

Palaeobiogeography of the upper Cenomanian–lower Turonian macroinvertebrates of the Sergipe Basin, northeastern Brazil

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Abstract: The upper Cenomanian–lower Turonian macroinvertebrate fauna of the Sergipe Basin, northeastern Brazil, is dominated by molluscs. In particular, ammonites and bivalves are abundant, with the latter representing the predominant benthic group. The Sergipe macroinvertebrates show low degrees of endemism; all groups have strong affinities with faunas described from other areas, in particular the southern Tethys. The biogeographic pattern suggests that, besides migration along a north–south connection of the early Atlantic, many groups migrated along an ephemeral, shallow trans-Saharan seaway, which connected the southern Tethys with the incipient South Atlantic.

Keywords: Upper Cretaceous, Palaeobiogeography, Macroinvertebrates, Sergipe, Brazil

1. INTRODUCTION

Molluscs form the dominant element among the macroinvertebrate faunas of the upper Cenomanian–lower Turonian marine deposits of the Sergipe Basin in northeastern Brazil. In general, the fauna is characterised by (1) a relatively high abundance of oysters in the lower part of the upper Cenomanian, (2) a relatively high abundance of ammonites and bivalves in the upper Cenomanian–lower Turonian, (3) the presence of a nearly monospecific echinoid fauna, (4) the lack or scarcity of many other important forms typically found on Tethyan platforms, for example rudists and corals, and (5) the absence of brachiopods.

As part of a study concerning the Cenomanian–Turonian transition in the Sergipe Basin, detailed palaeontological and stratigraphic investigations were carried out with an emphasis on the macrofaunas (SEELING, 1999; SEELING & BENGTON, 1999). Ammonites are generally the most abundant fossils in outcrop sections although the benthic biota are dominated by bivalves. However, with the exception of some extremely abundant upper Cenomanian oysters and lower Turonian species of the inoceramid genus *Mytiloides*, most bivalve species are scarce and usually represented by only a few specimens. Gastropods are less abundant and less diverse. The echinoid fauna of the transitional beds is characterised by a nearly monospecific occurrence of *Mecaster batnensis*

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(COQUAND, 1862), which is present in nearly all sections and locally reaches high abundance.

A problem in palaeobiogeographic interpretation of the Sergipe material is the scarcity of well-preserved specimens. The implications of this and other general methodological issues were discussed by BENGTON & KAKABADZE (1999). However, even if the Sergipe material is far from optimal and insufficient, for example, for the application of statistical methods, many macroinvertebrates have proved to be useful for identifying palaeobiogeographic affinities.

The Sergipe macroinvertebrates show strong affinities with faunas described from coeval beds of south Tethyan and African basins (e.g., Egypt, Tunisia, Algerian Sahara, Niger, Nigeria, Cameroon, Congo, Angola). The composition of the Sergipe faunas suggests that, in addition to migration along a north–south connection in the equatorial Atlantic, many groups migrated along an ephemeral shallow trans-Saharan seaway, which connected the southern Tethys with the incipient South Atlantic.

2. GEOGRAPHICAL AND GEOLOGICAL SETTING

The Sergipe Basin *sensu stricto* is the southern part of the Sergipe–Alagoas Basin in northeastern Brazil, between 9° and 11° 30' S and 35° 30' to 37° W. It is situated south of the São Francisco River, in the eastern, coastal part of the state of Sergipe (Fig. 1). The

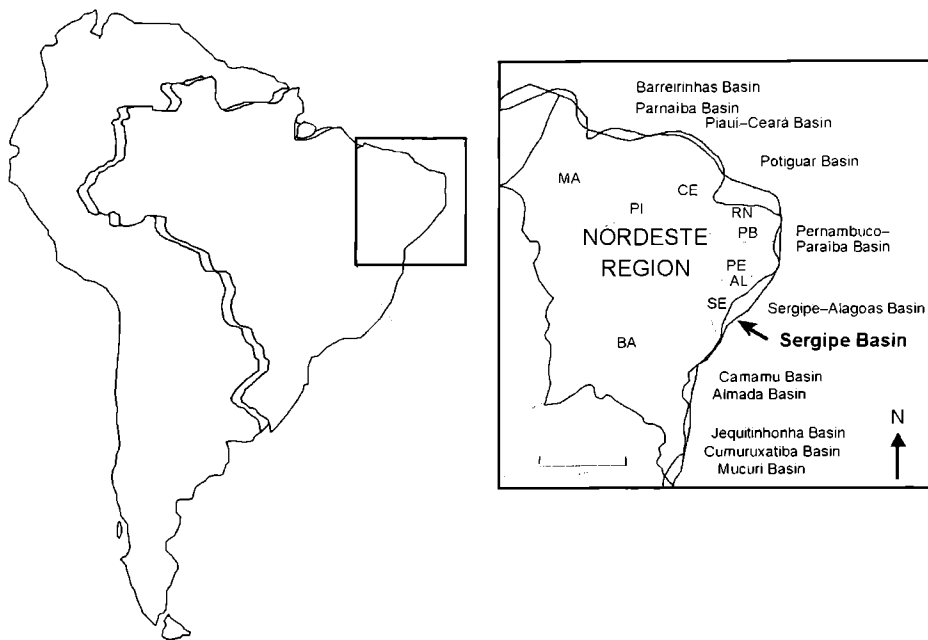


Fig. 1: Location of the Sergipe Basin and adjacent South Atlantic basins in northeastern Brazil.

basin comprises approximately 6000 km² onshore and an additional 5000 km² offshore. The onshore part occupies an approximately 16 to 50 km wide and 170 km long coastal strip (KOUTSOUKOS, 1998).

The Sergipe Basin is one of the numerous Mesozoic tensional rift basins bordering the South Atlantic. It forms a half-graben, limited offshore to the southeast by the continental slope and bounded to the northwest by a system of normal faults. The basin consists of a series of minor half-grabens, with regional dips averaging 10–15° to the southeast (OJEDA & FUGITA, 1976). Its palaeogeographic setting is a direct consequence of the strong tectonic activity in this area since the beginning of rifting between South America and Africa in the Early Cretaceous (OJEDA, 1982).

The geological evolution and the development of the marine Cretaceous of the Sergipe Basin have been discussed at length by several authors. For more detailed information the reader is referred to OJEDA & FUGITA (1976), OJEDA (1982), BENGTSOON (1983) and KOUTSOUKOS et al. (1993), among others.

3. MATERIAL

The material for this study was collected by P. B. and Suzana BENGTSOON (now University of Heidelberg) in 1971–1972 and 1977 and by J. S. and Simone WALTER (University of Heidelberg) in 1995 and 1996. The collections comprise several hundreds of ammonite and bivalve specimens and more than a hundred gastropods and echinoids. The ammonites were determined by P. B. and the bivalves and echinoids by J. S. Reliable determination of the gastropods is hampered by their mostly poor and incomplete preservation. J. P. LEFRANC (then Université de Montpellier, France; deceased in 1993) initially studied the gastropods collected in 1971–1972 and 1977. His preliminary determinations and draft descriptions (LEFRANC, 1977, in MS [1982]) were placed at our disposal. For the identification of the gastropods we tentatively rely on his identifications.

4. PALAEOBIOGEOGRAPHIC AFFINITIES OF SELECTED MACROINVERTEBRATE GROUPS

Besides Sergipe, Cenomanian–Turonian macroinvertebrates have been described or reported from some of the other Brazilian basins (Fig. 1). These include species from the estuarine facies of the Cenomanian–Santonian Itapecuru Formation of the Parnaíba Basin (KLEIN & FERREIRA, 1979), the Albian–Cenomanian Algodões Formation of the Camamu Basin (MAURY, 1925, 1937), the Albian–Cenomanian Açu Formation and the Turonian–Maastrichtian Jandaíra Formation of the Potiguar Basin (MAURY, 1925, 1934; BEURLEN, 1964, 1967), the Turonian–Campanian Beberibe Formation of the Pernambuco–Paraíba Basin (BEURLEN, 1961), and the upper Cenomanian of the Alagoas Basin (BENGTSOON & NORDLUND, 1987). Stage designations for the above mentioned formations are from ARARIPE & FEIJÓ (1995), FEIJÓ (1995), GÓES & FEIJÓ (1995) and NETTO et al. (1995). The echinoid faunas of the northeastern Brazilian basins were revised by SMITH & BENGTSOON (1991). The molluscan fossil record of the Brazilian Cretaceous basins was recently summarized by SIMONE & MEZZALIRA (1994) in a complete listing of all known Brazilian species.

Most of the Cretaceous macroinvertebrates reported from Sergipe and the basins mentioned above were originally described as new species, which gives the impression of a highly endemic Brazilian fauna. However, this is an artefact caused by the prevailing taxonomic concepts of earlier times, which led to taxonomic oversplitting. Our work has shown that the Upper Cretaceous of Brazil contains very few endemic molluscan species. This was discussed by BENGTON (1996, 1999) for ammonites and by SEELING & BENGTON (1999) for oysters. The same situation is true for echinoids, as discussed by SMITH & BENGTON (1991).

4.1. Ammonites

The upper Cenomanian–lower Turonian ammonite fauna of Sergipe is mainly composed of vascoceratids and pseudotissotiids of Tethyan affinity. This is true in particular for the Cenomanian–Turonian transitional beds. In older beds of the early to mid late Cenomanian and in younger beds of the mid to late early Turonian, vascoceratids and pseudotissotiids co-occur with widely distributed taxa that are known also from Boreal regions. This includes genera such as *Euomphaloceras* and *Thomelites* in the upper Cenomanian and *Watinoceras* and *Mammites* in the lower Turonian.

The Cenomanian–Turonian boundary fauna of Sergipe is most closely related to central-western and northern African basins, for example Nigeria, Niger (compare for example MEISTER, 1989; MEISTER et al., 1989, 1994; COURVILLE, 1989; COURVILLE et al., 1998; ZABORSKI, 1987, 1990, 1993, 1996), and Algeria (AMÉDRO et al., 1996; BUSSON et al., 1999). Thus, these basins are strongly dominated by vascoceratids and show similar faunal compositions, even at the specific level. On the other hand, direct comparison with the faunas of these African basins is hampered by the variable and diverging concepts of vascoceratid taxonomy, which complicates palaeobiogeographic interpretation.

There is less correspondence between the ammonite faunas of Sergipe and those of the west African coastal basins of Cameroon, Gabon and Angola than between the bivalve and echinoid faunas, respectively, of these regions. A reason may be the less advanced state of knowledge of the ammonites of these west African basins, in part owing to a scarcity of outcrops (Cameroon, Gabon), in part for military-political reasons (Angola). Also in contrast to the strong affinities recorded between the ammonite faunas of Sergipe and those of central and North Africa, there is less correspondence with other South American regions on the south-western margin of the equatorial Atlantic, for example Venezuela (RENZ, 1982) and Colombia (VILLAMIL & ARANGO, 1998), and with western North African basins such as Tarfaya (Morocco) (e.g., COLLIGNON, 1966; WIEDMANN & KUHN, 1996). At the generic level, the Sergipe lower Turonian ammonite fauna shows similarities to that of Colombia (VILLAMIL & ARANGO, 1998), Angola (COOPER, 1978; HOWARTH, 1985) and central Africa (ZABORSKI, 1990; COURVILLE et al., 1998). This includes the above mentioned genera, along with, for example, *Wrightoceras*, *Fagesia*, large coilopoceratids (*Hoplitooides*, *Coilopoceras*) and *Mitonia*, the latter known from Venezuela (RENZ, 1982). The palaeobiogeographic affinities of the most abundant ammonites of the upper Cenomanian and lower Turonian of Sergipe are illustrated in Figs. 2 and 3.

On biogeographical grounds, the ammonite succession of the upper Cenomanian–lower Turonian of Sergipe can be subdivided into three successive associations, all of low

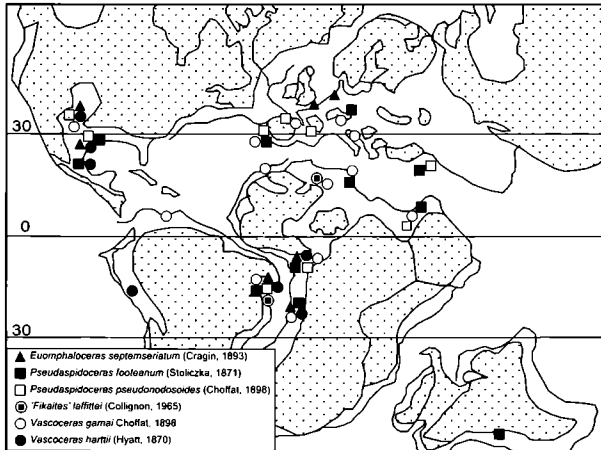


Fig. 2: Palaeobiogeographical distribution of selected upper Cenomanian ammonite species. Data from CHOFFAT (1889), PETRASCHECK (1902), GRECO (1915), FARAUD (1934), KARRENBERG (1935), BASSE (1937), WILLARD (1966), POLSAK (1967), BERTHOU & LAUVERJAT (1978), COOPER (1978), WIEDMANN & KAUFFMAN (1978), CHANCELLOR (1982), RENZ (1982), FÖRSTER et al. (1983), COBBAN (1984), LEWY et al. (1984), HOWARTH (1985), KENNEDY et al. (1987), KENNEDY et al. (1989), ZABORSKI (1990, 1995, 1996), KASSAB (1991), KENNEDY & COBBAN (1991), RAZGALLAH et al. (1994), AMÉDRO et al. (1996). Map based on BARRON et al. (1981), BARRON (1987), FUNNELL (1990) and DHONDT (1992).

diversity but displaying high abundances at several levels: (1) An upper Cenomanian fauna, mainly composed of widely distributed forms such as *Pseudocalycoceras harpax* (STOLICZKA, 1864) and *Thomelites* sp. succeeded by abundant *Euomphaloceras septemseriatum* (CRAGIN, 1893), *Pseudaspidoceras pseudonodosoides* (CHOFFAT, 1899) and *Vasoceras gamai* CHOFFAT, 1899. (2) An uppermost Cenomanian–lowermost Turonian southern Tethyan fauna composed of abundant *Vasoceras hartii* (HYATT, 1870) and *Pseudaspidoceras footeanum* (STOLICZKA, 1864) and less abundant '*Fikaites*' *laffittei* (COLLIGNON, 1965), succeeded by *Pseudotissotia nigeriensis* (WOODS, 1911), *Thomasites gongilensis* (WOODS, 1911) and *Pseudaspidoceras flexuosum* (POWELL, 1963). (3) A lower Turonian fauna containing mixed 'Boreal' and 'Tethyan' or cosmopolitan forms such as pseudotissotiids (*Wrightoceras* sp.), late vascoceratids (*Neoptychites cephalotus* (COURTILLER, 1860), *Fagesia* spp.) and *Watinoceras amudariense* (ARKHANGEL'SKIJ, 1916), *Kamerunoceras seitzi* (RIEDEL, 1932) and the near-endemic genus *Mitonia*, succeeded by *Mammites nodosoides* (SCHLÜTER, 1871) and *Kamerunoceras turoniense* (D'ORBIGNY, 1850). Diversity increases notably in the Turonian, with a corresponding decrease in specimen density at most levels.

From the Beberibe Formation of the Pernambuco–Paraíba Basin, the ammonite *Choffaticeras koeneni* (RIEDEL, 1932) has been reported (BEURLIN, 1961). The genus *Choffaticeras* has hitherto not been recorded from the Sergipe Basin, although it is well represented in the lower Turonian of the Tethys (Spain, France, Syria, Israel, Jordan),

Colorado, and various African basins (e.g., ZABORSKI, 1990; COURVILLE et al., 1996). Poorly preserved specimens of the genera *Mammites*, *Hoplitoides* and *Coilopoceras* were also reported from the lower–middle Turonian of the Potiguar Basin (BEURLEN, 1964). From the Alagoas Basin *Pseudocalycoceras* cf. *harpax* and *Kamerunoceras* sp. were described and assigned a late Cenomanian age (BENGTSON & NORDLUND, 1987).

The ammonite faunas reported from the above mentioned Brazilian basins differ in some respects from those of Sergipe, but (1) the Cenomanian–Turonian transitional beds are not exposed in any of these basins and (2) the incomplete documentation of these faunas makes comparison with Sergipe difficult and hampers interpretation of the causes of these apparent differences in occurrence.

4.2. Bivalves

A problem in palaeobiogeographic analysis of the upper Cenomanian–lower Turonian bivalve fauna of Sergipe is the scarcity and poor preservation of many taxa, in particular the heterodonts. Interpretation is possible only for some more abundant and better preserved groups.

At the generic level, the Sergipe bivalves show no endemism. All genera are well known from other regions and in many cases they are widely distributed, in particular in Tethyan regions or are cosmopolitan in the lower Upper Cretaceous. The degree of species endemism is low but increases slightly from the Cenomanian into the lower Turonian. Among the 47 bivalve species described from these beds, approximately 15% are endemic to Sergipe or at least represent species as yet unknown from other areas (SEELING, 1999).

KAUFFMAN (1973) discussed the palaeobiogeography of Cretaceous bivalves and introduced a concept of palaeobiogeographical units based on this group. According to this, the Sergipe Basin belongs to the South Atlantic Subprovince within the South Temperate Realm (KAUFFMAN, 1973, figs. 1, 2). However, the upper Cenomanian–lower

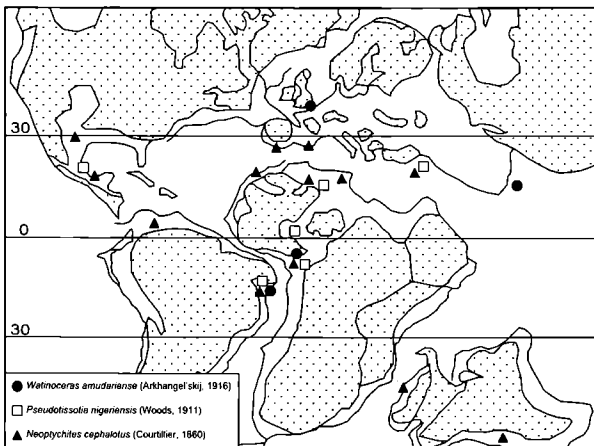
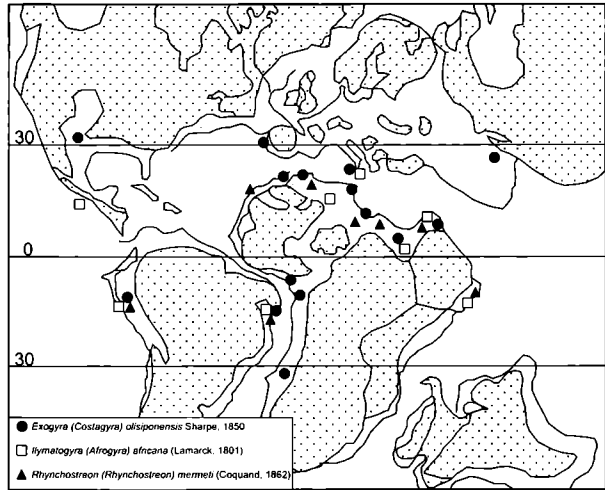


Fig. 3: Palaeobiogeographical distribution of selected lower Turonian ammonite species. Data from FREUND & RAAB (1969), WRIGHT & KENNEDY (1981), COBBAN (1984), LEWY et al. (1984), ZABORSKI (1987, 1990), COURVILLE et al. (1991, 1998), KENNEDY & COBBAN (1991), MEISTER et al. (1994), AMÉDRO et al. (1996), VILLAMIL & ARANGO (1998). Map based on BARRON et al. (1981), BARRON (1987), FUNNELL (1990) and DHONDT (1992).

Fig. 4:
Palaeobiogeographical distribution of three selected oyster species. From SEELING & BENGTON (1999). Map based on BARRON et al. (1981), BARRON (1987), FUNNELL (1990) and DHONDT (1992).



Turonian bivalves of Sergipe show such close affinities to faunas of the southern Tethyan regions that, using KAUFFMAN'S (1973) nomenclature, the basin is better assigned to the Indo-Mediterranean region within the Tethyan Realm, or to the Mediterran–Caucasian Subrealm, using the nomenclature of WESTERMANN (2000).

4.2.1. Oysters

In the Cenomanian of Sergipe oysters are the predominant bivalve group. They are generally well preserved and may reach high abundances. The palaeontology, stratigraphy and palaeobiogeographic affinities of Cenomanian oysters from Sergipe were discussed by SEELING & BENGTON (1999). Moreover, the distribution of this group in the Cretaceous Tethys was summarized by DHONDT (1992), MALCHUS (1996) and DHONDT et al. (1999). The Sergipe oysters show similar distribution patterns to those of the other benthic invertebrates, i.e. the fauna is composed of widely distributed to cosmopolitan species [e.g., *Rastellum diluvianum* (LINNÉ, 1767), *Pycnodonte (Phygraea) vesiculosa* (SOWERBY, 1823)] and of species with a strong South Tethyan affinity, for example *Ilymatogyra (Afrogyra) africana* (LAMARCK, 1801), *Exogyra (Costagyra) olisiponensis* SHARPE, 1850, *Rhynchostreon (Rhynchostreon) mermeti* (COQUAND, 1862). The palaeobiogeographic distribution of the latter species is given in Fig. 4.

4.2.2. Inoceramids

The upper Cenomanian–lower Turonian inoceramid fauna of Sergipe is composed of widely distributed taxa. In the Cenomanian, three species of *Inoceramus* occur sparsely (SEELING, 1999), closely related to the cosmopolitan *I. crippei* and *I. pictus* lineages. The same applies to the very abundant basal Turonian *Mytiloides*, which is represented by

cosmopolitan species of the *Mytiloides labiatus* (SCHLOTHEIM, 1813) group [e.g., *M. kossmati* (HEINZ, 1930), *M. mytiloides* (MANTELL, 1822)] (HESSEL, 1988; SEELING, 1999).

BEURLÉN (1961) reported *M. labiatus* from the Beberibe Formation of the Pernambuco–Paraíba Basin, then assigned to the lower Turonian. Today, the Beberibe Formation is considered to range into the Campanian. The specimen, which bears no. 117 in the Universidade Federal de Pernambuco collections, was examined briefly by P. B. in March 1982. The determination of BEURLÉN (1961) as *M. labiatus* must be seen as at least doubtful. BEURLÉN (1964, 1967) also described *M. labiatus* from the Potiguar Basin and, judging from the sketchy illustrations, this assignment is also doubtful. Re-examination of the original material is needed for a conclusive determination.

KLEIN & FERREIRA (1979) described two poorly preserved bivalve fragments from the Cenomanian of the Paraíba Basin and classified them as *Inoceramus* sp. They discussed the affinities with *M. labiatus*. HESSEL (1984), however, considered the specimens to be representatives of a different bivalve family.

4.2.3. Other bivalves

Most of the bivalves other than oysters and inoceramids represent a southern Tethyan fauna, which has its strongest affinities with northern and western African regions. This is demonstrated by the palaeobiogeographic distribution of selected species (Fig. 5).

A number of Cenomanian and Turonian bivalve species have been reported from other Brazilian basins. This includes 28 species from the Potiguar Basin, 10 from the Camamu Basin, 3 from the Paraíba Basin, and 2 species from the Pernambuco–Paraíba Basin (SIMONE & MEZZALIRA, 1994). At species level, there is no correspondence with the Sergipe fauna, but several genera occur in common, such as *Modiolus*, *Isognomon*, *Plicatula*, *Neithea*, *Corbula*, *Pholadomya*, and *Liopistha* (SIMONE & MEZZALIRA, 1994). Judging from the literature, at first sight the faunas of these basins seem to show much higher degrees of endemism and with few exceptions all species are solely reported from there. This is in sharp contrast to the Sergipe fauna, which shows very little endemism

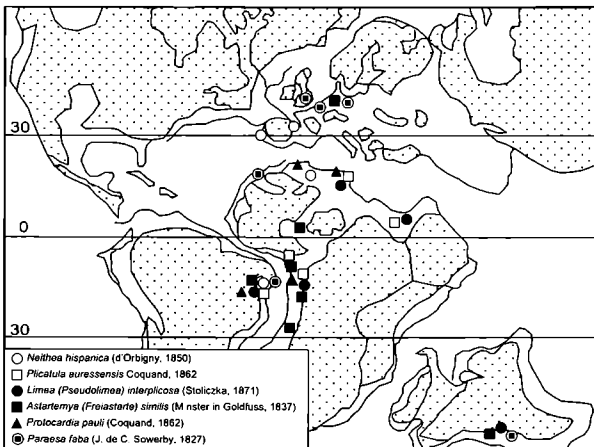


Fig. 5: Palaeobiogeographical distribution of selected bivalve species. Data from d'ORBIGNY (1844), COQUAND (1862), STOLICZKA (1870), HOLZAPFEL (1889), WOODS (1905), PERVINQUIÈRE (1912), RIEDEL (1932), BARBER (1956) DARTEVELLE et al. (1957), FRENEIX (1966, 1972), DHONDT (1973, 1981, 1992). Map based on BARRON et al. (1981), BARRON (1987), FUNNELL (1990) and DHONDT (1992).

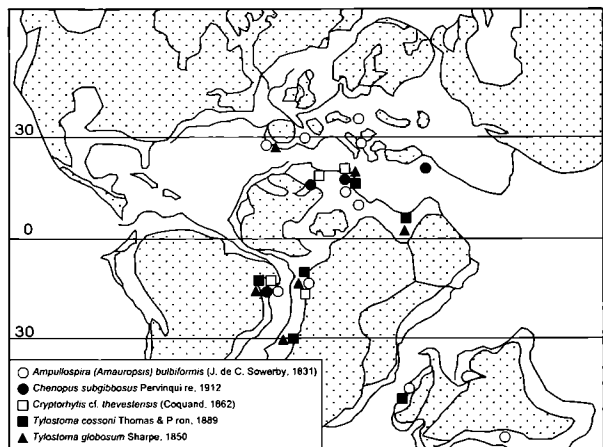
and is strongly dominated by widely distributed taxa. However, without access to the original material it is difficult to ascertain whether these faunas indeed represent higher levels of endemism or if this is an artefact as a result of taxonomic misinterpretation. These faunas are in need of revision.

4.3. Gastropods

At the generic level, the upper Cenomanian–lower Turonian gastropods of the Sergipe Basin show no endemism. All the genera are widely distributed and some are probably cosmopolitan. However, at the species level, in particular in the lower Turonian, there is some endemism, as indicated by LEFRANC (in MS, 1982). He described some species as new, which he had initially (LEFRANC, 1977) taken to be closely related to mainly northern African species. According to his notes, approximately 30% of the Sergipe Cenomanian–Turonian species are new, but the state of preservation of the gastropod material hampers reliable taxonomic assignment.

Nevertheless, the Sergipe gastropods show striking affinities with northern African faunas, for example from Tunisia (compare PÉRON, 1890–1891; PERVINQUIÈRE, 1912) or the Algerian Sahara (compare COQUAND, 1862; LEFRANC, 1977). There are also affinities with faunas of the west African coastal basins from Cameroon to Angola. Half of the species identified in our material have also been described from these basins (DARTEVELLE & BREBION, 1956). Some taxa closely related to those from Sergipe, have also been described from the Upper Cretaceous of Europe, notably from France and Austria (Gosau) (e.g., D'ORBIGNY, 1843–47; KOLLMANN, 1985). Affinities with the Western Interior Basin of North America are not as close (e.g., SOHL, 1964, 1987; KOLLMANN & SOHL, 1979; SOHL & KOLLMANN, 1985). The palaeobiogeographical distributions of five selected species are illustrated in Fig. 6, reflecting the close relationship of the Sergipe species to northern and western African gastropod faunas. Besides these, a form very similar to *Peruviella* sp. occurs in the Turonian of Cameroon. *Turritella* (*Haustator*) *carregeozica* and *Ringinella*

Fig. 6:
Palaeobiogeographical distribution of selected gastropod species. Data from COQUAND (1862), PÉRON (1890–1891), PERVINQUIÈRE (1912), RIEDEL (1932), DARTEVELLE & BREBION (1956), LEFRANC (1977). Map based on BARRON et al. (1981), BARRON (1987), FUNNELL (1990) and DHONDT (1992).



pinguiscula are Brazilian species. The same possibly applies to *Pterocera* cf. *decussata* and *Nerinea* sp., both most probably representing new species endemic to Sergipe (LEFRANC, in MS, 1982).

A total of 38 gastropod species have been described from the lower Upper Cretaceous of other Brazilian basins, mainly from the Potiguar Basin. As with the bivalves, there is little correspondence between Sergipe and the other Brazilian basins. Endemism is apparently higher in Sergipe, although this may be masked by the lack of modern revisions.

4.4. Echinoids

Five echinoid species have been described from the upper Cenomanian–lower Turonian of Sergipe (SMITH & BENGTON, 1991; SEELING, 1999): *Phymosoma?* sp., *Tetragramma deshayesi* (COTTEAU, 1864), *Micropedina olisiponensis* (FORBES, 1850), *Mecaster batnensis* and *M. batnensis* transitional to *Mecaster fourneli* (COQUAND, 1862). The fauna is strongly dominated by *M. batnensis*, which has a nearly monospecific occurrence in the Cenomanian–Turonian boundary beds. The Sergipe fauna at this time appears to be an impoverished Algerian fauna (NÉRAUDEAU & MATHEY, 2000).

M. batnensis is common in various regions of the southern Tethys, for example Portugal, Morocco, Algeria, Tunisia, Egypt and Syria (SMITH, 1992). It has been reported from the upper Cenomanian of the Iullemeden Basin in Niger, central West Africa (MATHEY et al., 1995) and is also known from the Turonian of Texas (COOKE, 1955). The palaeobiogeographic distribution of this species (Fig. 7) shows great similarities with that of the bivalve and gastropod faunas discussed above (compare Figs. 4–6). Thus *M. batnensis* is also a typical northern African species of the south Mediterranean Tethys that most probably migrated into the basin along an open trans-Saharan seaway.

The Cretaceous echinoids described from other Brazilian basins have been discussed by SMITH & BENGTON (1991). These include faunas from the upper Turonian–Santonian

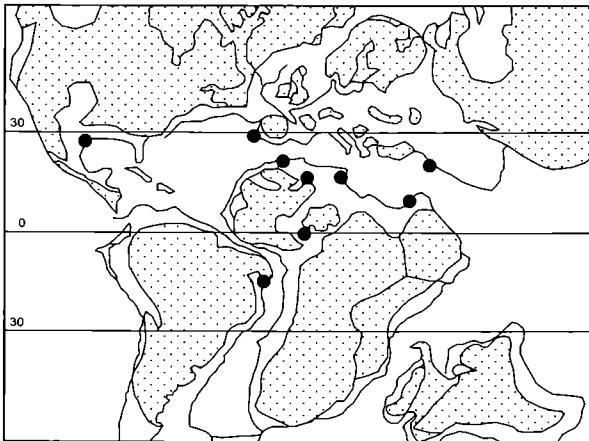


Fig. 7: Palaeobiogeographical distribution of *Mecaster batnensis*. For sources see text. Map based on BARRON et al. (1981), BARRON (1987), FUNNELL (1990) and DHONDT (1992).

or Campanian? of the Potiguar Basin, the Maastrichtian of the Pernambuco–Paraíba Basin, and the Aptian? or Albian of the Camamu Basin (Bahia). BEURLIN (1966) described two species from the Aptian or Albian of the Araripe Basin. For more information on Cretaceous echinoids from these basins, the reader is referred to SMITH & BENGTON (1991). It should be noted that no echinoids have so far been reported from Cenomanian–Turonian transitional beds outside Sergipe.

4.5. The conspicuous absence of some macrofossil groups

Although the Sergipe macroinvertebrates show strong affinities with those of the southern Tethys, there are also clear differences. Thus, rudists, corals, brachiopods, calcareous sponges and several microfossil forms commonly associated with these, for example large benthic foraminifera, and bryozoans, normally occur on the North and South Tethyan platforms (MATHEY et al., 1995) but are absent or very scarce in Sergipe. These groups also occur on the North Saharan platforms, although less frequently (LEFRANC, 1977). In this respect, the Sergipe Basin shows analogous characteristics with the Niger ramp (see MATHEY et al., 1995).

During the late Cenomanian to early Turonian, there was a sharp decline in the diversity of rudists (PHILIP, 1998), which coincided with the age boundary and also concerned associated forms such as those mentioned above (PHILIP & AIRAUD-CRUMIÈRE, 1991). Furthermore, rudists normally colonise shoals, where reefs can form. The absence of rudists and allied organisms from the Sergipe Basin can probably be explained by the general decrease of diversity, combined with morphological and palaeogeographical characteristics of the Sergipe Basin as a homoclinal ramp in the incipient South Atlantic Ocean, which at this time was connected to the Tethys by a narrow and only temporarily open seaway.

Brachiopods are among the rarest invertebrates in the Cretaceous of Sergipe. For example, in the Cenomanian to Coniacian of the basin only four specimens, of which three are lingulids, all from the same locality, have been found to date (HOLMER & BENGTON, 1996), and Albian terebratulids are restricted to one or two localities only (FONSECA et al. 2000). These unusual occurrences at only a few localities suggest that favourable conditions for these infaunal organisms were only locally present. The scarcity of brachiopods in the Upper Cretaceous of Sergipe was discussed by HOLMER & BENGTON (1996), who suggested two possible reasons for this: (1) Oxygen deficiency of bottom waters, thought to have existed in the basin. Low oxygen levels at the sediment-water interface would exclude all but a few, more tolerant, infaunal brachiopod taxa. (2) The extremely short-lived larval stage of articulate brachiopods, which may have hindered dispersal of this group into the opening South Atlantic Ocean. To explain the lack of brachiopods from the Niger ramp, MATHEY et al. (1995) discussed further possible causes, such as competition with a pioneer bivalve-dominated epifauna and/or excessive turbidity of bottom waters. They also mentioned extensive to mutual exclusion between brachiopods and epifaunal bivalves, mainly Ostreidae and Gryphaeidae, in the Cenomanian and Turonian of the northern Tethys.

5. DISCUSSION

The Cenomanian–Turonian macroinvertebrate faunas of the Sergipe Basin show strong Tethyan affinity. This is particularly true for the benthic groups of bivalves, gastropods and echinoids. The affinities of the ammonites differ somewhat from these groups. Besides Tethyan elements, there are also ammonite groups that show affinities with faunas of the Western Interior Basin of North America. This difference in distribution patterns is probably a result of different modes of life, where the more mobile ammonites were able to cross the southern North Atlantic, which already was a wide and deep oceanic basin at this time. Besides Tethyan elements, cosmopolitan taxa are also present, for example some groups of ammonites, some upper Cenomanian oysters and lower Turonian *Mytiloides*.

During the Cenomanian–Turonian transition, there was a sea-level highstand in the Sergipe Basin (SEELING, 1999; SEELING & BENGTSON, 1999). This transgression had consequences for the faunas of the basin, for example *Mytiloides* became the dominant genus among the bivalves and *Mecaster batnensis* among the echinoids. Moreover, among ammonites the Tethyan influence was strongest at this time. It is probable that before this transgression the migration of ammonites into the early South Atlantic mainly took place along the equatorial seaway, which was at least temporarily open. Ammonite and foraminifer data indicate surface-water connections between the south and central Atlantic as early as in the late Aptian (BENGTSON & KOUTSOUKOS, 1992). Data from the Gulf of Guinea and from adjacent African basins suggest that mid- or deep-water circulation between the equatorial and South Atlantic existed at least since the late Albian (PLETSCH et al., 1996; WAGNER & PLETSCH, 1999). The faunal exchange along a trans-Saharan Seaway was minimal, if any, at these times, but increased during the latest Cenomanian–early Turonian sea-level rise (COURVILLE et al., 1998). Initially, conditions were too shallow for ammonites, which were able to spread along the trans-Saharan seaway only during deeper water conditions in latest Cenomanian times. This is in agreement with results of COURVILLE et al. (1998) who reported different, successive periods of south–north (from the Saharan platforms) and north–south (from the Atlantic margin) directed colonisation of the Benue Trough in Nigeria by ammonites. For example, these authors reported the south to north directed migration of *Euomphaloceras* from the Atlantic margin into the Benue Trough in late Cenomanian times, whereas the end Cenomanian transgressive phase in latest *Neocardioceras juddii* Zone time was characterised by a north to south colonisation of the Benue Trough by groups related to the Saharan Vascocheratinae (COURVILLE et al., 1998).

A similar pattern of changing migration routes into the basin is not indicated by the other invertebrate fossil groups. Bivalves, gastropods and echinoids show a constant, strong South Tethyan influence from mid-Cenomanian times onwards. They appear to have also migrated along the trans-Saharan seaway at times of shallow waters, when this was apparently impossible for ammonites. The South Tethyan benthic groups and the vascocheratid ammonites represent Mediterranean warm-water faunas (WIEDMANN, 1976) that were able to spread along the shallow, tropical trans-Saharan seaway. In contrast to this, the above mentioned 'Boreal' ammonites represent colder-water faunas (WIEDMANN, 1976) and to migrate into the warm South Atlantic they needed the deeper waters of the equatorial Atlantic seaway.

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