

Georges Demathieu. - *Contribution to the ichnology and understanding of the evolution of reptiles during the Triassic period.*

The Triassic appearance of autopodial specializations in archosaurian reptiles makes the study of vertebrate footprints from this period particularly interesting. These specializations have an influence on footprints, such that new ichnological genera appear. This structural evolution, underway in the Lower Triassic, developed throughout the period and beyond. From the 5-digit autopodium in primitive thecodonts where the 4th digit was longer, the general result was a reduction of the outer digits and lengthening of the median digit relative to the foot.

We compare the information provided by ichnology and osteological paleontology for this period.

DATA FROM OSTEOLOGICAL PALEONTOLOGY

1) *Distribution of genera (thecodonts and dinosaurs).* Thecodonts comprise about fifty genera (55) throughout the Triassic. They debut in the Upper Permian (*Archosaurus*) and become extinct at the end of the Triassic. Dinosaurs appear in the Middle Triassic but disappear in the Upper Cretaceous. About forty genera in the Triassic (42).

Thecodonts are represented by 10 genera in the Lower Triassic, 15 in the Middle, and 30 in the Upper. In comparison, dinosaurs are slightly better represented in the Upper Triassic: 36 genera versus 6 in the Middle. One should not attach too strict a value to these numbers, because of the differing interpretations of authors regarding synonymy and generic definitions.

2) *Information concerning the evolution of autopodia.* The autopodial skeletons of Triassic reptiles are relatively well understood. In the Lower Triassic: for the few thecodonts in number, there are practically no relevant differences; in the Middle Triassic, there is a greater representation of thecodonts with the beginnings of specialization: predominance of the 3rd digit and tarsal modifications (*Euparkeria*, *Prestosuchus*, *Ticinosuchus*). Appearance of theropod dinosaurs (*Triassolestes*, *Ischisaurus*, *Herrerasaurus*) in the Upper Triassic: reduction of outer digits in certain thecodonts and dinosaurs.

DATA FROM ICHNOLOGY

1) *Distribution of ichnological genera.* Ichnological genera do not correspond to zoological genera. Remaining within the fixed limits of paleozoology, the distribution of genera belonging to the crocodyloid and dinosauroid groups are studied.

In the Lower Triassic the crocodyloid group is represented by 4 genera, including the genus *Chirotherium* which includes 15 species; in the Middle Triassic, there are six crocodyloid genera and 3 dinosauroid, located mostly on the northeast edge of the Massif central, as well as in Largentière and Nottinghamshire; in the Upper Triassic, the two groups contain 14 and 29 genera, respectively, but bipedal thecodonts might have left dinosauroid footprints.

Comparing thecodont and dinosaur genera with ichnological genera, a relative symmetry between the two is found.

2) *Information provided by the footprints of autopodia.* The majority of *Chirotherium* prints reveal that their maker might have had a relatively straight tarsus and a relatively less mobile tarso-zeugopodian articulation, and confirm in particular the outlines of the reliefs and the variability of the length of the 5th digit. In this genus from the end of the Lower Triassic, prints appear (*Ch. bornemanni*) that undergo a reduction of the outer digits. With the Middle Triassic *Sphingopus*, this reduction is accentuated so that only 3 digits are practically functional. *Ch. coureli* marks the shifting of maximal support of the autopodium under the first 3 digits and functional reduction of the 5th. In the same epoch the rather timid appearance of tridactyl prints is seen (*Anchisauripus*). In the Keuper the prints are mostly dinosauroid, which are those known from the Upper Triassic of Connecticut, the Rhaetian of Vendée, or the Keuper of Anduze or Basutoland. In the latter localities, note the existence of massive tetradactyl or pentadactyl tracks that show the appearance of a new foot skeleton construction. The study of prints of the anterior autopodia, often more poorly preserved, only slightly adds to the complementary elements.

CONCLUSION. The ichnological information differs noticeably from that provided by paleontology. These data do not contradict, but, if our interpretation is correct, ichnology could furnish more advanced information in all the Triassic beds. *Ch. barthi* and especially *Ch. bornemanni*, a little older than *Euparkeria*, show more specialized skeletons than the latter. *Sphingopus* reveals a structure that is only found in the Upper Triassic *Hesperosuchus*; likewise for the tridactyl prints of the Middle Triassic. In the

Upper Triassic of Cévennes and Basutoland, in addition to tridactyl prints, it seems that massive prints can be attributed to sauropods (F. Ellenberger).

This "advance" of ichnological information over classic paleontological information seems to be confirmed in all the Triassic beds. To remark on this further, skeletons show us that thecodonts, at their maximum development, attain their greatest specialization in the Upper Triassic, while coelurosaurian theropods, for example, show a still more specialized development during this epoch. These elements, added to the preceding comparison of genera, imply that thecodonts and dinosaurs (at least theropods) were separated early on.

F. Ellenberger and L. Ginsburg envisioned "an explosive phase of evolution while still at a pseudosuchian stage" for the saurischians. The data provided by ichnology lead us to think that this stage must have been advanced, perhaps from the 2nd part of the Lower Triassic, and that the explosion must have taken place in primitive pseudosuchians such as proterosuchids.