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Short review of the Saurischia and their natural interrelationships

by Friedrich von Huene

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The oldest saurischians are the coelurosaurs; which are known since the time of the Buntsandstein.

The coelurosaurs are also the most primitive saurischians, with close resemblances to some pseudosuchians, e.g. *Saltoposuchus*[1], with a calcaneum that bears a process ["gespornten Calcaneus" in the original text].The Triassic coelurosaurs are mainly bipedal, all digitigrade and long-necked animals with an elongated pubis. Some used the hands in slow locomotion (as do kangaroos), all had a process on the calcaneum. The hand touched the ground only if both feet were moved simultaneously in short steps, never if the feet moved in an alternating fashion. The hand is relatively large, and the fifth finger was not reduced in the Triassic; its morphology still closely resembles that of the hands of pseudosuchians.

Based on tracks, Soergel showed that pseudosuchians were abundant in the Buntsandstein; he also found tridactyl coelurosaur tracks in Thuringia.

The elongated neck and the tendency towards a tridactyl foot indicate terrestrial and cursorial habits. In pseudosuchians the tendency towards a tridactyl foot is already present; the 3rd toe is the longest, and 1 and 5 are short and hang down. Such a pseudosuchian is surely not arboreal, and it did not evolve from arboreal forms, since it still has dermal armour.

Five families of coelurosaurs are present in the Triassic. The most primitive are the ammosaurids, which are also closely related to the oldest pachypodosaurs, the most primitive prosauropod *Thecodontosaurus antiquus* and the most primitive carnosaur *Palaeosaurus*. The number of cervical vertebrae is 9, just one vertebra more than in pseudosuchians. The second family, Hallopodidae, is characterised by a bird-like foot, a long lower limb and a short upper limb segment in the hindlimbs; these were probably saltators, thus they moved their limb simultaneously. The third family, Procompsognathidae, and the fourth, Zanclodontidae, are highly specialised; the genus Tanystrophaeus belongs to the latter family. The fifth family, Podokesauridae, are those that are most adapted for a cursorial lifestyle. Fifteen genera and twenty-two species of coelurosaurs are known from the Triassic of Europe, North America, and Africa.

Fifteen genera, representing the three families Coeluridae, Ceratosauridae, and Compsognathidae are known from the Jurassic.

From the Cretaceous, we also know fifteen genera within the three families Coeluridae, Compsognathidae, and Ornithomimidae; thus, there are a total of approximately 45 genera and 60-70 species of coelurosaurs.

The pachypodosaurs are derived from primitive coelurosaurs, and in the beginning of the evolutionary history of this group, it is hard to tell carnosaurs from prosauropods. Both occur almost simultaneously in the Middle Triassic. Carnosaurs are always rarer than prosauropods and later sauropods. Their differentiation is relatively small. Only since the

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[1] Acta Zool. II 1921. 330-403

Jurassic are the typical carnosaur characters well developed: the head is enlarged and the neck shortened.

The oldest carnosaurs are almost indistinguishable from prosauropods. *Palaeosaurus* probably still used quadrupedal locomotion at slow speeds; during running it was bipedal with alternating strides. In the Jurassic and Cretaceous, the forelimb is shortened, it becomes 4-, 3- and 2-fingered (*Gorgosaurus*). The tibia remains relatively long, but always shorter than the femur.

In the Triassic, two families with a total of 9 genera are present. Only the megalosaurids are known with three closely related genera from the Jurassic; in the Cretaceous, the diversity is higher again, with 9 genera within five families; one of them, the dinodontids, which include *Tyrannosaurus*, *Gorgosaurus*, and similar forms, are the largest and fiercest carnivores of all time.

The prosauropods are obviously of very similar origin as the carnosaurs; in the beginning there is only a slight difference in the diet. Together with the sauropods, they form a natural group. The most primitive prosauropod was probably quadrupedal, but had the ability for bipedal locomotion with alternating strides. This is *Thecodontosaurus antiquus* from Lettenkohle-equivalent beds of England.

Eleven genera of prosauropods, including a total of 25 species, are known from the Triassic; they represent four families. The most primitive family are the thecodontosaurids with five genera of small to medium sized bipedal animals which moved with alternating strides. The ratio humerus/femur is 0.76-0.57 : 1; the ratio tibia/femur 0.65-0.9 : 1. Thus, the forms are variable. The next family are the plateosaurids, with nine species within the one genus. They are strictly [literally translated: extremely] bipedal and show a very long neck and small skull, with small, homodont teeth, as in the thecodontosaurids. The forelimbs are approximately 2/5th the length of the hindlimbs and the metatarsus is relatively long. They are so far only known from western Europe. The equivalent forms in South Africa are the plateosauravids with three genera and six species; they are more heavily [literally: ungainly] built and have longer forelimbs. The most interesting family are the melanorosaurids with two genera, also from South Africa. They have short, stout limbs of solid built (i.e. almost no internal cavities), with rather long forelimbs (4 : 5) and elongate, cavernous trunk vertebrae. The melanorosaurids were probably secondarily quadrupedal and - based on the solid built of the limbs - probably had an amphibian lifestyle.

The origin of sauropods is probably to be found close to them, but, unfortunately, we do not have any knowledge about their evolution in the Liassic and oldest Dogger [Middle Jurassic]. The major change from the melanorosaurids towards the oldest sauropods is the pronounced adaptation for secondary quadrupedalism: the metatarsus is shortened and the foot semi-plantigrade, whereas the metacarpus is elongated and the hand digitigrade, with a cylindrical arrangement of the metacarpals. Furthermore, the lower leg is even more shortened, although it is not shorter than in some thecodontosaurids. The pectoral girdle is moved 2-3 vertebrae backwards, whereas the number of presacral vertebrae stays the same; in the later evolution of sauropods, it is moved further backwards, and only in late forms, an increase in the number of presacral vertebrae may be present. Within the evolution of sauropods, changes in proportions are found which are almost greater than those between prosauropods and sauropods. The skull of some sauropods, including *Brachiosaurus*, *Camarasaurus*, and *Helopus* is very similar to that of prosauropods, whereas *Diplodocus* and the titanosaurids show major changes in the proportions.

Thus, the sauropods descended from their ancestors by the means of a change in lifestyle; the major morphological changes from prosauropods to sauropods took place at the end of the Triassic, and we can follow it in detail.

The sauropods include approximately 30 genera within some half dozen families. They rule the Middle and Late Jurassic and the Early Cretaceous, and then they die out, with the exception of one family. These are the titanosaurids, which arise from the most primitive Jurassic sauropods in the Late Cretaceous [Huene probably wants to say that they are morphologically very close to the most primitive Jurassic sauropods, but are just known

from the Late Cretaceous]; they evolve during the Late Cretaceous with some further differentiation and dominate the end of this epoch unto the Danian. The largest terrestrial animal of all times, *Antarctosaurus giganteus* from Patagonia, with a femoral length of 2.32 m belongs to this family.

I would like to add two comments on the systematic nomenclature:

Since I think that I am able to show that saurischians and ornithischians arose from different pseudosuchians, and in a dissimilar way, they must be regarded as separate orders, being not closer related to each other than saurischians to birds or saurischians to crocodiles. Therefore, I reject the uniting term "Dinosauria". It is also not possible to restrict the name to one of the two orders, since Richard Owen included representatives of both orders in his initial definition.

As we have seen, the saurischians are divided into two separate groups (suborders): the coelurosaurs and the other branch that arose from them in the Middle Triassic, the pachypodosaurs.; the latter immediately separate into the carnosaurs (Triassic to Upper Cretaceous) and the prosauropods (Triassic) and their descendants, the sauropods (Jurassic and all of the Cretaceous); at the beginning, these two groups are very similar. The sauropods arise from the prosauropods at the end of the Triassic. Marsh included the coelurosaurs and a part of the pachypodosaurs, the carnosaurs and prosauropods, in his "Theropoda". However, since it is not possible to restrict this name to one of the groups, or to give it a strongly modified definition a posteriori; since this separation was furthermore shown to be unnatural, the name "Theropoda" should vanish altogether.

Discussion:

Mr. M. Frank:

In reference to the comments of Pompeckj, who pointed out that the evolution of the separate forms occurred simultaneously throughout the world, we should be reminded that the correlation of sediments throughout the world is based on their faunas. We should thus be cautious to come to the opposite conclusion and say: since the same fossils occur in sediments of the same age throughout the world, the evolution of the faunas must have been simultaneously.

Freiherr v. Huene:

I would rather explain the simultaneous occurrence of closely related sauropods in North America and Deutsch-Ostafrika [Tanzania] by migration, rather than separate evolution; the time involved is still often underestimated. What is usually called a narrow "horizon" in stratigraphy probably still includes a very long timespan. It is often noted, that a world wide distribution might be achieved within the same horizon that also documented the first occurrence. On the other hand, it seems that often simultaneous changes occur in not closely related groups, like "fashions" at a certain time, for example similar modifications of the pelvis in ornithischians, birds, crocodiles, and pterosaurs in the mid-Mesozoic. This can only be explained by homoplasy.