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The “South Gondwana Fauna” in the Jurassic – an example of the utility of marine Ostracods for palaeobiogeography and palaeogeographic researches

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Abstract

The present article is a review of a palaeobiogeographic analysis of Jurassic Ostracods from East Africa, India and Madagascar and includes also some general remarks on palaeobiogeography, biodiversity and Ostracod ecology.The palaeobiogeographic study shows the high significance of this microfossil group for the reconstruction of palaeogeographic processes, particularly plate tectonic developments and sea level changes. The “South Gondwana Fauna” (SGF) was established in the early Middle Jurassic in a shallow marine rift basin between Madagascar, India and East Africa (Gulf of Madagascar) which was a result of early rifting processes between East- and West Gondwana. The maximum diversity of this fauna was reached during the late Middle Jurassic due to geographic expansion of the basin caused by successive rifting and rising sea level. The strong endemic character of the fauna was related to the peripheral geographic position of the Gulf of Madagascar at the southern Tethyan margin. In the late Middle and Upper Jurassic the SGF shows a biogeographic separation between East Africa and Madagascar/India and increasing endemism which may be affected by a deepening of the gulf and/or by the appearance of other environmental migration barriers between these areas.

Keywords: *Palaeobiogeography, Palaeobiodiversity, Jurassic, Ostracods, Gondwana, Plate Tectonics.*

Introduction

Controlling mechanisms of biodiversity and biogeography in Earth history

The research on biodiversity in Earth history has become an increasingly significant part of palaeontologic research during the last decades. It has been shown that rapid and strong fluctuations in past biodiversity (mass extinction events) as a result of ecologic “catastrophes” occurred several times in Earth history and severely affected the Earth biosphere.

The biodiversity is controlled by a number of biologic, ecologic and geologic processes. At the global scale and over long geologic periods the adaptive radiation, speciation and extend of habitats (“adaptive space”) were the most important factors (Benton, 1990). At a smaller geographic scale and over short geologic periods some of the important controls were the quality and availability of natural resources (e.g. quantity and heterogeneity of food; number, variability and heterogeneity of habitats). Other important factors are climatic conditions (e.g. average temperature, seasonal temperature variability, precipitation). There have been controversy discussions about the impact of geographic distribution patterns (provincialism) on the palaeobiodiversity. According to Valentine (1980) the number of bioprovinces was a major factor for the global biodiversity in the Phanerozoic. Later studies, however suggest that adaptive space and the number of ecologic niches were more important than provincialism (Benton, 1990).

Several palaeobiogeographic analyses (e.g. Boucot, 1975; Valentine, 1989; Jablonski, 1986; Skelton, 1993) have also shown that the geographic range, particularly the proportion of endemic and pandemic taxa correlates with the long term extinction rate (background extinction). Taxa with limited areal distribution, population size and high ecologic specialization are more vulnerable to ecologic fluctuations and show therefore a higher extinction rate than pandemic and cosmopolitic groups (Brown, 1995; Erwin, 1998). The relative proportion of marine endemic and pandemic taxa are largely controlled by sea level change, climate and plate tectonics.

Discussion

Ecology of Late Palaeozoic to recent benthic marine Ostracoda (overview)

Marine Ostracod groups are affected by a number of ecologic factors. The most important factors are salinity, oxygen concentration, water temperature, water turbulence and substrate conditions. These conditions have therefore a strong impact on ostracod distribution and diversity.

Oxygen concentration

One of the most important ecologic factor for marine Ostracods is the oxygen concentration. According to morphologic and palaeoecologic studies taxonomic groups of Ostracods show different tolerance to low oxygen concentration (Adamczak, 1969; Whatley, 1991; Lethiers & Whatley, 1994). The Platycopina and probably also representatives of the Metacopina and Palaeocopida were able to withstand periods of dysoxic conditions ("kenoxic events") at the sea floor. This ability of the Platycopina was explained by the fact that this group is able to increase the water circulation within the carapace by vibration of their branchial plates. Studies of modern platycopids, however could not prove that this group is in fact more tolerant to oxygen deficiency than other modern Ostracod groups such as Cytherocopina or Bairdiocopina (Dingle, 1995; Smith & Horne, 2002; Horne, 2003). Micropalaeontologic studies of Lethiers & Whatley (1994) suggested that at least some of the metacopid and palaeocopid ostracods were also filter feeders and therefore tolerant to oxygen deficiency. This hypothesis was supported by significant changes in the relative abundance of palaeocopid, and metacopid ostracods in the Upper Devonian - Lower Carboniferous interval (climate change: icehouse– greenhouse) and platycopid Ostracods during the Cenomanian-Turonian oceanic anoxic event (Lethiers & Whatley,1994; Jarvis *et al.*, 1988; Horne, Jarvis & Rosenfeld,1990; Babinot & Crumière-Airaud,1990). Both periods are characterised by drastic changes of sea water oxygen concentration. The latter authors also stated that the low abundance of deposit feeding Ostracods (Cytherocopina and Bairdiocopina) in the Lower and Middle Palaeozoic could be due to a relative low atmospheric and oceanic oxygen concentration during this time interval.

Salinity

Another important ecologic factor for Ostracods is salinity. Since the Late Palaeozoic different Ostracods groups have adapted to brackish and freshwater environments. The Leperditicopida are recorded from Early-Middle Palaeozoic intertidal environments and were probably tolerant to abnormal salinity. A first attempt to colonize marginal marine habitats with abnormal salinity is reported from the Upper Devonian (Knox & Gordon, 1999). In the Early Carboniferous the Darwinuloidea and Carbonitoidea invaded non-marine environments (Carbonel *et al.*, 1988; Horne, 2003).In the Mesozoic several Ostracod groups invaded brackish and non-marine environments at different times. In the Triassic to Middle Jurassic interval several representatives of the Cytherocopina (Limnocytheridae and Cytherideidae) are recorded from fresh and brackish water deposits. The third main and most successful adaption to non-marine conditions by the Cypridoidea occurred in the Late Jurassic (e.g. Whatley, 1990a, 1992; Horne, 2003). Furthermore, several other groups of Mesozoic marine Cytherocopina show a tolerance to salinity variations (marine Euryhaline taxa).

Several brackish Ostracod species of the Cytherocopina and Cypridocopina show characteristic ecophenotypic structures such as hollow tubercles. It has been suggested that these tubercles may be an adaption (increasing carapace volume) to the lower specific gravity of surrounding water (Van Morkhoven, 1962). but it is not yet clear which processes are responsible for these structures. Other ecophenotypic structures related salinity were detected at the recent species *Cyprideis torosa* which shows different types of sieve pores at different water salinities (Rosenfeld & Vesper, 1977).

Recent marine Ostracods can be assigned to four groups showing different salinity tolerance: 1. marine euhaline taxa, 2. marine euryhaline taxa, 3. marine brackish taxa, 4. limnic-brackish taxa. The reconstruction of salinity tolerance of fossil Ostracods taxa is mainly based on quantitative analysis of Ostracod assemblages, associated micro- and macrofossil groups and sedimentologic data. In many cases the true salinity range of Ostracods taxa may not be recorded because of post-mortem transport which happens quite frequently in marginal marine environments. The salinity tolerance of Jurassic Ostracods has been studied since several decades (e.g. Oertli, 1963; Kilenye & Allan, 1968; Brenner, 1976; Rohr, 1976; Ware & Whatley,1981; Malz *et al.*, 1985; Neale, 1988; Wakefield, 1995; Mette, 1997).

Water temperature

The temperature tolerance of Mesozoic Ostracods is poorly known and mainly based on data of lithofacies and associated fossils. Representatives of the Bairdiacopina with sculptured carapace are generally interpreted as inhabitants of shallow and warm water environments, particularly carbonate platforms (Crasquin-Soleau & Depeche, 1993;

Whatley, 1988). One of the most characteristic thermophile taxon is the genus *Cytherelloidea* which is today most abundant in shallow water of tropical and subtropical regions. There are several Eurytherm genera such as *Cytherella* which are recorded from Mesozoic shallow marine and deeper water environments. The temperature tolerance of Quaternary marine Ostracods has been studied by a number of detailed quantitative palaeoecologic analysis (e.g. Cronin, 1979, 1981; Hazel, 1988). Some analysis suggest that the Sr/Ca and Mg/Ca ratios of fossil Ostracod carapaces may be also useful for palaeotemperature reconstructions (Cronin *et al.,* 1999).

Substrate

Substrate conditions are also a significant ecologic factor for marine Ostracods. There are, however only few studies on the substrate tolerance of Mesozoic marine Ostracods. They benthic Ostracods can generally be differentiated into taxa which are living in phytal habitats, shallow burrowing forms living in the interstitial pore-water of sandy substrates and epibenthic taxa which prefer either fine-grained or coarse-grained sea bottoms. Many Ostracods show morphologic adoptions to substrate conditions. The phytal taxa include representatives of the Paradoxostomatidae and Xestoleberididae. Interstitial Ostracods are characterized by small size and often show an elongate carapace shape (Danielopol & Wouters, 1992). Many epibenthic inhabitants of soft substrates show a broad ventral sgkjn b u0 rface with wing-like lateral extentions of the carapace (Elofson, 1941). The preference of Ostracods for certain types of substrate is also related to the different content of detritic food (Hulings & Puri, 1964). Most taxa prefer relatively fine-grained silty-clayey substrates because of the relative high concentration of organic detritus. Coarse sandy substrates show usually much less diverse Ostracod associations.

Bathymetry

The bathymetric distribution of Ostracods is not directly controlled by the water depth but by those ecologic factors which are related to water depth, particularly water temperature, light intensity and oxygen availability at different bathymetric levels. The distribution of many recent marine Ostracod taxa is relatively well-known (e.g. Whatley, 1988). The strong temperature gradient between the neritic zone and the bathyal cold water masses represents an effective migration barrier of recent Ostracods at the species level (Benson, 1988). Recent deep marine Ostracod groups include the Eucytheridae and Krithidae. Most recent Ostracods of the deep sea are descendants of neritic taxa which migrated into bathyal environments in the Late Cretaceous and Palaeocene (Benson, 1969, 1975; Coles *et al.*, 1990). At the species level recent Ostracods show a strong affinity to different water masses (Dingle & Lord, 1990, Ayress *et al.,* 1997).

The thermal oceanic migration barrier was probably much less effective during the Mesozoic because of thermosphaeric conditions and a much weaker thermocline. There is little evidence of a thermal faunal barrier in Mesozoic Ostracod assemblages. The occurrence of Palaeozoic Ostracod taxa in Middle Triassic deep-water sediments however suggest the existence of deep marine refugia where these taxa could survive during the Late Palaeozoic and Early Mesozoic (Mette, Honigstein & Crasquin, 2015). The Jurassic deeper marine Ostracods are largely represented by Bytherocytheridae, Cytheruridae (e.g. *Cytheropteron, Monoceratina*) and Eurytherm genera of the Platycopina and Bairdiacopina such as *Cytherella*, smooth-shelled Bairdidae (e.g. *Bairdia, Bythocypris*). Other typical inhabitants of the deep water were *Cardobairdia* and *Pontocyprella*.

Palaeobiogeography and evolution of the South-Gondwana Fauna in the Jurassic

The unique character of Jurassic marine faunas from the southern Tethys which are known as "Ethiopian Province" was already recognized several decades ago (Arkell, 1956; Hallam,1969). Today this palaeobiogeographic province represents one of the classical examples of Mesozoic marine provincialism in the shallow-sea realm. A number of palaeobiogeographic studies were concerned with cephalopods (e.g. Cariou, 1973, Enay, 1980). Later increasing attention has been paid to benthic fossil groups such as bivalves (e.g. Heinze, 1996) and Ostracods. The latter group is, due to their mode of life very well suited for palaeobiogeographic analyses. Because Ostracods have no planktic larval stage and are predominantly benthic they can be highly indicative of palaeogeographic changes such as plate movements which has been demonstrated by a number of palaeobiogeographic studies (e.g. Krömmelbein & Wengner, 1966; Schallreuter & Siveter, 1985).

Jurassic Ostracods of the “Ethiopian Province” were studied for the first time by Grekoff (1963). Later Middle and Upper Jurassic ostracods from Tanzania and India were described (Bate, 1975; Lubimova, Guha & Mohan, 1969). A first analysis of the palaeobiogeography of Ostracods in South Gondwana was carried out by Dingle (1988).This study came to the conclusion that the geographic distribution pattern and diversity of the Ostracods were largely controlled by the Middle Jurassic rifting between East and West Gondwana, namely the opening of a shallow marine rift basin at the southern Tethys margin (Gulf of Madagascar) and the Early Cretaceous opening of the South Atlantic. Since then a number of taxonomic research from India, Madagascar, Somalia, Tanzania, Australia and South America has significantly increased the knowledge on Jurassic Ostracods in Gondwana (Rafara, 1990; Ballent, 1990, 1991, 1992; Lord *et al.,* 1993; Mette, 1993; Malz & Oertli,1993; Whatley & Ballent,1994; Ballent & Whatley, 1995a, 1995b, 1996, 2000a, 2000b; Khosla *et al.*, 1997; Sames, 2002; Mette & Geiger, 2004a, 2004b, 2004c). Additionally several Ostracod assemblages have been described from North Africa, Israel and Saudi Arabia (Charriere *et al.,*1994; Mette, 1995, 1997; Basha, 1980; Rosenfeld *et al.*, 1987a, 1987b; Rosenfeld & Honigstein,1991, 1998; Bischoff, 1990a, 1990b; Depeche *et al.*,1987).

The data from Madagascar (Mette, 2004a, 2004b; Mette & Geiger, 2004a) have shown that a diverse “South Gondwana Fauna (SGF)” (sensu Dingle, 1988) was much earlier established than previously thought. The Bajocian ostracods from Madagascar, South America and Australia show a high correspondence in their taxonomic composition, particularly because of the occurrence of the genus *Paradoxorhyncha*which is only recorded from these regions and probably migrated along the southern shores of Gondwana and into the “Gulf of Madagascar” (Fig. 1).

These faunal links show that the SGF originated in the early Middle Jurassic. The occurrence of other Ostracod taxa suggest that at least a part of the fauna immigrated from the north (Europe, North Africa, Arabia) into the “Gulf of Madagascar”.

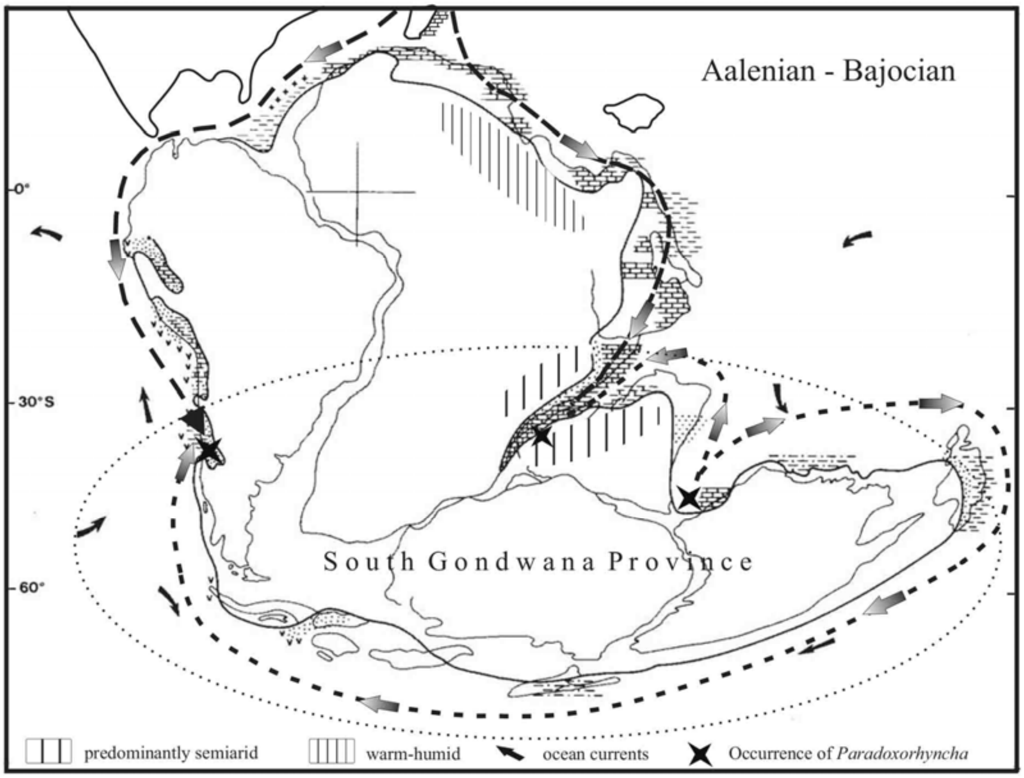

Figure 1. Ostracod species migration and palaeoclimate in the Aalenian-Bajocian of Gondwana (from Mette 2004b). Palaeoclimatic data from Frakes, Francis and Syktus 1992, Dina 1996, Uhmann 1996 and Aberhan *et al.* 2002. Palaeogeographic map after Barron et al. (1981), Scotese (1991) and Riccardi (1991).

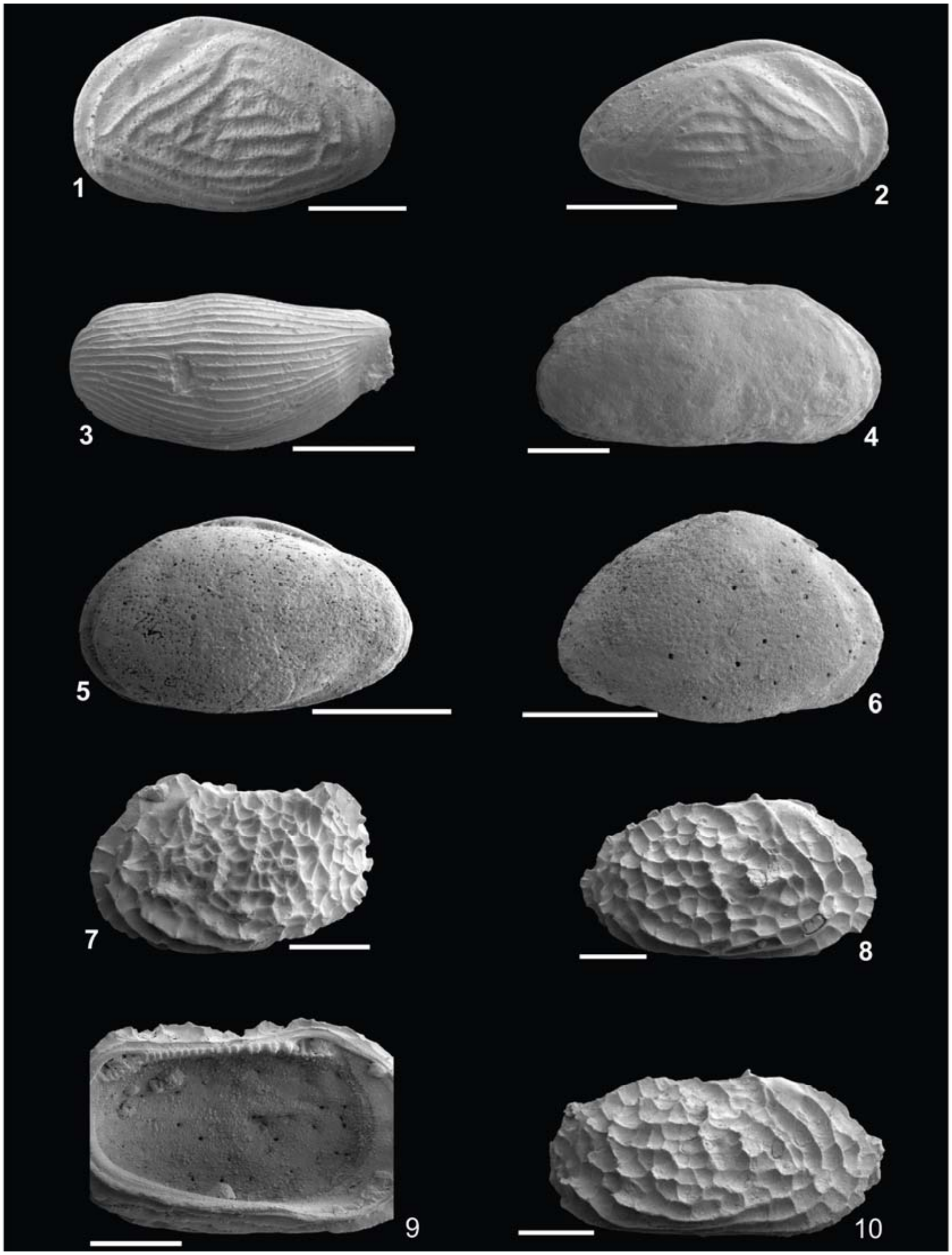

Plate 1. Characteristic ostracods of the Middle and Upper Jurassic, 1. *Ektyphocythere* sp.1, female, left valve, Sakaraha section, Bajocian; 2. *Ektyphocythere* sp.1, female, right valve (of carapace), southern Majunga Basin, Beronono section, Bajocian; 3. *Striatojonesia striata* (Triebel and Bartenstein, 1938), left valve, southern Majunga Basin, Beronono section, Bajocian; 4. *Fabanella* ? sp.1, female, right valve (of carapace), Anjeba section, Middle-Upper Bathonian; 5. *Paradoxorhyncha malgachica* Mette 2004, female, left valve (of carapace), Analamanga section, Bajocian.6. *Paradoxorhyncha malgachica* Mette 2004, female, right valve, Analamanga section, Bajocian; 7. *Australophocythere malgachica* Mette 2004, female, left valve, Dangovato section, Upper Oxfordian; 8. *Australophocythere malgachica* Mette 2004, female, right valve, Andrea section, Middle Oxfordian; 9. *Australophocythere malgachica* Mette 2004, female, left valve, internal view, Dangovato section, Upper Oxfordian; 10. *Australophocythere malgachica* Mette 2004, male, right valve, Andrea section, Middle Oxfordian. 1-6: Scale bar 100 μm; 7-10: Scale bar 200 μm

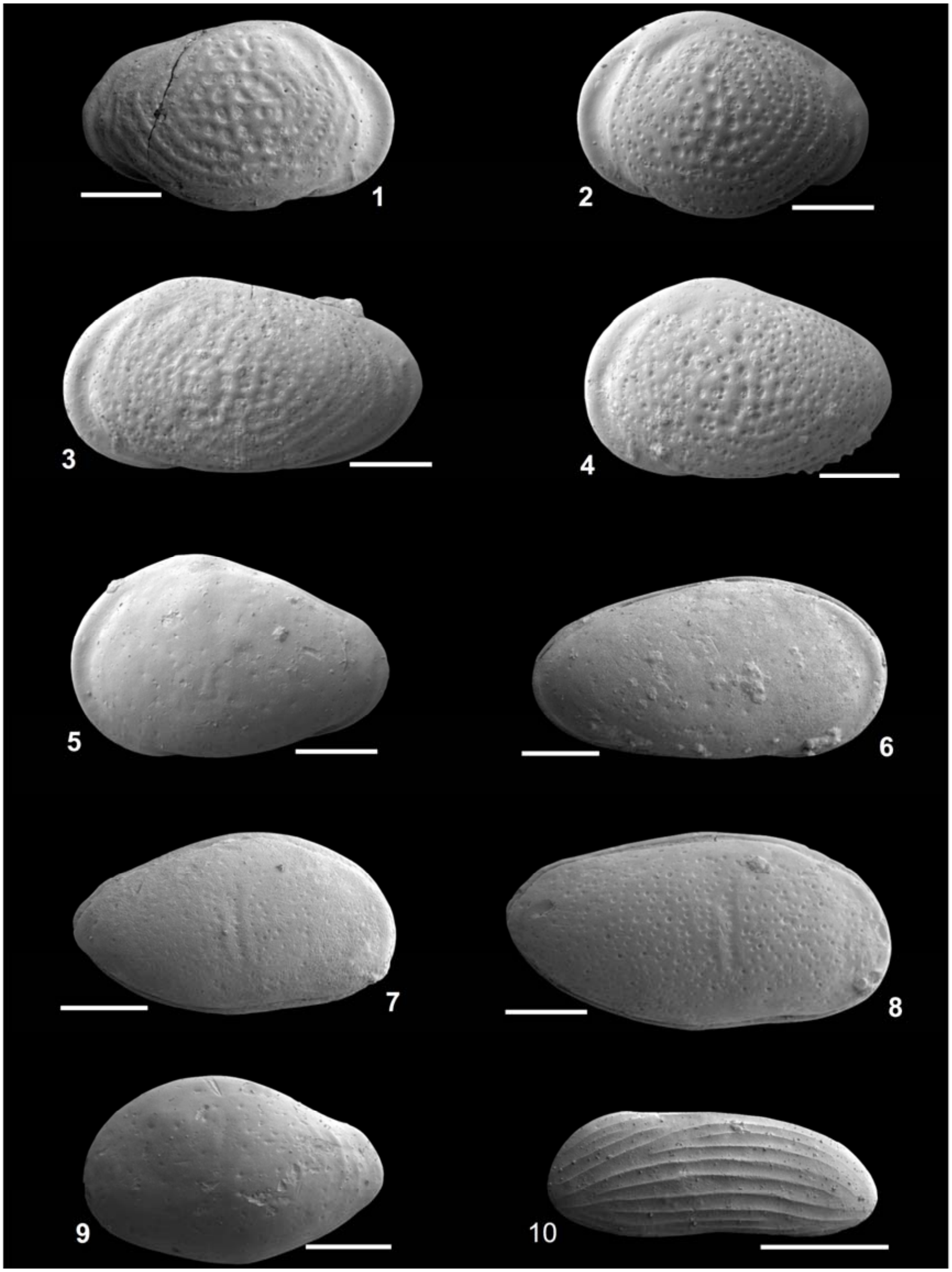

Plate 2. 1. *Majungaella ventriosa* Mett 2004, female, right valve, Andrea section, Middle Oxfordian; 2. *Majungaella ventriosa* Mette 2004, female, left valve, Andrea section, Middle Oxfordian; 3. *Majungaella microperforata* Mette 2004, male, left valve, Andrea section, Middle Oxfordian. 4. *Majungaella microperforata* Mette 2004, female, left valve, Andrea section, Middle Oxfordian. 5. *Majungaella glabra* Mette 2004, female, left valve, Andrea section, Middle Oxfordian; 6. *Majungaella glabra* Mette 2004, male, right valve (of carapace), Andrea section, Middle Oxfordian; 7. *Pirileberis tenuisulcata* Mette 2004, female, right valve (of carapace), Dangovato section, Upper Oxfordian; 8. *Pirileberis tenuisulcata* Mette 2004, male, right valve (of carapace), Dangovato section, Upper Oxfordian; 9. *Pirileberis tenuicostata* Mette 2004, female, left valve (of carapace), Andrea section, Middle Oxfordian; 10. *Mandawacythere* sp.1, male, left valve, Ankilimena section, Middle Oxfordian. Scale bar 200 μm

Sedimentologic and palaeoecologic data (Mette & Geiger, 2004a) point to a shallow to marginal marine environment with salinity variations in the Bajocian of Madagascar.

A completely different Ostracod fauna and different palaeobiogeographic pattern (Fig. 2) is recorded from the late Middle Jurassic. It includes several endemic genera and species which probably originated due to the onset of rifting and widening of the "Gulf of Madagascar". A number of new species were described from the Callovian of Madagascar (Mette & Geiger, 2004b). This rapid evolution and diversity increase was probably also a result of the late Middle Jurassic sea level rise, increase of shallow normal marine habitats and high nutrient availability in combination with evolutionary developments in the Progonocytheridae (improvement of hinge structures, increase of tactile hairs) which probably improved their ecologic success in turbulent shallow marine environments. The sedimentologic and palaeoecologic data point to an open shelf environment and normal marine conditions during the late Middle Jurassic (Mette & Geiger, 2004b). The high endemism was caused by the peripheral palaeogeographic position of the rift basin at the southern Tethyan margin.

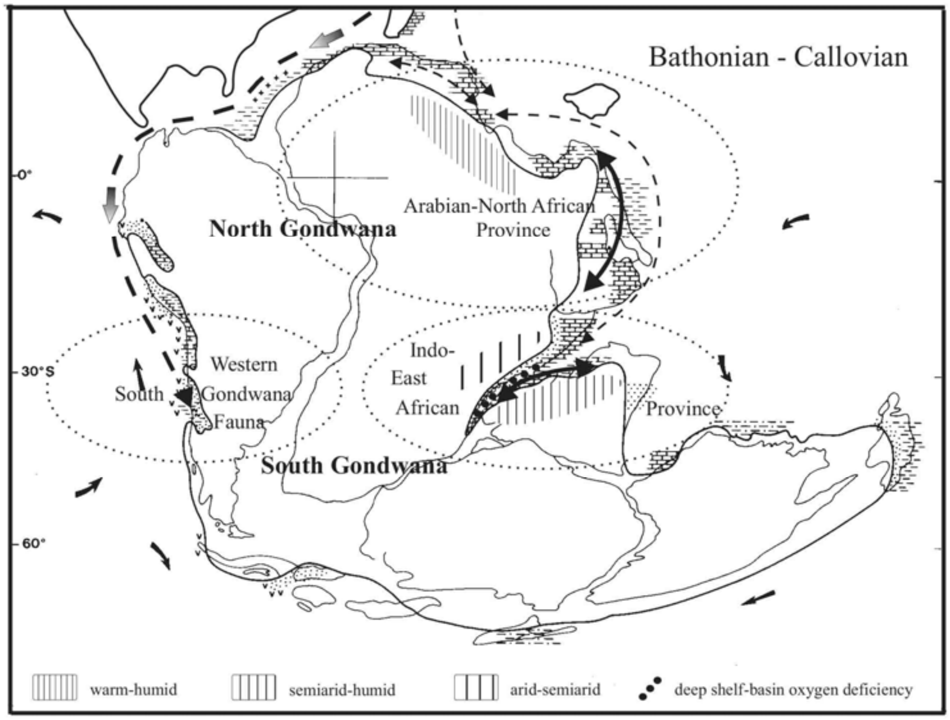

Figure 2. Ostracod species migration and palaeoclimate in the Bathonian-Callovian of Gondwana (from Mette 2004b). Palaeoclimatic data from Frakes, Francis and Syktus 1992, Dina 1996, Uhmann 1996 and Aberhan *et al.* 2002. Palaeogeographic map after Barron *et al.* (1981), Scotese (1991) and Riccardi (1991).

After the onset of sea floor spreading between East Africa and Madagascar/India occurred a splitting of the SGF into a western (Tanzania) and eastern Ostracod fauna (Madagascar/India) and increasing endemism (Mette, 2004b). This separation suggests that the "Gulf of Madagascar" acted as a migration barrier during the late Middle and Late Jurassic (Fig. 3). It is however not clear how this marine gulf could effectively inhibit the migration. One possibility is that the water depth of the basin was sufficient to act as a migration barrier for the shallow marine Ostracods. Another possibility is the existence of oxygen-poor water masses in the deeper part of this basin. The Oxfordian to Kimmeridgian Ostracod assemblages of Madagascar lived in an open shelf environment with sea level changes. In the late Middle Jurassic and Late Jurassic the SGF shows also a successive separation from the North African / Arabian Ostracod assemblages (Figs. 2, 3). This differentiation could be due to regional climatic conditions, as supposed by earlier author and / or due to ocean currents.

The palaebiogeographic developments of the

SGF had also a strong impact on the taxonomic diversity (Fig. 4). A first diversity peak is recorded in the Bajocian. The Ostracod diversity of the SGF reached the maximum in the Callovian and rapidly decreased in the Kimmeridgian-Tithonian.

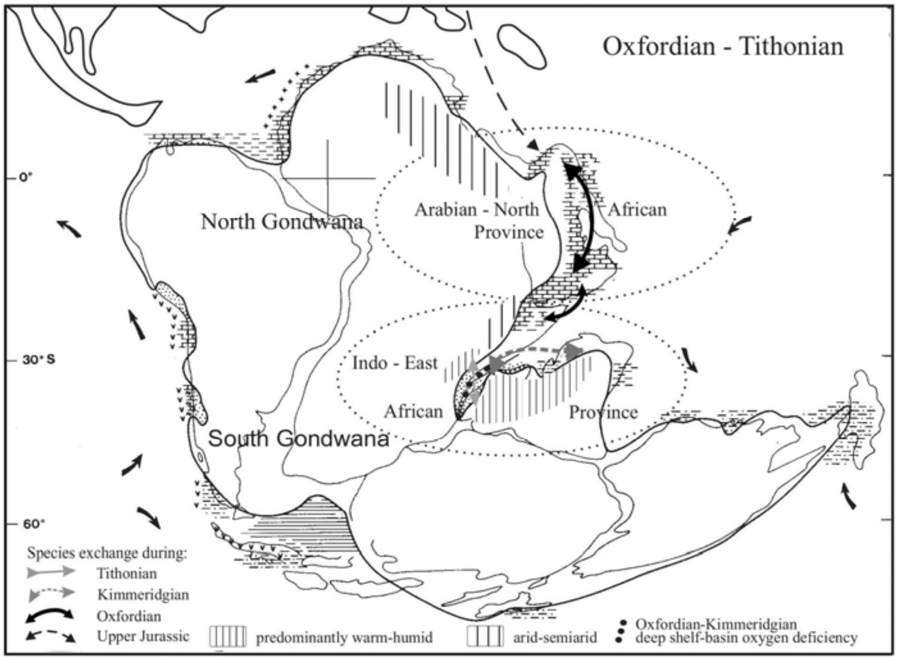

Figure 3. Ostracod species migration and palaeoclimate in the Oxfordian-Tithonian of Gondwana (from Mette 2004b). Palaeoclimatic data from Frakes, Francis and Syktus 1992, Dina 1996, Uhmann 1996 and Aberhan *et al.* 2002. Palaeogeographic map after Barron *et al.* (1981), Scotese (1991) and Riccardi (1991).

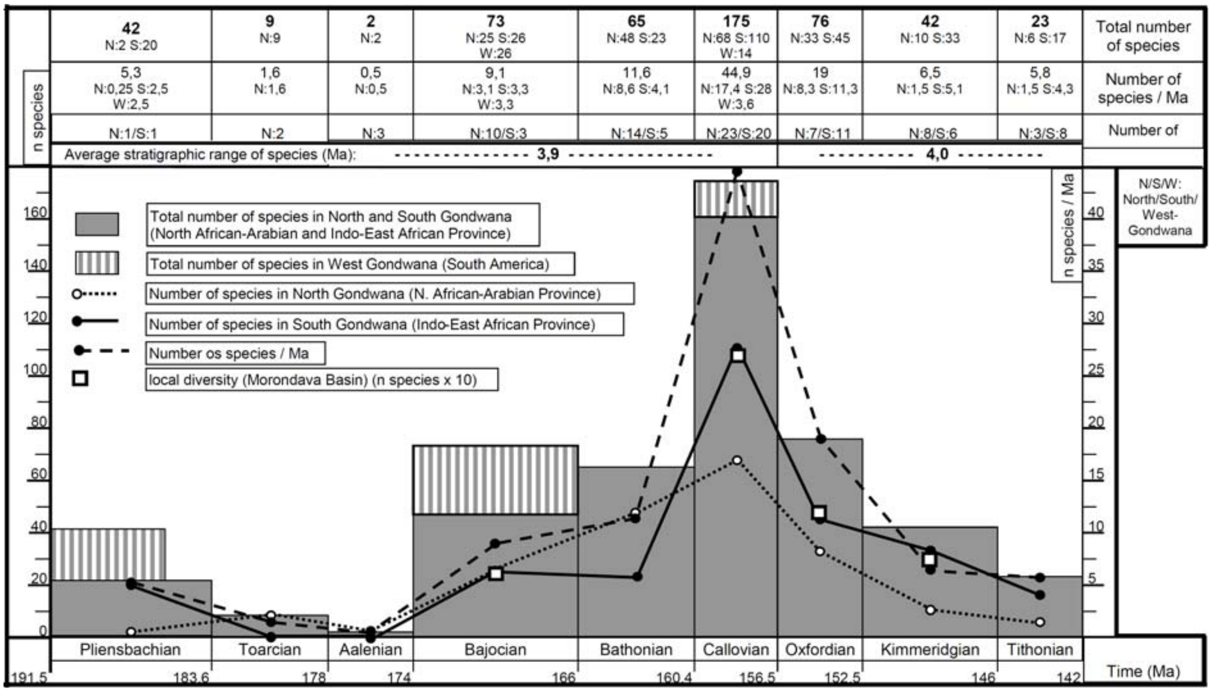

Figure 4. Pliensbachian - Tithonian ostracod species diversity in Gondwana. Local diversity is defined as average species diversity of the assemblages. The intensity of micropalaeontologic research is indicated by the number of investigated sections (from Mette 2004b).

A similar trend was observed with regard to the species origination and extinction rates. The diversity trend of the SGF is very different from the global Ostracod diversity trend (Whatley, 1990b) which shows a stepwise diversity increase during the Jurassic (Fig. 5). This difference is due to the fact that the global trend was primarily effected by sea level changes and intrinsic factors (evolutionary adoptions) of the Ostracods (Whatley, 1990b) but the diversity trend and evolution of the SGF was largely controlled by regional plate tectonic processes (opening of the Gulf of Madagascar).

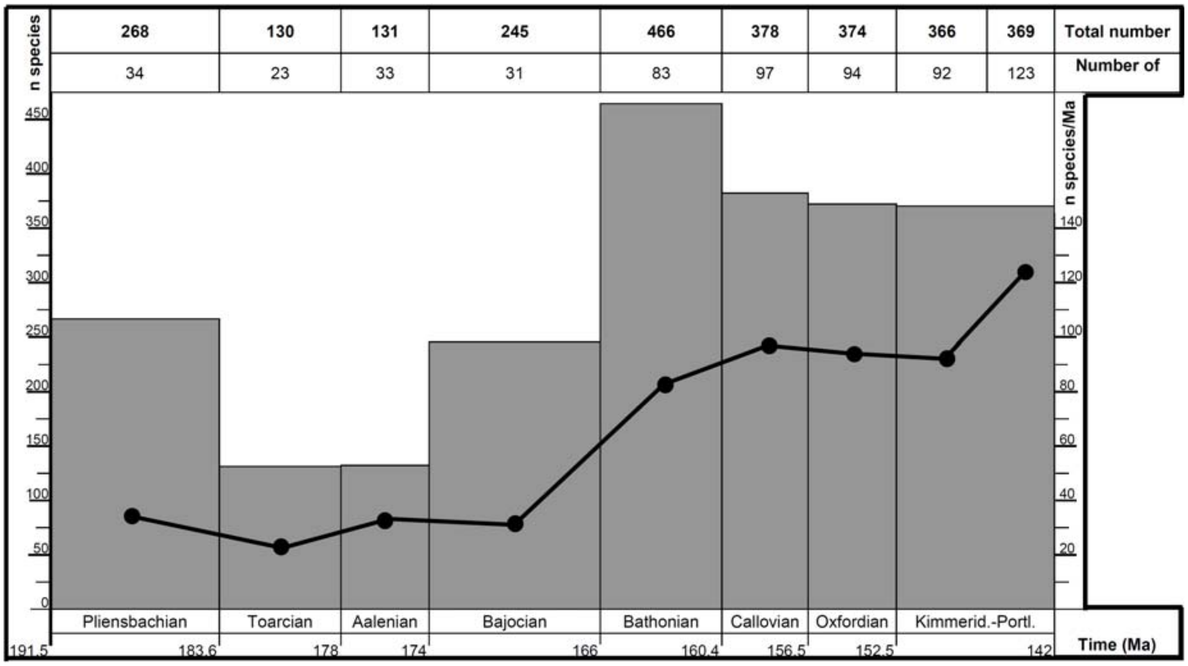

Figure 5. Global Pliensbachian – Tithonian ostracod species diversity. The data were adopted from Whatley 1990b and subsequent publications (from Mette 2004b.(

Conclusion

The evolution of the SGF in the Jurassic can primarily be explained by the palaeogeographic development of Gondwana. It`s palaeobiogeography and diversity were a product of the onset of tectonic separation between East and West Gondwana the opening of a new marine basin, the Gulf of Madagascar,and the global sea level rise. According to the present data (Mette, 2004a, b; Mette & Geiger,2004a, b, c) the late Middle and Upper Jurassic Ostracod assemblages of Madagascar were not affected by environmental deterioration such as oxygen deficiency, temperature or salinity changes. Salinity variations are, however, recorded from the Bajocian.

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