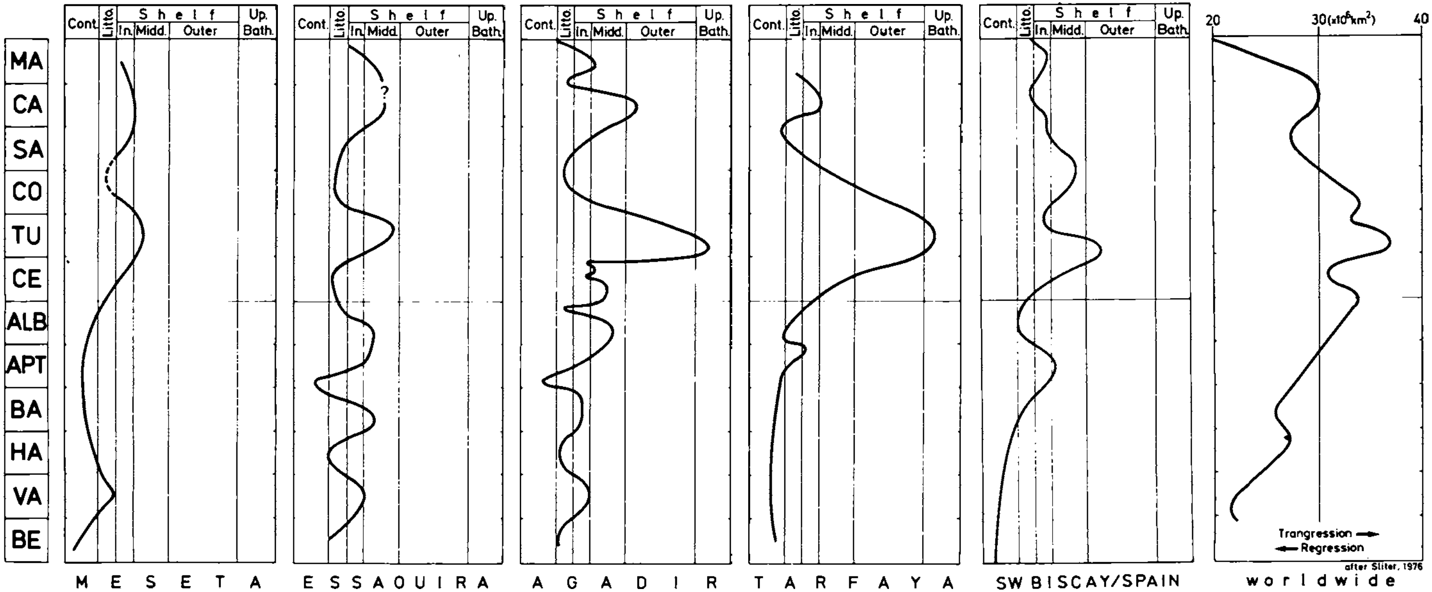
With the global Cenomanian peak transgression, micro-associations exhibit a complete faunal replacement from benthic to planktonic associations, even recognizable or traceable into restricted continental seas (Wiedmann et al. 1978). The complete foodchain of plankton-feeders and their predators immediately evolved, not least of which were the ammonites. Since the transgression, which started in the late Albian, involved most of the shelf areas, the ammonites reached their peak diversity and possibly also their peak density at that time.

An interesting example is the mid-Cretaceous transgression onto the Alpine, Helvetic, and Carpathian shelves, where the transgression interrupts the evolution of the Urgonian carbonate platforms. It is related to condensation, formation of

Text Fig. 9. Episodes of passive margin development, Agadir-Essaouira Basin, Morocco (from Wiedmann 1982).

A. Late Triassic graben with calc-alcaline volcanics.
B. Early Liassic evaporitic rifting stage.
C. Early spreading of early Dogger.
D. Spreading and early carbonate shelf development, late Dogger.
E. Early Malm carbonate platform development.
F. Early Cretaceous platform drowning, prograding delta cones, early turbidites, initial diapirism.
G. Turonian peak subsidence, pelagisation event, with continuing turbiditic sedimentation and salt diapirism.

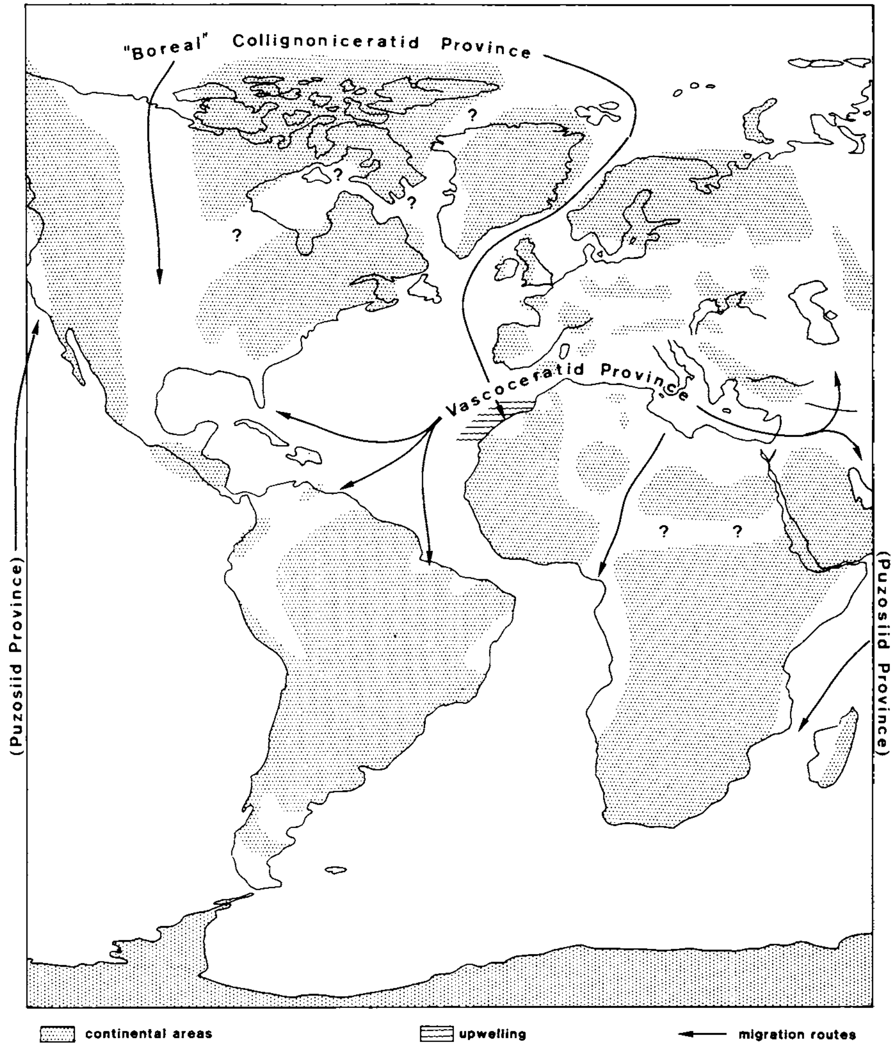

W
ESSAOUIRA- AGADIR BASIN
E
G TURONIAN
HIGH ATLAS
F EARLY CRETACEOUS
ESSAOUIRA-AGADIR BASIN
MOROC. MESETA
E EARLY MALM
D LATE DOGGER
ESSAOUIRA-AGADIR BASIN
?
C EARLY DOGGER
CENTRAL ATLANTIC RIFT
B EARLY LIAS
NOVA SCOTIA
SCOTIAN SHELF
SW MOROCCO
MOROC. MESETA
E ATLAS SEAWAYS (TETHYS)
A LATE TRIASSIC



Text Fig. 10. Global and local sea level fluctuations in the Cretaceous Morrocan coastal basins (from Wiedmann et al. 1978).

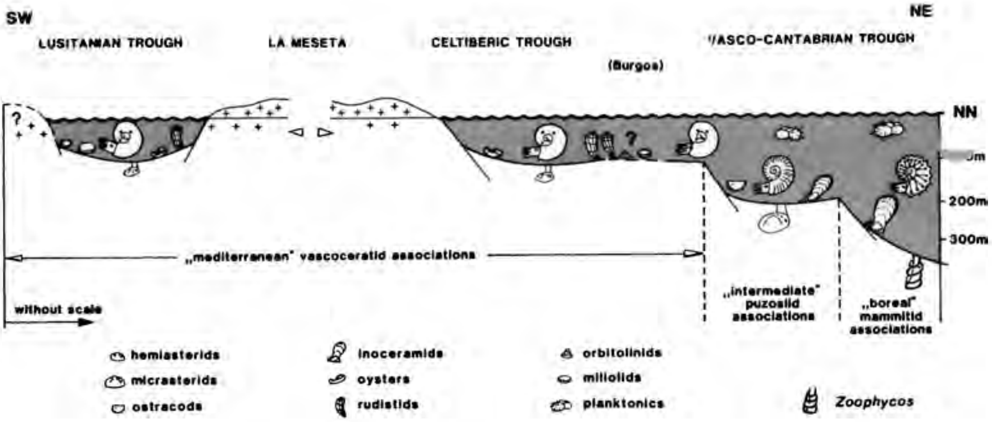
hardgrounds, and glauconite and phosphate deposition (Bergner et al. 1982, Gebhard 1983, Marcinowski & Wiedmann, this vol.) due to the rapidly decreasing terrigenous input from the likewise submerged, previous source areas.

As mentioned above, due to the opening of seaways contemporaneously with this transgression, Lower Cretaceous provincialism disappeared and a cosmopolitan fauna developed in late Albian to middle Cenomanian time.



Text Fig. 11. Turonian paleogeography around the Atlantic (after Barron et al. 1981, Smith et al. 1981, Kauffman 1984, and own observations), ammonite provinces and migration routes.

It is interesting to note that the maximum transgression during late Cenomanian to early Turonian time was again linked to increasing provincialism (Text Figs. 11, 12, 13). This provincialism is easily explained by the development of large continental seas and seaways (Trans-Sahara seaway, Western Interior Basin) or very shallow marginal seas (around the Iberian Meseta). Nevertheless, within these shallow seas, most of which graded into open oceans, very different and specialised ammonite associations could develop: In the subtropic to tropic shallow seas they were mainly formed by unornamented groups with simplified pseudoceratitic suture lines, e.g., *Neolobites* and *Vascoceras* in the Cenomanian, *Pseudotissotia* and *Wrightoceras* in the Turonian, *Tissotia, Tissotioides* and *Hemitissotia* in the Coniacian, and *Lenticeras* in the Santonian. In Spain and Portugal these faunas were detected in the shallow Lusitanian, Celtiberian, and southern Basco-Cantabrian troughs, where they are associated with oysters, rudistids, larger foraminifera, miliolids, agglutinants, and ostracods. In the Basco-Cantabrian Trough these "Tethyan" associations, which developed only in times of maximum transgression are replaced towards the north (provinces of Alava and Biscaya) by associations of puzosiids (*Pachydesmoceras, Parapuzosia*), placenticeratids, by acanthoceratids in the Cenomanian, and mammitids in the Turonian. The replacement is related to northerly increasing water depth. In addition, oysters and rudists become replaced by inoceramids, while within the foraminifera the first planktonics join the still prevailing benthic associations. Furthermore, rich associations of irregular echinoids (*Micraster*) occur locally (Text Fig. 12). Further north, in the present-day coastal areas of the provinces of Biscaya and Guipuzcoa, turbiditic sedimentation prevails, and water depth increases again. Associations pass gradually into the so-called "Temperate" ammonite associations with acanthoceratids, mammitids, pachydiscids, abundant inoceramids, and exclusively planktonic foraminifera.



Text Fig. 12. Depth and temperature(?) control of ammonite distribution in the late Cenomanian - early Turonian of northern Spain and Portugal (after Wiedmann 1975b).

These mid-Cretaceous examples are of special importance since they document the problem of utilizing eco-morphotypes in ammonites. Contrary to the belief that smooth (leiostraceous) forms are related to greater water depth, a direct relationship between the simplification of ammonite sculpture and suture line and the decrease of water depth (= increase of water temperature) can be demonstrated (Wiedmann 1975b, 1976, Wiedmann & Kauffman 1978). It is interesting to note that these strongly specialized groups were unable to survive the next environmental change, i.e., the subsequent marine regression.

In contrast to the general opinion that ammonite diversity and provincialism increase during times of regression, it is finally shown that times of transgressions also favour ammonite provincialism (Marcinowski & Wiedmann, this. vol.). It is related to water depth and presumably water temperature at depth. This can be interpreted as a further indication of a bottom-related life habit of ammonites, since the temperature gradient is more pronounced at the seafloor.

4. Climate

That temperature played indeed a major role in ammonoid distribution and provincialism is likewise obvious from Text Fig. 4. The Hoplitinid Faunal Province of the Albian in Temperate northern Europe, which was dominated by trachyostraceous ammonite associations, was connected by a variety of open seaways with the Tethyan Realm, which was dominated at that time by leiostraceous ammonite groups (phylloceratids, lytoceratids, desmoceratids, and knemiceratids). Both were separated by a relatively sharp boundary running parallel to the Albian paleoequator.

Not as easy to explain, however, is the presence of northern Temperate and especially North American ammonite faunas in the mid-Cretaceous (Cenomanian to Coniacian) of southern Morocco in the Tarfaya-El Aaiun Basin (Text Figs. 11, 13, 14). Here the typical Tethyan associations of molluscs (pseudoceratitic ammonites, oysters, and rudists), which are still present in the northern and central part of Morocco, are again replaced by associations of Temperate ammonites (*Tarrantoceras, Selwynoceras,* and *Otoscaphites* (see Text Fig. 13)), inoceramids, and astartids. Unlike in northern Spain, the Temperate genera and species occur south of the Tethyan ones, and — more importantly — both faunas were buried and most probably spent their life under equivalent bathymetric inner shelf conditions.

The peculiarity of these Tarfayan faunas was first detected by Collignon (1967). An explanation given by Choubert et al. (1972), was that of the pre-drift connection between North America and northwestern Africa. But meanwhile we know that the North Atlantic was open in the Cenomanian for at least 3000 km (Text Fig. 11). An interesting second theory was developed by Reyment (1969) who believed in an alternating tilting of the North African plate to permit alternating transgressions with immigration of Temperate faunas from the west and of Tethyan ones from the east. This faunal alternation should, however, be provable in stratigraphic sections. For this reason new field work was initiated, allowing the following conclusions (Einsele & Wiedmann 1975, 1982, 1983, Wiedmann 1976, Wiedmann et al. 1978b, 1982b):

The Tarfaya Cretaceous is represented by a single sedimentary cycle (Text Fig. 10). Sedimentation starts with a "Weald-like", thick series of continental to deltaic sandstones and conglomerates of early Cretaceous age. The subsequent marine transgression is represented by greenish marls and nearshore shell beds of late Albian age. Cenomanian, Turonian, and Coniacian sediments consist of thin-bedded black marls and shales alternating with well-bedded limestones or more or less silicified concretionary layers. These types of sediments were deposited during the peak transgression on the African Plate. The Santonian and Campanian are again characterized by nearshore shell beds. Marine sedimentation terminates with deposition of the phosphatic Cretaceous-Tertiary boundary beds of the El Aaiun Basin. This means that similar depth conditions, i.e., sedimentation on the inner shelf, persisted through the whole sequence, even at the peak transgression. Characteristics of the laminated black marls include the high amounts of organic matter (up to 10% Corg), silica (which is probably derived from opaline skeletons of diatoms and radiolarians), phosphate (250-4600 ppm P_2O_5), heavy metals, and calcium carbonate (35-99%), as well as the absence of shell beds and the scarcity of bioturbated layers.

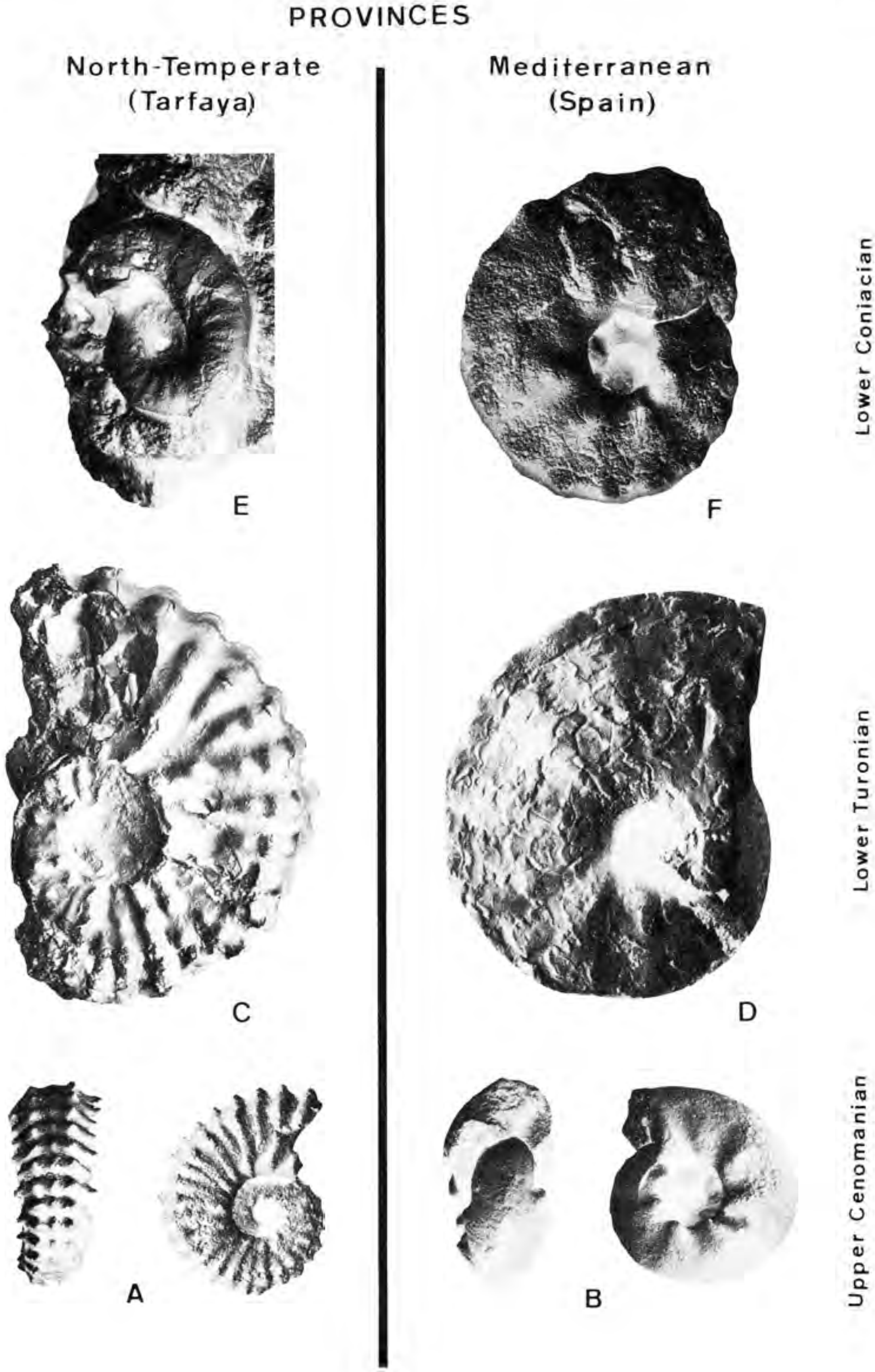
More interesting, however, are the faunal peculiarities of these black marls, i.e., the total absence of Tethyan ammonites, oysters, rudistids, or benthic microfaunas, and the appearance of Temperate ammonites, inoceramids, globigerinoid planktonics associated with heterohelicids, calcareous nannoplankton, and calcispheres.

From all the sedimentological and faunal observations, Reyment's hypothesis can easily be rejected. The mid-Cretaceous sequence is stratigraphically complete, layers with Tethyan faunas were not observed.

If we look for similar sedimentological and faunal features in the Recent, these can be detected in areas of coastal upwelling. Upwelling conditions give indeed the only reasonable explanation for the very uncommon distribution pattern of Temperate ammonites in the center of the Tethyan Realm. This means that (1) temperature was one of the controlling factors for ammonite distribution; (2) climate and current systems of the North Atlantic are believed to have been similar in the mid-Cretaceous to those existing now (Text Fig. 14); and (3) black shale sedimentation on the Morrocan shelf has to be genetically separated from similar Cenomanian-Turonian black shales of the North Atlantic deep ocean (Kuhnt et al. 1986), largely deposited below the CCD and possibly caused by a global oxygen minimum zone (Schlanger & Jenkyns 1976).

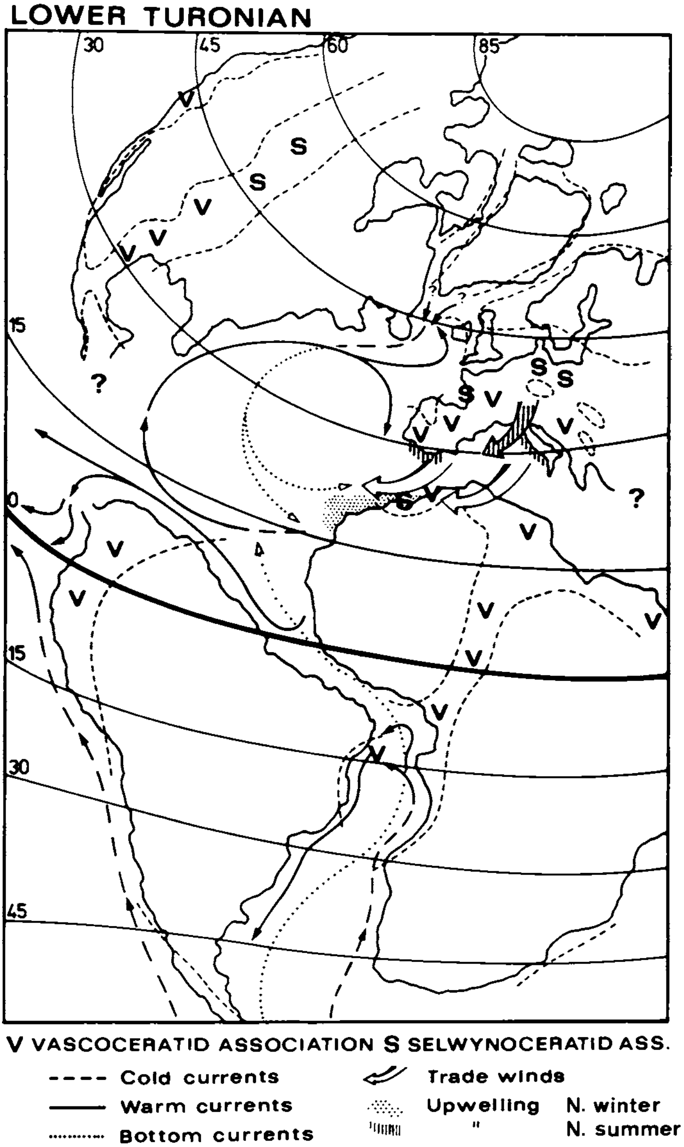
Text Fig. 13. Index ammonites of the mid-Cretaceous of the Mediterranean compared with those of the Tarfaya Basin.

- I. North Temperate species of Tarfaya
    - A. *Tarrantoceras wrighti* Coll. SGM coll. Upper Cenomanian, Oued Ougnane Tel-li. 2/3.
    - C. *Selwynoceras reymenti* Coll. SGM coll. Lower Turonian, Oued El Ouaar. 1/2.
    - E. *Otoscaphites* cf. *bladenensis* (Schlüter). GPIT 1649/7. Lower Coniacian, Sebkha Houiselgua. 1.5×.
- II. Mediterranean species from northern Spain
    - B. *Vascoceras diartianum* (D'Orb.). GPIT 1649/8. Upper Cenomanian, Ganuza (Navarra). 2/3.
    - D. *Wrightoceras submunieri* Wiedm. GPIT 1471/2. Lower Turonian, Picofrentes (Soria). 2/3.
    - F. *Tissotioides haplophyllus* (Redt.). GPIT 1649/9. Lower Coniacian, Masa (Burgos). 2/3.


PROVINCES
North-Temperate
(Tarfaya)
Mediterranean
(Spain)
E
F
Lower Coniacian
C
D
Lower Turonian
A
B
Upper Cenomanian

5. Ammonite mode of life and extinction

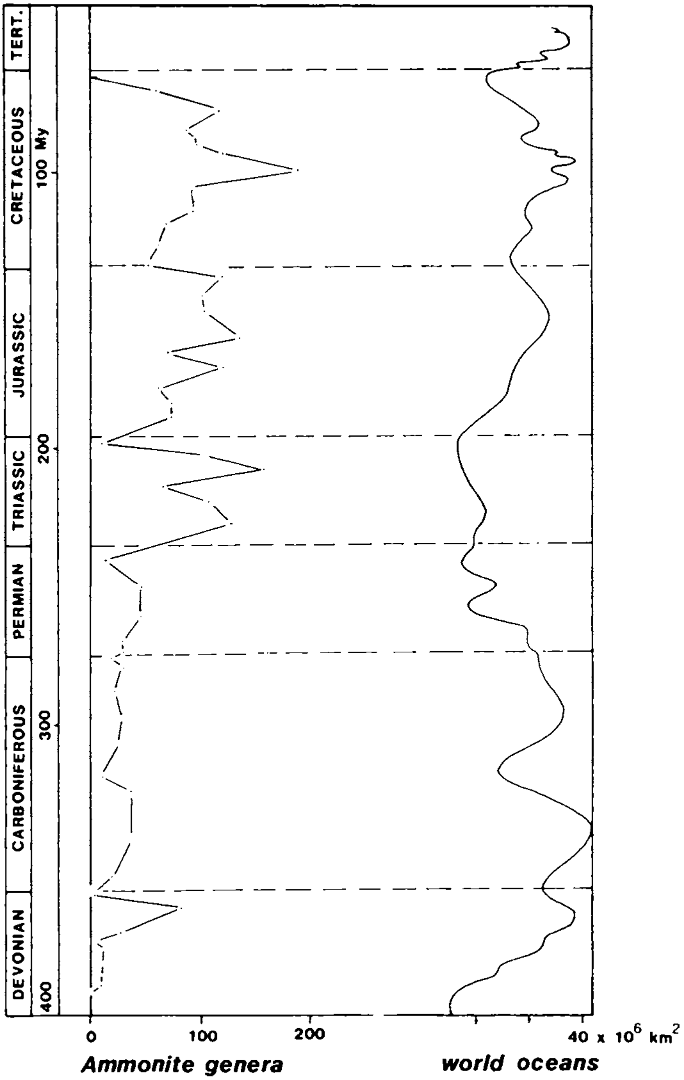
Although our knowledge of the mode of life of ammonites is still very limited, we have seen that two factors controlled and greatly affected ammonite evolution and diversification, i.e., sea level changes and temperature. From observations of the



Text Fig. 14. Significance of Lower Turonian ammonite provincialism for oceanic circulation in the Atlantic and the driving wind system (from Thurow et al. 1982).

Basco-Cantabrian Trough, we can possibly conclude that ammonites had an epibenthonic life habitat. The main area of ammonite distribution through time was shallow marine inner shelves on which ammonite record reaches its peak.

In turn, the ammonite extinction pattern should be related to the ammonite mode of life. Studying the Mesozoic extinctions (Wiedmann 1968, 1969, 1970, 1973a, 1973b, 1973c, 1975a), it has become obvious to the author, that global re-

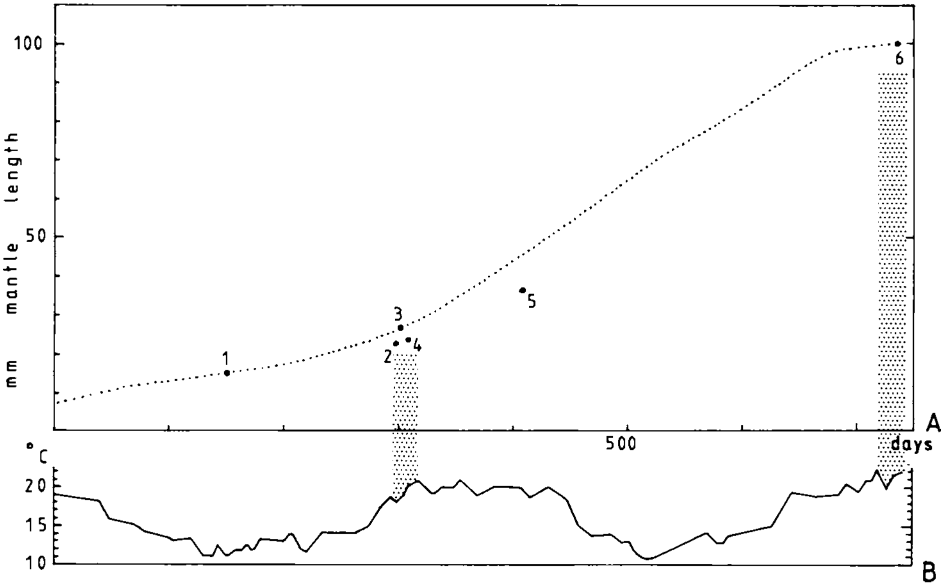


Text Fig. 15. The parallelity in the course of ammonite diversity (from House 1985) and global sea level fluctuations (after Yanshin 1973, Sliter 1976), from the Devonian to the Cretaceous.

gressions did indeed affect ammonite life most markedly (Text Fig. 15). Naturally, marine regressions become most effective only in shelf areas, the favoured biotopes of trachyostraceous ammonites. The basinal habitat of leiostraceous groups (like the ophiceratids, phylloceratids, lytoceratids, or haploceratids) explains not only why these groups were less affected by the great faunal caesuras at the system boundaries, but also why new phylogenetic lines in ammonites (of Scythian, Hettangian, or Valanginian ages) generally start with smooth leiostraceous forms (Wiedmann 1973c, fig. 11).

New investigations on the final decline of ammonites (Ward & Wiedmann 1983, Ward et al. 1986, Wiedmann, this vol.) support the idea of an intimate interrelationship between the pattern of sea level changes and ammonite diversity. The decline of ammonites during the Upper Cretaceous exactly parallels the curve of late Cretaceous regressions and transgressions. It was shown at the same time that — although diminished — all four groups of Cretaceous ammonites (phylloceratids, lytoceratids, ammonitids, and heteromorphs) persisted into the late Maastrichtian (Wiedmann this vol., fig. 7).

These observations do not devalue the opinion (Birkelund & Hakansson 1982, Wiedmann 1986, this vol.) that the biocollapse at the Cretaceous-Tertiary boundary was the result of a much more comples scenario. Changing temperature (Douglas &



Text Fig. 16. Reduced growth rates in *Sepia officinalis* cultivated under extreme diet and continuous light conditions (from Wiedmann & v. Boletzky 1982).

A. Cuttlebone growth curve of 6 specimens. Black circles mark time of death.

B. Course of temperature during the experiment. Note, that the specimens 2, 3, 4 and 6 died after increasing temperature.

Savin 1975, Thierstein & Berger 1978, Birkelund & Hakansson 1982, Hsü et al. 1982, Smit & ten Kate 1982) may have contributed to the final collapse as well, while controversy continues about the nature and value of the cosmic Iridium event (Alvarez et al. 1980, Hsü 1980, Smit 1982). These two last mentioned events are restricted to a very short episode at the Cretaceous-Tertiary boundary itself, and, thus, have nothing to do with the decline and extinction of ammonites which started and finished much earlier (Hancock 1967, Wiedmann 1969, 1986, this vol., Ward & Wiedmann 1983, Ward et al. 1986).

6. Experiments on living cephalopods

To gain a better understanding of environmental factors controlling cephalopod life and distribution, experiments using Recent *Sepia* are being conducted (v. Boletzky & Wiedmann 1978, Wiedmann & v. Boletzky 1982). Minimum food supply and other stress situations were found to have the following morphological expression in the *Sepia* cuttlebone: dwarfism with septal crowding, a phenomenon which is common in ammonites at times of decline (Wiedmann 1969, 1970, 1973a). Rises in temperature also seem to be a lethal factor in sepiid life (Text Fig. 16), but further research is needed.

7. Summary

In summary:

1. Early rifting and spreading of grabens and oceanic basins affected ammonite life only to a very limited extend. The breaking-up of continents and the opening of new seaways facilitated ammonite migration, reduced endemisms and provincialism, and produced cosmopolitan realms.
2. Plate motion and plate tilting may occasionally produce similar situations but are without any significant importance for ammonite evolution.
3. The development of active continental margins, island arcs with pronounced volcanic activity, and volcanoclasic sedimentation did not favour ammonoid life.
4. The development of Atlantic-type passive continental margin is of more interest in this discussion, since shelf and epicontinental seas played a major role in ammonoid evolution. Some episodes (evaporitic and euxinic stages, formation of deltaic cones, carbonate ramps, and platforms) were found to be less adequate for ammonite life than others (major transgressions and phases of subsidence).
5. Thus, the main interest of our investigations was directed toward these global (and local) sea level changes which can be best detected in marginal seas. The graph of ammonite diversity during the Upper Cretaceous parallels the curve of global sea level changes. As the transgression proceeds, cosmopolitan species prosper, but at peak transgression (late Cenomanian/early Turonian), ammonite diversity and provincialism increase again. Most of the species prospering during transgressive episodes were unable to regenerate from their extreme adaption and became extinct during subsequent regressions.

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6. Temperate was also found to be an important factor controlling ammonite life, more so than geographic isolation. It is not, however, possible to relate the final decline of ammonites in the late Cretaceous to fluctuations in temperature or to the cosmic Iridium event, both restricted to the very end of the Cretaceous.

7. Promising preliminary experiments on the environmental factors controlling growth and life in sepiids may stimulate continued research in this direction. This is probably the only way to make sure which factors might have favoured or limited ammonite life.

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Abbreviations used:

GPIT	Geologisch-Paläontologisches Institut, Tübingen
NMB	Naturkunde-Museum, Basel
SGM	Service Géologique du Maroc, Rabat
USNM	U.S. National Museum N.H., Washington D.C.

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