Mind the "Middle Jurassic" gap
Bone versus track record in dinosaurs

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Up to now studies on vicariance biogeography or cladistic biogeography of dinosaurs have been performed with body fossils only. In the Triassic and Early Jurassic these methods have produced rather coherent patterns, probably due to the existence of Pangaea. They show a large cosmopolitan community of herrerasaurids, coelophysoids, prosauropods and basal ornitischians (Holtz et al. 2004).

The fossil record of body and trace fossils of dinosaurs in the Middle Jurassic consists of rather limited information. Today more than hundred locations are known to contain either trace or body fossils. Although scattered, they occur on all continents except on Antarctica. The best record including all stages comes from Europe where all groups of dinosaurs are present, whereas all other continents show only very few localities. A limited record is known from Africa and Australia. The break up of Pangaea is also recorded in the dinosaur communities resulting in only six taxa that are globally distributed. However, the global record indicates the presence of ceratosaurs, basal spinosaurs and carnosaurs among theropods, stegosaurs and various sauropods among herbivore dinosaurs.

If the bone and track record are combined a different pattern emerges. In the Aalenian the only skeletal and track record comes from Europe, in the Bajocian again Europe and Australia indicate skeletal remains of theropods and sauropods, whereas footprints indicate the presence of sauropods in all continents except Asia; theropod tracks are present in North America, Asia and Australia. The Bathonian indicates a skeletal record of theropods in Europe, Africa and Asia, sauropods in Europe and Asia and ornitischians in Europe only. The track record indicates theropods in North America and confirms the presence of theropods, sauropods and ornithischians in Europe and theropods and sauropods in Africa. In the Callovian sauropod remains are present on all continents except Australia, theropods occur in South America, Europe, Africa and Asia, whereas ornithischians are found in Europe and Asia only. The track record adds sauropods to North and South America. Combining the record of both body and trace fossils gives a somewhat different picture, although we are far away to link particular trackways to specific vertebrate taxa. In this paper we would like to focus on similarities and differences in the global track record.

The Middle Jurassic dinosaur fossil record is poor and incomplete record during this time interval, when many dinosaur groups radiated. Recent discoveries of coeval dinosaur tracksites from Portugal, the United States and England have greatly enhanced our understanding.

We report here on an important skeletal and trace fossil record from Morocco that greatly enhances our understanding of global distribution of ichnotaxa. Lapparent (1955) described two partial postcranial skeletons, the sauropod *Cetiosaurus mogrebensis* and the theropod *Megalosaurus mersensis* from the El Mers area. These localities could be relocated and can be placed in the uppermost part of the El Mers Formation. Furthermore, Charroud & Feddan (1992) noted the presence of large sauropod bones from the Bathonian Gypsum marls of Boulhafa some 15 km west of El Mers. We report herein the first dinosaur tracks from the Middle Atlas Mountains in two different stratigraphic units with a total of thirteen different levels.

The first set of track localities lies in the middle of the Ich Timellaline and J'bel Bou Akrabène Formation (Bathonian). Outcrops in the canyon of

the Oued Tamghilt east of El Mers, have yielded three localities that contain an important set of dinosaur trackways. So far tridactyl footprints and trackways attributed to theropods have been found. Smaller footprints (Footprint Lenght: 15 – 30 cm) show slender toes, larger footprints (FL: 40 cm) have blunt toes and can be attributed to the ichnogenus *Megalosauripus*. Furthermore, we have mapped a series of very large sauropod trackways (pes length up to 130 cm) that are narrow gauged (sensu Lockley et al. 1994). Size, trackway width as well as missing toe or pollex impressions suggest the ichnogenus *Breviparopus*. The second set of trackbearing surfaces has been located at the base of the El Mers Formation (Late Bathonian to?Callovian). Here mainly small theropod footprints (FL: 20 cm) have been observed; isolated footprints of large sauropods (FL: 100 cm) have also been recorded. Sedimentary structures as well as abundant remains of wood indicate a deposition in a shallow siliciclastic tidal flat.

The vertebrate ichnofacies of the El Mers area is in many ways similar to the one encountered in the Iouaridène and Taguelft basin in the High Atlas (400 km to the west). All the localities show the presence of the narrow-gauged ichnotaxon *Breviparopus* indicating the presence of very large but slender eusauropod. *Megalosauripus* attributed to a large theropod is equally present in all these deposits in Morocco. In comparison with other Middle Jurassic localities (England, USA, Portugal) the Moroccon sites display the highest diversity of track morphotypes. However, there are striking similarities and differences. Whereas the ichnotaxon *Megalosauripus* has been found in England and Marocco, but is missing in Western North America, a small but very peculiar ichnotaxon *Carmelopodus* can be found in England, Morocco as well as in the USA. Furthermore, a medium sized theropod morphotype (FL 20 cm) occurs in all the areas as well. These theropods were apparently widespread on all three continents. The narrow gauge sauropod ichnotaxon *Breviparopus* is so far restricted to North Africa. In Europe (Portugal, England) only the narrow gauge sauropod ichnotaxon *Parabrontopodus* can be found. Furthermore trackways of wide-gauge sauropods in England demonstrate the presence of titanosauridform sauropods, not present elsewhere. These observations clearly demonstrate, that in the Middle Jurassic of Europe and North Africa different sauropod taxa occured, despite the lack of detailed information on skeletal taxa. On the other hand theropod of different sizes were apparently widespread in North Africa, Europe and the USA.

Combining the bone and track record in specific time slices can greatly improve our knowledge and fill the gap of apparently missing data. Nevertheless, in the past many authors have argued that those gaps in the vertebrate record reflect a taphonomic megabias related to sea level fluctuations. Many researchers speculated that for instance Mid Cretaceous eustatic highstands did reduce the number of low land areas suitable to the preservation of terrestrial faunas ((Smith 2001)). This is in clear contrast, f.e. to the eustatic high in the Campanian/ Maastrichtian that shows an increasing number of localities when compared to the Mid Cretaceous eustatic low stands with only few known occurrences. Fara (2002) compared estimates of sea-level variations, land surfaces and the proportions of Lazarus tetrapod taxa in the Late Jurassic to Eocene interval and found a negative correlation. Taking into account the record of dinosaur trace and body fossils from the so called “Middle Jurassic” gap, we see that almost all stages show the presence of the group and the Callovian with a sea level highstand has the best track and body fossil record. We think that the apparent missing record during the Middle Jurassic is mainly due to sample bias.

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