

The Systematic Position of the African Theropods
***Carcharodontosaurus* Stromer 1931 and *Bahariasaurus* Stromer**
1934

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Abstract: The systematic position of the Egyptian theropod genera *Carcharodontosaurus* Stromer 1931 and *Bahariasaurus* Stromer 1934 from the Cenomanian of the Bahariya-Oasis is reviewed. The genera show several similarities to allosauroids and can therefore be referred to the superfamily Allosauroidea (Currie and Zhao, 1993). Both genera are also similar to each other, especially in possessing pleurocoelous caudal vertebrae. This character, which is not found in any other theropod, allows the reference to a separate family of theropod dinosaurs, Carcharodontosauridae Stromer 1931. The origin of carcharodontosaurids will probably be found in primitive allosauroids of the Middle to Upper Jurassic. Three lines of large theropods existed in the Cretaceous: the ceratosaurian abelisaurids in South America, the allosauroid carcharodontosaurids in Africa and the coelurosaurian tyrannosaurids in North America and Asia.

Introduction

In the first half of this century, several expeditions under the direction of Dr. Ernst Stromer to the Bahariya Oasis in the Egyptian desert discovered a rich fauna from the Cenomanian (Stromer, 1936). Included in this fauna were numerous remains of theropod (Stromer, 1915, 1931, 1934, 1936) and sauropodomorph (Stromer, 1932, 1934, 1936) dinosaurs.

The material permitted the description of two new theropods: *Spinosaurus aegyptiacus* Stromer 1915, und *Bahariasaurus ingens* Stromer 1934. Stromer also erected the new genus *Carcharodontosaurus* Stromer 1931, to which he referred the genus *Dryptosaurus saharicus* Deperet and Savornin 1927. The holotype of *Dryptosaurus saharicus* was an individual tooth.

In 1989 colleagues published the special research volume 69 “Geowissenschaftliche problems of arid districts” describing new discoveries of vertebrate fossils in northern Sudan (Buffetaut et al., 1990). In the following years several expeditions under the direction of Dr. Christa Werner revealed a rich Wirbeltierfauna of Cretaceous age (Werner, 1994). Included in this fauna were dinosaurs, which Dr. Werner kindly entrusted to me for research. Since some of these elements are similar to *Bahariasaurus*, questions about the systematic position of these animals and the closely related genus *Carcharodontosaurus* resulted.

Unfortunately, the entire material from the Bahariya oasis was destroyed in an air raid during the second World War, so that a new investigation of the systematic position of *Carcharodontosaurus* and *Bahariasaurus* is made here, based only on the data published by Stromer (1931, 1934, 1936).

Previous conceptions of the systematics of *Carcharodontosaurus* and *Bahariasaurus*

Stromer erected a new family, Carcharodontosauridae (1931) for the genus *Carcharodontosaurus*, which along with *Bahariasaurus*, he regarded as members of the Theropoda. In Stromer's opinion a close relationship between *Carcharodontosaurus* and *Bahariasaurus* did not exist (Stromer, 1934).

This opinion was also followed by Lapparent (1960), who placed *Bahariasaurus* in the family Megalosauridae, and *Carcharodontosaurus* in the Tyrannosauridae (Lapparent, 1960: S. 26-27). Huene (1948, 1956) referred *Carcharodontosaurus* to the Allosauridae, and erected the monotypic family Bahariasauridae Huene 1948 for *Bahariasaurus*.

In contrast, Romer (1966) held the opinion that both genera were more closely related with each other, since he placed both in the family Megalosauridae. Romer's classification was followed by Steel (1970) and Carroll (1988).

Molnar et al. (1990) regarded the two African theropods as Carnosauria incertae sedis, whereby Carnosauria consisted of the families Allosauridae and Tyrannosauridae. *Carcharodontosaurus* and *Bahariasaurus* share different characteristics with the Allosauridae and Tyrannosauridae, such that their classification into one of the two families was impossible (Molnar et al., 1990: S. 198).

Bonaparte (1991) held the contrary opinion that the two genera of Stromer's were not similar to the Laurasian Carnosaurs, but more closely related

to the South American Abelisauridae and Noasauridae, though the details of *Carcharodontosaurus* and *Bahariasaurus* were not discussed.

A new systematic review of the Theropoda by Holtz (1994) places the Abelisauridae in the Ceratosauria, and removes the Tyrannosauridae from Molnar et al.'s (1990) Carnosauria and assigns it to the Coelurosauria. Unfortunately, Holtz did not consider the systematics of the theropods from the Bahariya Oasis.

Sereno et al. (1994) also did not consider the two African taxa in the modification of the analysis of Holtz.

A goal of this work is to clarify the systematic position of *Carcharodontosaurus* and *Bahariasaurus* with the Theropoda. As a framework the cladogram of Holtz (1994) as modified by Sereno et al. (1994) is used (fig. 1). Since different cladistic approaches to theropod systematics differ strongly in the evaluation of the characteristics supporting them (Paul, 1984; Gauthier, 1986; Russell and Dong, 1993a; Holtz, 1994), this investigation will be a classical comparison of the African theropods with other genera. During the final classification one tries nevertheless to utilize shared derived characteristics.

The elements described by Stromer

To begin with a summary of the elements of the two genera described by Stromer (1931, 1934) is given.

Carcharodontosaurus: Reliable elements belonging to

Carcharodontosaurus are a fragment of the braincase, both nasals, fragments of the left maxilla, several teeth, three cervical vertebrae, one caudal vertebrae, a proximal fragment of a rib, a haemal arch, a fragment of the left ischium, both pubes (damaged), both femora (damaged), and a left fibula. In addition, Stromer (1934) included an ilium, however, its referral to *Carcharodontosaurus* is still questionable. In addition to the description and illustration of this ilium (Stromer, 1934: S. 45; Table III, Fig. 15), the orientation of the bone given by Stromer can also be doubted. Instead of a right ilium in medial aspect, it could be a left ilium in medial aspect, so that the side Stromer regarded as cranial is actually caudal. Stromer's identification of cranial and caudal was based on a border on the caudal part which was compared to a similar border on *Gorgosaurus* (= *Albertosaurus*). Such a border is however on the cranial medial side of ilia from *Allosaurus* (Madsen, 1976: Plate 47B) and *Tyrannosaurus* (Osborn, 1916: Fig. 10A). If one interprets this ilium as a left, rather than a right ilium, then this element loses some of the peculiarity to which Stromer (1934: S. 45-46) refers. Whether this interpretation is correct, cannot be proven any longer unfortunately, therefore this element is hardly used for comparison.

Bahariasaurus: The holotype of *Bahariasaurus* (Stromer, 1934) consists of two dorsal vertebrae, a neural arch, three sacral vertebrae, a rib fragment, both pubes and an ischium fragment. In addition, Stromer (1934) also referred a cervical vertebrae, five additional dorsal vertebrae, thirteen caudal vertebrae, an

isolated neural arch, an ilium fragment, five pubes, two further ischium fragments, as well as with a question mark one scapula, coracoid, two femora, and one fibula. The entire described material is considered here, however the elements of the shoulder girdles are consulted only a little for comparison.

The relationship of the two Egyptian genera to each other

Stromer (1934) did not accept a close relationship between *Carcharodontosaurus* and *Bahariasaurus*. If one examines the described material in regard to today's conceptions of systematics, and thus for the evaluation of characteristics, there are important things in common. Thus the two genera divide some characteristics, which are important within the Theropoda for their systematic classification (s. u.): Strongly opisthocoelous cervical vertebrae (probably related to large size) with only one pair of pleurocoels, proximally and distally reduced pubis symphyses (so that in both the pubes only contact in the middle part of the shafts), cranially curved pubis (fig. 2G, H, I), separate obturator processes of the ischium (fig. 4G, H), and a widened and anteriorly offset from the femoral shaft lesser trochanter ("wing-like lesser trochanter" in the English literature; Fig. 5E, F; vergl. Molnar et al., 1990). A further and very important characteristic is the presence of pleurocoels in the caudal vertebrae of *Carcharodontosaurus* and *Bahariasaurus*, a characteristic which has not been described so far in other theropods. This characteristic, unique to the two African genera, suggests a close relationship. The differences

between both genera were allowed to frame which family to place them within. A characteristic to which Stromer (1934) particularly referred, the dorsally oriented ball joint of the femur of *Carcharodontosaurus* is probably due to the statics of the legs and thus the large weight of the animal. The apparent differences in the orientation of the lesser trochanter (Fig. 5E, F) probably resulted from the diagenetic squeezing of the bones, which Stromer (1931, 1934) mentioned.

Comparisons with other theropods

To clarify the systematic position of *Carcharodontosaurus* and *Bahariasaurus*, the following data published by Stromer (1931, 1934, 1936) are compared with that of other theropod groups. Also, very fragmentary remains from the Cenomanian of Northern Sudan will be considered that are similar to *Bahariasaurus* (Werner, 1994; Rauhut, in prep). Within the Theropoda, well-known representatives are consulted for comparison, decreasing the possibility of the overvaluation of differences. However, with this arises the partial difficulty in recognizing large convergences.

Comparisons with Ceratosaurians: If one compares the two African theropods with the Upper Jurassic Ceratosaur *Ceratosaurus nasicornis*, there are clear differences. The cervical vertebrae of *Ceratosaurus* are cranially flat, caudally concave, and have two pairs of pleurocoels (Gilmore, 1920), while those of *Carcharodontosaurus* and *Bahariasaurus* are clearly opisthocoelous and have only one pair of pleurocoels. However, the presence of strong opisthocoelous

vertebrae could be due to the large size of the animals, so that the taxonomic meaning of this characteristic is questionable (Molnar et al., 1990; Norman, 1990).

Only the dorsal vertebrae of *Bahariasaurus* were described (Stromer, 1934). These differ from the American genera by the possession of pleurocoels. The caudal vertebrae of *Ceratosaurus* possess a deep longitudinal pit on the ventral surface (Gilmore, 1920; Madsen, 1976), which is present in other Ceratosaurs (Rowe and Gauthier, 1990). Stromer (1934) mentioned a ventral pit in the caudal vertebrae of *Bahariasaurus*, this pit is from tail vertebrae from cf. *Bahariasaurus* from chalks of Northern Sudan, and is not as clear as in *Ceratosaurus*, but does not resemble that very flat surface of *Allosaurus* (Madsen, 1976: Fig. 8). Stromer (1931) does not mention a ventral pit in the description of *Carcharodontosaurus*.

Important differences are in the pelvis. The pubis of *Ceratosaurus* curves caudally (Fig. 2A), which occurs within the Ceratosauria frequently (Rowe and Gauthier, 1990) and possibly represents a plesiomorphic characteristic of the Theropoda. In contrast, the pubis of *Carcharodontosaurus* clearly curves cranially (Fig. 2G; Stromer, 1931: Table I, Fig. 13) and the pubes of *Bahariasaurus* seem to be slightly cranially curved (Fig. 2H, I; Stromer, 1934: Table II, Fig. 1a, 3b). Also, the pubes of *Ceratosaurus* contact over their whole distal half, with the exception of a short interruption of the symphysis distally (Fig 3A), the pubic symphysis at the distal ends of the pubic shafts of the African

genera is missing (Fig 3E; in *Bahariasaurus* a symphysis is only present at the caudal ends of the distal pubic boots, this region is damaged in *Carcharodontosaurus*). Since different primitive theropods (e.g. *Herrerasaurus*; Novas, 1993), as well as Prosauropods (Galton, 1990) possess a continuous pubic symphysis, its reduction is considered a derived characteristic. A further derived characteristic of the pubes of *Bahariasaurus* is the absence of an obturator foramen (Fig. 2I). In *Ceratosaurus* a foramen completely surrounded by bone is present (Fig. 2A; Gilmore, 1920).

Despite their fragmentary preservation the ischia of the African genera clearly show an obturator process separate from the pubic process of the ischium (Fig. 4G, H; Stromer, 1931, 1934); a derived characteristic, which is absent in *Ceratosaurus* and all other Ceratosaurs (Fig. 4A, B; Gilmore, 1920; Rowe and Gauthier, 1990).

Further differences in the femur are in the orientation of the lesser trochanter as well as the extensor pit. The African genera possess a widened lesser trochanter that is clearly set off from the femoral shaft (Fig. 5E, F). In *Ceratosaurus* the lesser trochanter is low and separate from the bone shaft and does not appear thorn-like in cranial view (Fig. 5A). This orientation is primitive and is present in most Ceratosaurs, as well as *Herrerasaurus* (Novas, 1993). The extensor pit is deep in Stromer's two theropods, while it appears rather flat in *Ceratosaurus*. This characteristic could be related to the large size of these animals, so its taxonomic value is questionable.

Due to the listed differences, a close relationship between the African theropods and *Ceratosaurus* and earlier Ceratosaurs can be excluded.

The close relationship with the Abelisauridae proposed by Bonaparte (1991) is likewise improbable.

Stromer (1934) already referred to differences in the posterior cranial region of *Carcharodontosaurus* and the two Indian theropods *Indosaurus* and *Indosuchus* interpreted as Abelisaurids (Molnar, 1990; Bonaparte, 1991).

As in *Ceratosaurus*, the cervical vertebrae of *Carnotaurus* have two pairs of pleurocoels (Bonaparte et al., 1990). Besides this are the very low neural spines of *Carnotaurus*, which rise only on the posterior half of the neural arch, while those of *Carcharodontosaurus* and *Bahariasaurus* arise from the entire neural arch (Stromer, 1931, 1934). As in *Ceratosaurus*, the cervical vertebrae of *Carnotaurus* are platycoelous or only slightly opisthocelous (Bonaparte et al., 1990).

A similarity between *Carnotaurus* and *Bahariasaurus* is the presence of pleurocoels in the dorsal vertebrae. Other serious differences (s. u.) however, suggest that this represents convergence.

Differences in the caudal vertebrae include the orientation of the transverse processes, which are oriented dorsolaterally in *Carnotaurus* (Bonaparte et al., 1990; Bonaparte, 1991), and laterally in the African genera on the other hand. The orientation of the facets for the haemal arches is also different, as the distal joint is not bent ventrally in *Carnotaurus*, as it is in the

Egyptian theropods. Furthermore, the joint surfaces of *Carnotaurus* are situated at the same height, while those of *Bahariasaurus* and *Carcharodontosaurus* are shifted against one another (Molnar et al., 1990). In the caudal vertebrae of cf. *Bahariasaurus* from the Wadi Milk Formation of Sudan the neural canal is clearly broader and higher in relation to the vertebral body than in *Carnotaurus* (Fig. 6A, C).

Again important differences are in the pelvis. The caudal part of the dorsal border of the ilium of *Carnotaurus* is approximately straight, while both sides of the dorsal border of the element referred to *Carcharodontosaurus* by Stromer (1934), regardless of the orientation, are ventrally curved. The pubis of *Carnotaurus* is straight, instead of cranially curved (Fig. 2B), and is clearly missing an obturator process separate from the pubic process (Fig. 4B). Besides, an obturator foramen completely surrounded by bone is present in the South American genus (Bonaparte et al., 1990).

The femur of *Carnotaurus* possesses a widened lesser trochanter set off from the bone shaft (Fig. 5b), however, the cleft between the lesser trochanter and the bone shaft seems to be clearly lower and different than in the African genera, so that the shape of the lesser trochanter may be a result of convergence related to large size.

Due to these clear differences, particularly regarding the number of pleurocoels in the cervical vertebrae and the presence of an obturator process, a

close relationship between the African theropods and any ceratosaur can be excluded. Thus the two genera were allowed to belong to the Tetanurae.

Comparisons with “Torvosaurus”: The most primitive group of the Tetanurae are, following Sereno et al. (1994), the Torvosauroidae. Sereno et al. (1994) placed within this group the African theropod *Afrovenator* based on some derived characteristics (possession of a tertiary antorbital fenestra, a clear obturator process on the ischium separated from the pubic process), and some other genera so far too little known (*Spinosaurus*, *Baryonyx*), or in need of revision (*Eustreptospondylus*). This group in the family Torvosauridae is limited, the best known representative being *Torvosaurus* from the Upper Jurassic of North America (Galton and Jensen, 1979; Britt, 1991). With regard to the femur the genera *Megalosaurus* is also consulted, which is possibly closely related to *Torvosaurus* (Britt, 1991; though see Holtz, 1994).

The maxillary interdental plates of *Torvosaurus* are fused with one another, a characteristic which is also present in *Carcharodontosaurus*. The medial edge of the alveoli formed by these plates is clearly over the lateral border (Britt, 1991), while the interdental plates of *Carcharodontosaurus* at least between the alveoli are at the level of the lateral edge (Stromer, 1931: Table I, Fig. 6A).

The cervical vertebrae of *Torvosaurus* show, like the cervical vertebrae of all Tetanurae (with the possible exception of *Microvenator*; Ostrom, 1970), only one pleurocoel per side (Britt, 1991). Like those of *Carcharodontosaurus* and

Bahariasaurus they are strongly opisthocoelous, and have a flat ring around the convex proximal surface, a characteristic which does not occur in the African forms (Stromer, 1931, 1934). This difference could mean that the development of the opisthocoelus cervical vertebrae of *Torvosaurus* represents convergence.

The dorsal vertebrae of *Torvosaurus* possess pleurocoels that are larger in the caudal region than in the cranial region (Britt, 1991), while in *Bahariasaurus* the opposite seems to be the case (compare Stromer [1934] illustration Table II, Fig. 24a with the dorsal vertebrae in Table II, Fig. 14a).

The caudal vertebrae of *Torvosaurus* are very similar to those of the theropods from the Bahariya Oasis, except for the absence of pleurocoels.

The pubes of *Torvosaurus* show a long symphysis as well as a completely enclosed obturator foramen (Fig. 2c), and the ischia is missing an obturator process separate from the pubic process (Fig. 4C; Galton and Jensen, 1979). In these characteristics the American genera is more primitive than *Carcharodontosaurus* and *Bahariasaurus*. However, the pubis of *Torvosaurus* is slightly curved cranially (Fig. 2C; Galton and Jensen, 1979).

The femur of *Torvosaurus* is unknown; Molnar et al. (1990: Fig. 6.29i) illustrated a femur probably belonging to *Megalosaurus* as possessing a low and widened lesser trochanter, which seems to be clearly more primitive than those of the African genera.

In summary, torvosaurids show some derived characteristics, which occur in *Carcharodontosaurus* and *Bahariasaurus* (cranially curved pubis, low and

widened lesser trochanter), but lack others (reduced pubis symphysis, obturator process). A characteristic that is possibly a synapomorphy of the Torvosauridae, a flat ring around the cranial facet of the cervical vertebrae, is missing in the African genera.

Comparisons with Allosauroids: The sister-group of the Torvosauroidea, following Sereno et al. (1994), is the Neotetanurae (Avetheropoda sensu Holtz, 1994), which consists of the Allosauroidea and the Coelurosauria. Allosauroidea sensu Sereno et al. (1994) consists of some single kinds, along with the families Sinraptoridae and Allosauridae, which were already placed in this group by Currie and Zhao (1993). Their best-known representatives, *Sinraptor* and *Allosaurus*, are separately treated here, since some clear anatomical differences exist between them.

An important similarity between *Carcharodontosaurus* and *Sinraptor* is in the form of the antorbital fossa. In the Chinese genus a part of this fossa is on the nasal (Currie and Zhao, 1993), a characteristic that Sereno et al. (1994) consider a synapomorphy of the Allosauroidea. In other theropods the nasal forms either the dorsal edge of the fossa (e.g. *Ceratosaurus*; Gilmore, 1920: Plate 18), or does not contact it (e.g. *Tyrannosaurus*; Molnar et al., 1990: Fig 6.1H). Stromer (1931) mentioned a lateral recess in the description of the nasals of *Carcharodontosaurus*. In the skull reconstruction (Stromer, 1936: Fig. 9A) it is clear to see and in the same position as the nasal portion of the antorbital fossa in *Sinraptor* and *Allosaurus*. Thus, it is very probably that a part of the dorsal

section of this fossa is on the nasal (Fig. 7A, B). Pneumatic foramina in the nasals, which occur in *Sinraptor* and *Allosaurus*, are apparently missing in *Carcharodontosaurus* (Stromer, 1931: S. 6).

In *Sinraptor* the interdental plates of the maxilla are clearly separate (Currie and Zhao, 1993), which is different than in *Carcharodontosaurus*. However, the holotype of *Sinraptor* is a subadult individual, so this characteristic may depend on the ontogenetic stage of the animal.

The Chinese genus possesses strongly opisthoceolous cervical vertebrae with only a single pleurocoel, which occurs in *Torvosaurus* and the African genera. The cranial dorsal vertebrae of *Sinraptor* have pleurocoels, but none are present in the caudal dorsal vertebrae of this genus. Thus, this characteristic seems to be more similar in *Sinraptor* and *Bahariasaurus* than *Torvosaurus*. A strong constriction between the articular surfaces, which was described by Stromer (1934) for the dorsal vertebrae of *Bahariasaurus*, is also present in *Sinraptor* (Currie and Zhao, 1993: Fig. 16G).

The only described caudal vertebrae of *Sinraptor* differs from those of the African genera in that the joint surfaces, when articulated, are in such a manner that the caudal end lies dorsal to the cranial end. With the joint surfaces articulated in *Bahariasaurus* and *Carcharodontosaurus* the opposite is true.

Important similarities between *Sinraptor* and the theropods from the Bahariya Oasis are in the pelvis. The pubes of the Chinese genus not only are slightly cranially curved (Fig. 2E), they also lack a symphysis at their distal end

(Fig. 3C). Only the caudal ends of the distal expansion (pubic foot) seem to have fused, as is also the case in *Bahariasaurus*. The pubic foot of *Bahariasaurus* strongly resembles that of *Sinraptor* (Fig. 2E, H) in its form, such that the latter may belong in the same genus (Currie and Zhao, 1993). Since the pubic foot of *Torvosaurus* has an identical cross-section (Galton and Jensen, 1979; Currie and Zhao, 1993), this form seems to represent the plesiomorphic condition within the Tetanurae.

Sinraptor has an obturator notch in the place where the obturator foramen would be (Fig. 2E). In this regard it is similar to the condition in *Bahariasaurus*, however in this genus the obturator notch is substantially broader (Fig. 2i). (Whether this notch is really homologous with the obturator foramen is uncertain, since some other theropods possess notches below the obturator foramen; e.g. Fig. 2A).

The ischium of *Sinraptor* has an obturator process clearly separate from the pubic process (Fig. 4E), a further important similarity with the African theropods. The femur of the Chinese genus has a clearly widened lesser trochanter set off from the bone shaft, which is quite comparable in its shape to that of *Bahariasaurus* and *Carcharodontosaurus*.

Sinraptor seems to be more closely related to the African genera than the other theropods discussed so far. Differences are mainly in the orientation of the articular surfaces of the caudal vertebrae and the presence of the narrow obturator notch in the Chinese genus.

In *Allosaurus fragilis* from the Jurassic of North America, part of the dorsal portions of the antorbital fossae are also on the nasals (Madsen, 1976: Plate 1), which show a clear resemblance to those of *Carcharodontosaurus*. In addition, the American genus shares with *Carcharodontosaurus* the fused interdental plates in the Maxillae (Madsen, 1976). Unlike in *Torvosaurus*, and similar to the African genus, the interdental plates between the alveoli are at the level of the lateral edge of the tooth row (Madsen, 1976; Britt, 1991).

Similarities are also in the teeth. *Carcharodontosaurus* has antapikal? arranged pits at the base of the individual denticles of its serrations (Stromer, 1931: Plate I, Fig. 1, 2), a characteristic, that has only been described so far in *Allosaurus* and the Tyrannosauridae (Rauhut and Kriwet, 1994).

The cervical vertebrae of the American theropod are strongly opisthocoelous and have only pleurocoel per side, just as the cranial dorsal vertebrae.

The caudal vertebrae of *Allosaurus* differ from those from Sudan referred to *Bahariasaurus* only by the absence of pleurocoels. They possess the same ventral keel with a very flat groove, the very strong constriction of the vertebral centrum between the articular surfaces, and large neural canals in relation to the vertebral centrum (Fig. 6B; Madsen, 1976).

The pubis of *Allosaurus* is cranially curved and has a shaft very similar to that of *Carcharodontosaurus* (Fig. 2F, G; Stromer, 1931: Plate I, Fig. 13A; Madsen, 1976: Plate 48A). As is missing in *Sinraptor* and the two African

genera, the pubic symphysis at the caudal part of the pubic foot is present in *Allosaurus* (Fig. 3D). The pubic foot of *Allosaurus* is clearly larger than in *Bahariasaurus* and *Carcharodontosaurus* and is triangular in cross-section (Madsen, 1976; Currie and Zhao, 1993).

The American genus also possesses an obturator notch, which is clearly broader than that of *Sinraptor*, and shows similarity with that of *Bahariasaurus* (Fig. 2F).

The ischium of *Allosaurus* also shows an obturator process clearly separated from the pubic process (Fig. 4F). The ischium of this theropod also shows a slim, elongated “neck” between the body of the ischium and its suture with the pubis (Fig. 4F), a characteristic that is also present in *Sinraptor* and the Lower Cretaceous Allosauroid *Acrocanthosaurus* (Stovall and Langston, 1950; Currie and Zhao, 1993). An identical “neck” is present in *Carcharodontosaurus* and *Bahariasaurus* (Fig. 4G, H).

The lesser trochanter of the femur of *Allosaurus* (Fig. 5D) is very similar to those of *Sinraptor*, and also *Carcharodontosaurus* and *Bahariasaurus*.

The two African genera thus show much similarity with *Allosaurus*, so that a close relationship can be accepted.

Similarities with Coelurosaurs: Comparison of the two theropods from the Bahariya Oasis with Coelurosaurs (sensu Holtz, 1994) becomes difficult, since most representatives of this group are much smaller than the two giant forms from Africa, and naturally, functional requirements of the skeleton are completely

different. There are however some differences in the pelvis, which are probably not related to large size. A continuous distal pubic symphysis is present in *Compsognathus* (Ostrom, 1978), the Dromaeosauridae (Ostrom, 1976), and the Troodontidae (Russell and Dong, 1993b). Osmolska et al. (1972) mentioned a distal separation of the two pubic shafts in the Ornithomimid *Gallimimus*, however these elements were very close together and because of the distal pubic foot a substantial symphysis seems to be present (Osmolska et al., 1972: Plate XLVI, Fig. 3). The obturator process in coelurosaurs is triangular and gradually transitions into the shaft of the ischium distally (e.g. Osborn, 1916; Ostrom, 1969; 1978). Although Molnar et al. (1990) mention a “subtriangular” obturator process in *Carcharodontosaurus*, Stromer (1931: S. 14) says more about this process: “Below it (the obturator process) is a small notch, as in *Antrodemus* (= *Allosaurus*)...”. This notch at the distal end of the process (Fig. 4E, F, G) is different than the gradual transition in coelurosaurs. The obturator process of the ischia of *Bahariasaurus* is damaged too badly to make a statement about its distal edge, though its form proximally seems to be very similar to *Carcharodontosaurus*. Their close relationship suggests a common derivation of this process.

Since *Carcharodontosaurus* and also *Bahariasaurus* were considered closely related to the Tyrannosauridae (Lapparent, 1960; Molnar et al., 1990), and this group was placed by Holtz (1994) within the Coelurosauria, more detailed examination is required.

According to Molnar et al. (1990) the parietals in *Carcharodontosaurus* form a sharp sagittal crest between the supratemporal fenestra (“supratemporal recesses confluent over the parietals”; Molnar et al., 1990: p. 198), a characteristic which also occurs in Tyrannosaurids; in *Allosaurus* these openings are separated by a horizontal plate of bone formed by the parietals (Madsen, 1976; Molnar et al., 1990). Stromer (1931) does not mention such a condition in his description, according to his reconstruction (Stromer, 1931: Plate I, Fig. 4A, B) the supratemporal fenestrae appear through the supraoccipital hump, which end rostrally in a broad plate, and is a separate condition, quite comparable to that of *Sinraptor* (Currie and Zhao, 1993: Fig. 7) and also *Allosaurus* (Madsen, 1976: Plate, 1, 2).

The interdental plates of the maxilla of Tyrannosaurus are not fused with each other (Osborn, 1912), as in *Carcharodontosaurus* and *Allosaurus*. However, they have teeth with antapikal? arranged pits at the base of the individual denticles of the serrations like the Tyrannosauridae (Currie et al., 1990; Rauhut and Kriwet, 1994).

Despite their enormous size, the cervical vertebrae of the Tyrannosaurids are only weakly opisthocoelous (Osborn, 1906; Molnar et al., 1990). Since opisthocoelous cervical vertebrae normally seem to be related to large size (Molnar et al., 1990; Norman, 1990) the apparent absence of this characteristic meant that the gigantic Tyrannosaurids probably had another (muscular?) way to

stabilize the neck. Thus, this characteristic represents an important difference with the African theropods.

A further connecting characteristic between the genera from the Bahariya Oasis and the Tyrannosauridae given by Molnar et al. (1990) is the presence of more amphicoelous cranial dorsal vertebrae, while those of *Torvosaurus*, *Sinraptor*, and *Allosaurus* are weakly opisthocoelous. The only dorsal vertebrae from *Bahariasaurus*, according to Stromer's (1934) data, are caudal dorsal vertebrae, so this characteristic is invalid. Besides, the vertebrae from Stromer's description are weakly opisthocoelous, though he describes them as platycoelous.

A difference in the caudal vertebrae of Tyrannosaurids and the African genera is in the position of the articular surfaces, which in Tyrannosaurids are not positioned against each other (Molnar et al., 1990). Molnar et al. (1990) indicated a connecting characteristic in the central lying neural spines with rear caudal vertebrae can also be rejected, since this extension is positioned in the middle tail vertebrae only as low, after distal rising edge (Stromer, 1934: p. 29; Plate II, Fig. 26a, b). The strong development of the transverse processes of these vertebrae, which, through a comparison with *Allosaurus* (Madsen, 1976), could have been between caudal 18-30, suggests that transverse processes were still present distally in the tail, while in Tyrannosaurids they disappear before the 16th caudal vertebrae (Molnar et al., 1990), as is the case in other coelurosaurs (Holtz, 1994).

The pubis of Tyrannosaurids is also cranially curved (Fig. 2D; Osborn, 1916), it has a cranial outgrowth to it proximally however (Fig. 2D; Osborn, 1916: Plate 27; Lambe, 1917: Fig. 16, 28), which is missing in the pubes of *Bahariasaurus* and *Carcharodontosaurus*. The pubic symphysis in Tyrannosaurids seems to be continuous distally (Fig. 3B; Lambe, 1917), although Osborn (1912) described a short distal interruption of this symphysis in *Tyrannosaurus*. The ischia of Tyrannosaurids shows the typical condition for coelurosaurs, with the obturator process gradually flowing into the shaft of the ischium distally (Fig. 4D), so that the same applies here for this group (contra Molnar et al., 1990).

Also, Tyrannosaurids possess a widened lesser trochanter, which is clearly set off from the shaft, however it reached the proximal end of the femur, and is thus clearly higher than those of the femora of the African theropods (Fig. 5C).

The superficial similarities between the genera from the Bahariya Oasis and the Tyrannosauridae could be due to the large size of the animals; a detailed comparison shows clear differences.

Summary of the Comparisons

All the following indicated characteristics refer to the two African genera.

The two African theropods differ from the Ceratosauria (sensu Holtz, 1994) in the presence of only one pair of pleurocoels in the cervical vertebrae,

the absence of a deep ventral pit in the caudal vertebrae, the reduction of the obturator foramen, the absence of a distal pubic symphysis, the presence of an obturator process clearly separated from the pubic process, and the form of the lesser trochanter.

Differences from the Torvosauridae are clear in the form of the interdental plates of the maxillae, the reduction of the obturator foramen, the absence of a distal pubic symphysis, as well as the presence of an obturator process separated from the pubic process.

Differences from the Tyrannosauridae are in form of the interdental plates of the maxillae, the more strongly opisthocoelous cervical vertebrae, the form of the neural spines in the distal caudal vertebrae, the presence of transverse processes distal to the 15th caudal vertebrae, the absence of a cranial outgrowth on the proximal pubic shaft, the absence of a distal pubic symphysis, the form of the obturator process, and the form of the lesser trochanter.

Non size-dependent differences from the Coelurosauria (sensu Holtz, 1994) are in the absence of a distal pubic symphysis, the form of the obturator process, as well as the presence of transverse processes distal to the 15th caudal vertebrae.

Similarities with the Allosauroidea (Currie and Zhao, 1993) are the absence of a distal pubic symphysis, the absence of an obturator foramen, the participation of the nasal in the dorsal edge of the antorbital fossa, the presence of an obturator notch, the form of the obturator process, the form of the obturator

process and the form of the lesser trochanter. Due to these characteristics, one can assign *Carcharodontosaurus* and *Bahariasaurus* to the superfamily Allosauroidea.

Within the Allosauroidea the two African theropods differ from the Sinraptorid *Sinraptor* in the form of the interdental plates of the maxillae, the width of the obturator notch, and the disalignment of the articular surfaces of the caudal vertebrae. Since they are very similar in these characteristics to the Allosaurid *Allosaurus*, and also share the long, slim neck of the pubic process of the ischium, they appear to be more closely related to the Allosauridae than the Sinraptoridae.

Carcharodontosaurus and *Bahariasaurus* particularly differ from all other theropods by a common characteristic: the possession of pleurocoels in the anterior caudal vertebrae. Since the pneumatization of the vertebral column often seems to be an important aspect in theropod systematics (e.g. Gauthier, 1986; Holtz, 1994), this characteristic appears to justify the erection of another family within the superfamily Allosauroidea. The systematic position of *Carcharodontosaurus* and *Bahariasaurus* can be represented therefore as follows:

Superfamily: **Allosauroidea** Currie and Zhao, 1993

The superfamily as proposed by Currie and Zhao (1993) contains only the two families Allosauridae and Sinraptoridae, and the Carcharodontosauridae are

included here. Sereno et al. (1994) assigned the theropod *Monolophosaurus jiangi* from the Middle Jurassic of Eastern Asia (Zhao and Currie, 1993) to this group. Its inclusion in this group appears questionable due to the primitive characteristics of the pelvis (a completely enclosed obturator foramen, lack of an obturator process separated from the pubic process). *Cryolophosaurus* from the Lower Jurassic of Antarctica (Hammer and Hickerson, 1994) is at present lacking a detailed enough description to examine its placement in the Allosauroidea (Sereno et al., 1994). Diagnostic characteristics of the Allosauroidea include the participation of the nasal in the antorbital fossa (this characteristic is also present in *Monolophosaurus*), the loss of an obturator foramen with the retention of an obturator notch, reduction of the distal pubic symphysis with retention of a symphysis at the caudal end of the pubic foot, the presence of an obturator process with a small notch between its distal end and the shaft of the ischium, separated from the pubic process, and the widened and clearly set off from the bone shaft ("wing-like") lesser trochanter, which extends dorsally to approximately the midpoint of the femoral head. It is worth mentioning that the reduction of the pubic symphysis in *Acrocanthosaurus* is apparently substantially less ?ausgepragt? than in other Allosauroids (Stovall and Langston, 1950).

Familie **Carcharodontosauridae** Stromer 1931

(=Bahariasauridae Huene 1948)

Diagnosis: Large Allosauroid theropods with pleurocoels in the anterior caudal vertebrae. Further autapomorphies of the Carcharodontosauridae could be the possession of straight tooth crowns, a triangular coracoid, as well as elongated dorsal vertebrae. While the first of these characteristics may only pertain to *Carcharodontosaurus*, and the second may only pertain to *Bahariasaurus*, the third, which Stromer (1934) described for *Bahariasaurus*, is at least suggested for *Carcharodontosaurus* by the presences of elongated proximal caudal vertebrae (Stromer, 1931).

Genus: *Carcharodontosaurus* Stromer 1931

Type species: *Carcharodontosaurus saharicus* (Deperet and Suvovnin, 1926)

Genus: *Bahariasaurus* Stromer 1934

Type species: *Bahariasaurus ingens* Stromer 1934

Origin and diversification of the Carcharodontosauridae

The Carcharodontosauridae appears to be, as already mentioned, the sistergroup of the Allosauridae. Several anatomical differences given by a detailed comparison between Carcharodontosaurids and Allosaurids, as well as the occurrence of *Allosaurus* in the upper Jurassic (Kimmeridgian), suggest that the separation of these two groups already took place in the middle Jurassic or in the older stages of the upper Jurassic. Janensch (1925) described some skeletal elements from large theropods from the Kimmeridgian of Tendaguru (Tanzania),

which he referred to *Allosaurus*. In addition he erected the species “*Megalosaurus*” *ingens* on the basis of very large teeth from the same discovery site (Janensch, 1920). These teeth have clearly ?antapikal? arranged pits at the base of the individual denticles of the serration edges (pers. Beob.), and are not similar to the teeth of *Allosaurus*, but are similar to those of *Carcharodontosaurus*. These remains from Tendaguru could represent early representatives of the Carcharodontosauridae.

Remainders from Carcharodontosaurids were described from the Cretaceous from different discovery sites in Africa (Fig. 8; see Weishampel, 1990: p. 109, 110, 138). If one does not consider the finds from Tanzania, then a temporal spread from the Aptian into the Coniacian-Turonian is present. The actual temporal range of this group could have been substantially longer however, the absence of evidence is probably because of the lack of dinosaur sites in the lower and upper Cretaceous of Africa.

Altogether, Carcharodontosaurids seem to have been very common in the Cretaceous of Africa: In the ten to fourteen sites in the Cretaceous of Africa, theropod remains assignable to this group are present (Fig. 8; Weishampel, 1990; Rauhut, in prep.). This suggests that the theropod fauna of the Cretaceous of Africa was clearly different than those of Laurasia and South America. Thus, three different lineages of large theropod of different origins are present in the Cretaceous: In South America the Abelisauridae evolved from the ceratosaurs of the upper Jurassic, in Africa large Allosauroids formed the top of

the food chain, and in Laurasia the giant Tyrannosauridae evolved from the smaller coelurosaurs. This consequence corresponds with the presence of an African line of the Torvosauroidae (Serenó et al., 1994). This acceptance is based on the referral of *Afrovenator* to the Torvosauridae, however. Whether this is true must await a detailed description of *Afrovenator*. The occurrence of possible Abelisaurids in India (*Indosaurus* and *Indosuchus*; Bonaparte, 1991), Europe (*Tarascosaurus*; LeLoeuff and Buffetaut, 1991), and in the uppermost Cretaceous of Africa (*Majungasaurus*; Molnar, 1990), speaks for some form of faunal connection between South America and Africa.

Only a few theropod remains from the Cretaceous of Australia are well-known, of which most are too fragmentary to make safe statements about their systematic position. Molnar et al. (1981) described remains of an Allosauroid that could also be closely related to the Carcharodontosauridae; further finds are necessary here in order to shed light on the relations of the Cretaceous theropod fauna of Australia.

Extended English Abstract.

The African theropod genera *Carcharodontosaurus* Stromer 1931 and *Bahariasaurus* Stromer 1934 were based on fragmentary skeletons from the Cenomanian of the Bahariya-Oasis of Egypt. The whole material was destroyed during the second world war. Therefore, the revision of the systematic position of these genera has to rely on the data published by Stromer (1931, 1934, 1936).

Molnar et al. (1990) regarded these genera as Carnosauria incertae sedis, somewhere in between allosaurids and tyrannosaurids. More recent theropod systematics ignore the two taxa from Africa (Holtz, 1994; Sereno et al., 1994). In this paper, the systematic position of the Egyptian theropods within the systematic scheme of Holtz, as modified by Sereno et al. (Fig. 1), is revised.

The two theropods share several characters which are important for their classification within theropods: strongly opisthocoelous cervical vertebrae (probably size related) with only one pair of pleurocoels, pubis-symphysis only found in the middle parts of the pubic shafts, but reduced proximally and distally (Fig. 3E; a symphysis is present in the caudal part of the pubic boot in *Bahariasaurus*, this region is damaged in *Carcharodontosaurus*), pubis bowed cranially (Fig. 2G, H, I), obturator process offset from the pubic process of the ischium (Fig. 4G, H), winglike lesser trochanter (Fig. 5E, F). A very important feature is the presence of pleurocoels in the anterior caudal vertebrae, a character which is not found in any other theropod. Therefore, the two genera are regarded as close relatives.

In the following comparisons, all characters refer to the two African theropods.

The genera from the Bahariya-Oasis differ from ceratosaurs (sensu Holtz, 1994) in the following characters: only one pair of pleurocoels present in cervical vertebrae, lack of a deep ventral groove in caudal vertebrae (see Madsen, 1976: Fig. 8; Rowe and Gauthier, 1990), loss of the obturator foramen, reduction of

distal pubic symphysis, presence of an obturator process of the ischium, winglike lesser trochanter. Therefore, a close relationship between ceratosaurs and the Egyptian genera can be excluded. Bonaparte (1991) argued, that the two genera are closely related to the advanced ceratosaur family Abelisauridae, based on the structure of the hind limbs. The pelvis of the abelisaurid *Carnotaurus* differs from that of *Bahariasaurus* and *Carcharodontosaurus* in all of the characters listed above (Bonaparte et al., 1990), and although *Carnotaurus* shows an aliform lesser trochanter, it differs significantly from that of the African theropods, suggesting convergence (Fig. 5B).

Sereno et al. (1994) named the Torvosauroida as the most primitive group of tetanuran theropods, to include *Afrovenator*, *Torvosaurus*, the spinosaurids and several other genera. Since *Afrovenator* shows some derived characters (presence of a promaxillary fenestra, *Sinraptor*-like obturator process on ischium), and spinosaurids are too incompletely known so far, the torvosaurids are here restricted to include *Torvosaurus* and maybe *Megalosaurus*, which seems to be a close relative of the former genus (Britt, 1991; but see Holtz, 1994). The systematic position of *Afrovenator* and the probable spinosaurid *Baryonyx* will hopefully be clarified by detailed studies of the specimens.

Differences between the genera described by Stromer and torvosaurids are found in the development of the interdental plates of the maxillary, the loss of the obturator foramen, reduction of the distal symphysis of the pubic shafts,

presence of an obturator process, which is offset from the pubic process of the ischium, and probably the exact shape of the lesser trochanter (based on material referred to *Megalosaurus*, Molnar et al., 1990: Fig. 6.29i).

Several authors suggested a close relationship between the African genera and tyrannosaurids (e.g. Lapparent, 1960; Molnar et al., 1990), which are now regarded as coelurosaurs (Holtz, 1994; Sereno et al., 1994). This relationship seems unlikely due to the following differences: supratemporal recesses not confluent over the parietals (contra Molnar et al., 1990), fused interdental plates in the maxilla, presence of strongly opisthocoelous cervical vertebrae (see below), the development of the neural spines in distal caudal vertebrae (contra Molnar et al., 1990), presence of transverse processes in caudal vertebrae distal to the 15th, reduction of the distal symphysis of the pubic shafts, small notch at the distal end of the obturator process (contra Molnar et al., 1990), lesser trochanter lower than greater trochanter.

If strongly opisthocoelous cervical vertebrae are related to large size (Molnar et al., 1990; Norman, 1990), the absence of this feature in even the largest tyrannosaurids might be an important difference, suggesting a different way of stabilizing the cervical vertebral column in this group.

Differences from smaller coelurosaurs include: reduction of the distal symphysis of the pubic shafts (this character may be present in ornithomimids; Osmolska et al., 1972), small notch at the distal end of the obturator process and more than 15 caudal vertebrae with transverse processes.

Comparing the two African genera with the allosauroid genera *Sinraptor* and *Allosaurus*, several similarities are found: nasal participation in the antorbital fossa (Fig. 7A, B), reduction of the distal symphysis of the pubic shafts, presence of an obturator notch, presence of a small notch at the distal end of the obturator process (may be plesiomorphic) and the shape and height of the lesser trochanter.

Therefore, *Carcharodontosaurus* and *Bahariasaurus* can be referred to the Allosauroidea Currie and Zhao, 1993. Within the Allosauroidea, both genera seem to be the sister group to the Allosaurids, due to the following characters: fused interdental plates in the maxillae, obturator notch wide (Fig. 2F, I), slender “neck” at the pubic peduncle of the ischium (Fig. 4F, G, H).

Since the pneumatization of the vertebral column often seems to be an important aspect in theropod classification (e.g. Gauthier, 1986; Holtz, 1994), the presence of caudal pleurocoels in both Egyptian genera allows their reference to a separate family of allosauroid theropods: Carcharodontosauridae Stromer 1931 (=Bahariasauridae Huene 1956). In contrast to Sereno et al. (1994), the Allosauroidea are here restricted to include the families Sinraptoridae, Allosauridae and Carcharodontosauridae.

The origin of this family may be found in theropods from the Kimmeridgian of Tendaguru (Tanzania), documented by remains assigned to *Allosaurus tendagurensis* and *Megalosaurus ingens* by Janensch (1920, 1925).

Carcharodontosaurids seem to be abundant in the Cretaceous of Africa (Fig. 8; see Weishampel, 1990), suggesting three lines of large theropods in the Cretaceous: the ceratosaurian abelisaurids in South America, the allosauroid carcharodontosaurids in Africa and the coelurosaurian tyrannosaurs in North America and Asia. This conclusion is quite similar to that reached by Sereno et al. (1994).

Literature Cited

Literatur

- BONAPARTE, J. F. 1991. The gondwanian theropod families Abelisauridae and Noosauridae. - *Historical Biology* 5: 1-25, Yverdon, Schweiz
- BONAPARTE, J. F., NOVAS, F. E. & CORIA, R. A. 1990. *Carnotaurus sastrei* BONAPARTE, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. - *Contributions in Science, Los Angeles County Museum*, 416: 1-41, Los Angeles, Calif.
- BRITT, B. B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. - *BYU Geology studies* 37: 1-72, Salt Lake City, Utah
- BUFFETAUT, E., BUSSERT, R. & BRINKMANN, W. 1990. A new nonmarine vertebrate fauna in the Upper Cretaceous of northern Sudan. - *Berliner geowissenschaftliche Abhandlungen (A)* 120.1: 183-202, Berlin
- CARROLL, R. L. 1988. Vertebrate paleontology and evolution. - W. H. Freeman & Co., New York, 698 S.
- CURRIE, P. J., RIGBY, J. K. Jr. & SLOAN, R. E. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada. - In: CARPENTER, K. & CURRIE, P. J. (Hrsg.): *Dinosaur systematics. Approaches and perspectives*: 107-125, Cambridge University Press, Cambridge, Mass.
- CURRIE, P. J. & ZHAO X.-J. 1993. A new carnosaur (Dinosauria, Theropoda) from the Jurassic of Xinjiang, People's Republic of China. - *Canadian Journal of Earth Sciences* 30: 2037-2081, Ottawa
- GALTON, P. M. 1990. Basal Sauropodomorpha - Prosauropoda. - In: WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (Hrsg.): *The Dinosauria*: 320-344, University of California Press, Berkeley, Calif.
- GALTON, P. M. & JENSEN, J. A. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. - *BYU Geology studies* 26 (2): 1-12, Salt Lake City, Utah
- GAUTHIER, J. 1986. Saurischian monophyly and the origin of birds. - In: PADIAN, K. (Hrsg.): *The origin of birds and the evolution of flight. Memoirs of the Californian Academy of Sciences* 8: 1-55, San Francisco, Calif.
- GILMORE, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. - *Bulletin of the United States National Museum* 110: 1-154, Washington D.C.
- HAMMER, W. R. & HICKERSON, J. 1994. A crested theropod dinosaur from Antarctica. - *Science* 264: 828-830, Washington D.C.
- HOLTZ, T. R. Jr. 1994. The phylogenetic position of the Tyrannosauridae: Implications for theropod systematics. - *Journal of Paleontology* 68 (5): 1100-1117, Lawrence, Kansas
- HUENE, F. von 1948. Short review of the lower tetrapods. - *The Royal Society of South Africa, Special publications; Robert Broom commemorative Volume*: 65-106; Johannesburg
- HUENE, F. von 1956. Paläontologie und Phylogenie der niederen Tetrapoden. - VEB Gustav Fischer Verlag, Jena, 716 S.
- JANENSCH, W. 1920. Über *Elaphrosaurus bambergi* und die Megalosaurier aus den Tendaguru-Schichten Deutsch-Ostafrikas. - *Sitzungsbericht der Gesellschaft der Naturforschenden Freunde Berlin* 1920: 225-235, Berlin
- JANENSCH, W. 1925. Die Coelurosaurier und Theropoden der Tendaguru-Schichten Deutsch-Ostafrikas. - *Palaeontographica (Suppl. 7)* 1: 1-99, Stuttgart
- LAMBE, L. M. 1917. The Cretaceous theropodous dinosaur *Gorgosaurus*. - *Memoirs of the geological Survey of Canada* 100: 1-84, Ottawa
- LAPPARENT, A. F. de 1960. Les dinosauriens du "Continental intercalaire" du Sahara central. - *Mémoires de la Société géologique de France (Nouvelle Série)* 88A: 1-57, Paris
- LELOEUFF, J. & BUFFETAUT, E. 1991. *Tarascosaurus salluvicus* nov. gen. nov. sp., dinosaure théropode du Crétacé supérieur du sud de la France. - *Geobios* 25 (5): 585-594, Lyon
- MADSEN, J. H. Jr. 1976. *Allosaurus fragilis*: A revised osteology. - *Utah geological and mineralogical Survey Bulletin* 109: 1-163, Salt Lake City, Utah
- MOLNAR, R. E. 1990. Problematic Theropoda: "Carnosaurs". - In: WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (Hrsg.): *The Dinosauria*: 306-317, University of California Press, Berkeley, Calif.
- MOLNAR, R. E., FLANNERY, T. F. & RICH, T. H. V. 1981. An allosaurid theropod dinosaur from the Early Cretaceous of Victoria, Australia. - *Alcheringa* 5: 141-146, Sidney
- MOLNAR, R. E., KURZANOV, S. M. & DONG Z. 1990. Carnosauria. - In: WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (Hrsg.): *The Dinosauria*: 169-209, University of California Press, Berkeley, Calif.

- NORMAN, D. B. 1990. A review of *Vectisaurus valdensis*, with comments on the family Iguanodontidae. - In: Carpenter, K. & Currie, P. J. (Hrsg.): Dinosaur systematics. Approaches and perspectives: 147-161, Cambridge University Press, Cambridge, Mass.
- NOVAS, F. E. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. - Journal of Vertebrate Paleontology 13 (4): 400-423; Lawrence, Kansas
- OSBORN, H. F. 1906. *Tyrannosaurus*, Upper Cretaceous carnivorous dinosaur (second communication). - Bulletin of the American Museum of Natural History 22: 281-296, New York, N.Y.
- OSBORN, H. F. 1912. Crania of *Tyrannosaurus* and *Allosaurus*. - Memoirs of the American Museum of Natural History 1: 1-30, New York, N.Y.
- OSBORN, H. F. 1916. Skeletal adaptations of *Ornitholestes*, *Struthiomimus*, *Tyrannosaurus*. - Bulletin of the American Museum of Natural History 35: 733-771, New York, N.Y.
- OSMÓLSKA, H., RONIEWICZ, E. & BARSBOLD, R. 1972. A new dinosaur, *Gallimimus bullatus* n. gen. n. sp. (Ornithomimidae) from the Upper Cretaceous of Mongolia. - Palaeontologia Polonica 27: 103-143, Warschau
- OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod dinosaur from the Lower Cretaceous of Montana. - Peabody Museum of Natural History, Bulletin 30: 1-165, New Haven, Conn.
- OSTROM, J. H. 1970. Stratigraphy and paleontology of the Cloverly Formation (Lower Cretaceous) of the Bighorn Basin area, Wyoming and Montana. - Peabody Museum of Natural History, Bulletin 35: 1-234, New Haven, Conn.
- OSTROM, J. H. 1976. On a new specimen of the Lower Cretaceous theropod dinosaur *Deinonychus antirrhopus*. - Breviora 439: 1-21, Cambridge, Mass.
- OSTROM, J. H. 1978. The osteology of *Compsognathus longipes* WAGNER. - Zitteliana 4: 73-118, München
- PAUL, G. S. 1984. The archosaurs: A phylogenetic study. - In: REIF, W.-E. & WESTPHAL, F. (Hrsg.): Third symposium on Mesozoic terrestrial ecosystems. Short Papers: 175-180, Attempto Verlag, Tübingen
- PAUL, G. S. 1988. Predatory dinosaurs of the world. - Simon & Schuster, New York, N.Y., 463 S.
- RAUHUT, O. W. M. in prep. Dinosaurier aus der "mittleren" Kreide des nördlichen Sudan.
- RAUHUT, O. W. M. & KRIWET, J. 1994. Teeth of a big theropod dinosaur from Porto das Barcas (Portugal). - Berliner geowissenschaftliche Abhandlungen (E) 13: 179-185, Berlin
- ROMER, A. S. 1966. Vertebrate paleontology (3. Ausg.). - University of Chicago Press, Chicago, 468 S.
- ROWE, T. & GAUTHIER, J. 1990. Ceratosauria. - In: WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (Hrsg.): The Dinosauria: 151-168, University of California Press, Berkeley, Calif.
- RUSSELL, D. A. & DONG Z.-M. 1993a. The affinities of a new theropod from the Alxa Desert, Inner Mongolia, People's Republic of China. - Canadian Journal of Earth Sciences 30: 2107-2127, Ottawa
- RUSSELL, D. A. & DONG Z.-M. 1993b. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. - Canadian Journal of Earth Sciences 30: 2163-2173, Ottawa
- SERENO, P. C., WILSON, J. A., LARSON, H. C. E., DUTHEIL, D. B. & SUES, H.-D. 1994. Early Cretaceous dinosaurs from the Sahara. - Science 266: 267-271, Washington D.C.
- STEEL, R. 1970. Saurischia. - Handbuch der Paläoherpetologie 14: 1-87, Stuttgart
- STOVALL, J. W. & LANGSTON, W. Jr. 1950. *Acrocanthosaurus atokaensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. - The American Midland Naturalist 43 (3): 696-728, Notre Dame, Ind.
- STROMER, E. 1915. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. - Abhandlungen der königlich bayerischen Akademie der Wissenschaften, mathematisch-physikalische Klasse 28 (3): 1-32, München
- STROMER, E. 1931. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. - Abhandlungen der bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung N. F. 9: 1-23, München
- STROMER, E. 1932. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 11. Sauropoda. - Abhandlungen der bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung N. F. 10: 1-21, München

- STROMER, E. 1934. Wirbeltier-Reste der Baharije-Stufe (unterstes Cenoman). 13. Dinosauria. - Abhandlungen der bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung N. F. **22**: 1-79, München
- STROMER, E. 1936. Baharije-Kessel und -Stufe mit deren Fauna und Flora. Eine ergänzende Zusammenfassung. - Abhandlungen der bayerischen Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Abteilung N. F. **33**: 1-102
- WEISHAMPEL, D. B. 1990. Dinosaurian distribution. - In: WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (Hrsg.): The Dinosauria: 63-139, University of California Press, Berkeley, Calif.
- WERNER, C. 1994. Die kontinentale Wirbeltierfauna aus der unteren Oberkreide des Sudan (Wadi Milk Formation). - Berliner geowissenschaftliche Abhandlungen (E) **13**: 221-249, Berlin
- ZHAO X.-J. & CURRIE, P. J. 1993. A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. - Canadian Journal of Earth Sciences **30**: 2027-2036, Ottawa

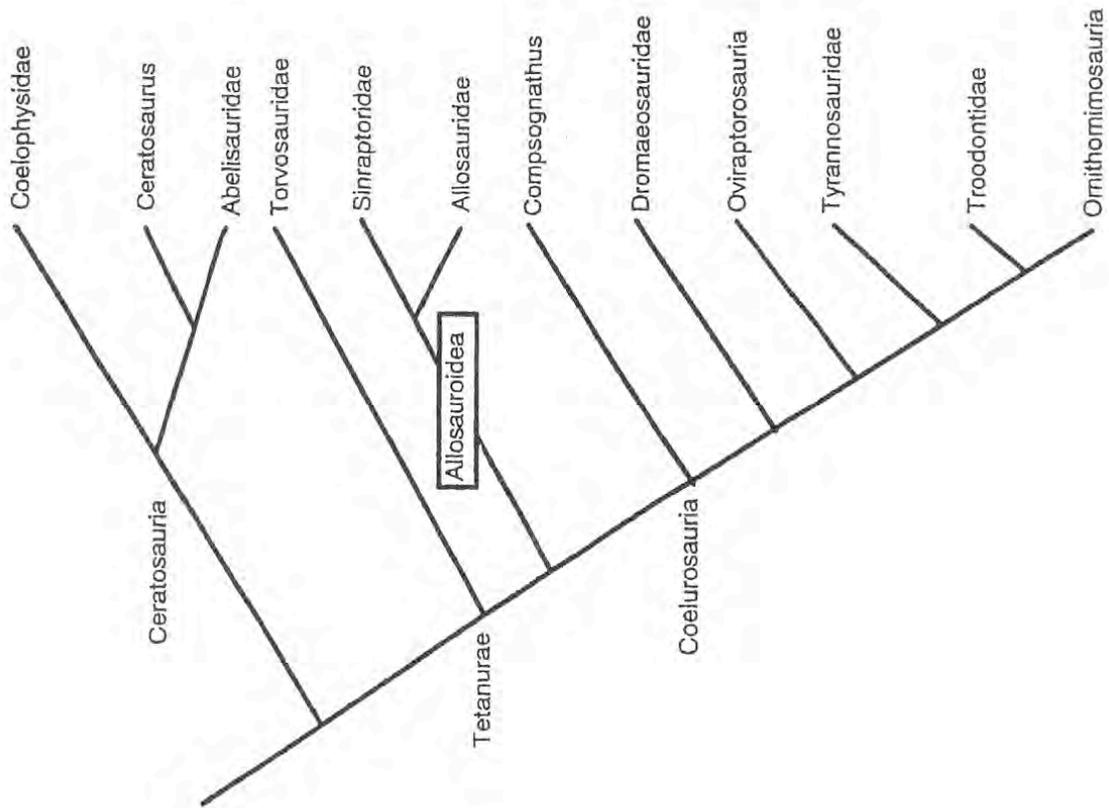


Fig. 1. Theropod systematics. Cladogram after Hotlz (1994), as modified by Sereno et al. (1994).

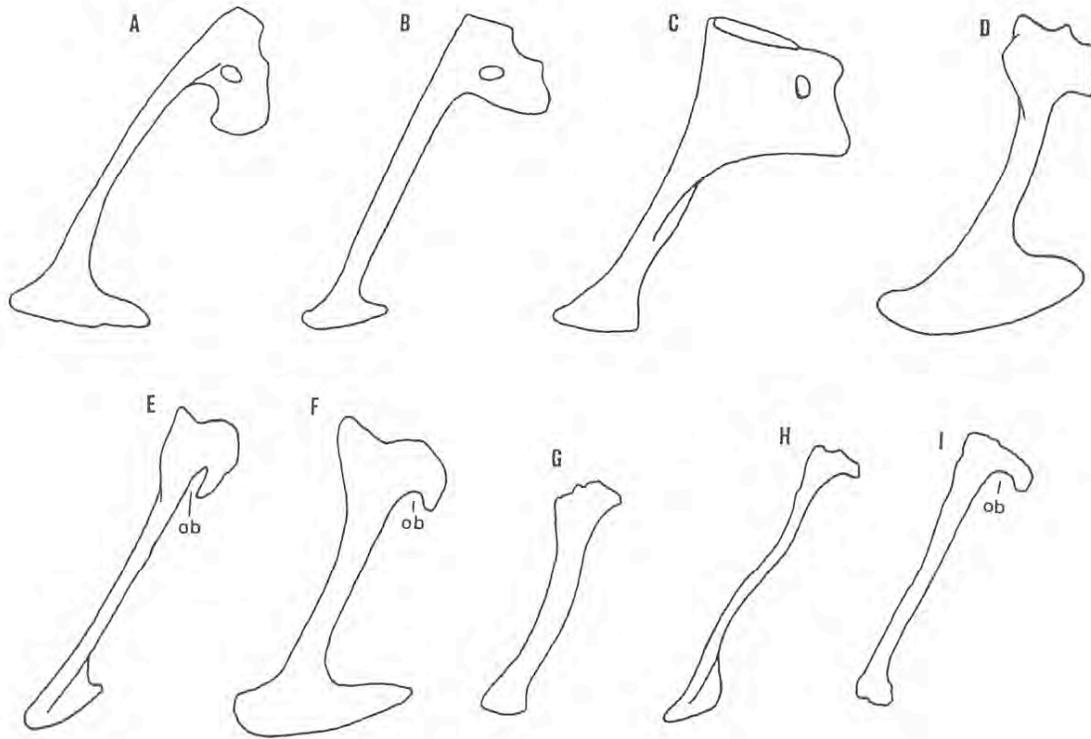


Fig. 2. Left pubis of several theropods in lateral view. A: *Ceratosaurus* (after Gilmore, 1920); B: *Carnotaurus* (reversed right pubis, after Bonaparte et al., 1990); C: *Torvosaurus* (after Galton and Jensen, 1979); D: *Tyrannosaurus* (reversed right pubis, after Osborn, 1916); E: *Sinraptor* (after Currie and Zhao, 1993); F: *Allosaurus* (after Madsen, 1976); G: *Carcharodontosaurus* (after Stromer, 1931); H, I: *Bahariasaurus* (after Stromer, 1934).

ob: Obturator notch. Not drawn to the same scale. The strange shape of the pubic shaft in *Bahariasaurus* (H) is most probably a result of diagenetic stresses.

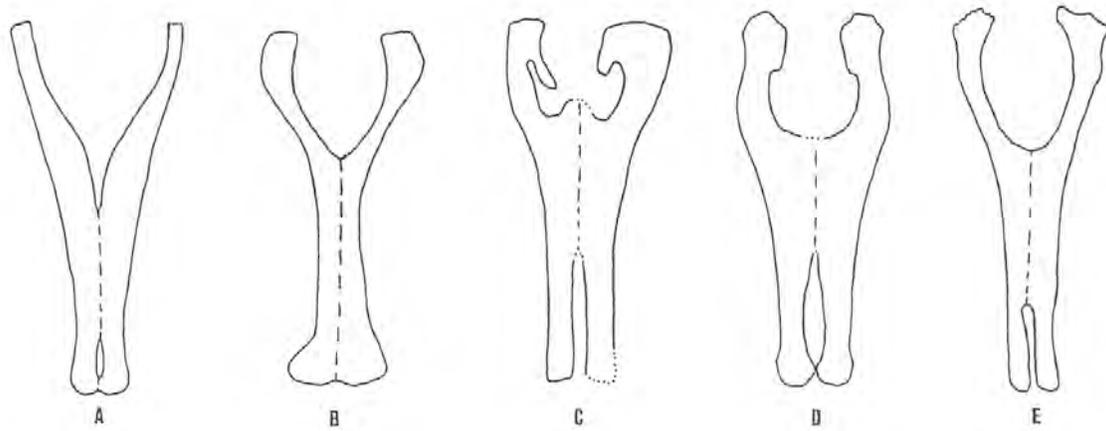


Fig. 3. Pubes of several theropods in cranial view, to show the reduction of the distal pubis symphysis in allosauroids. Symphysis in the caudal part of the pubic boot are not shown. A: *Ceratosaurus* (after Gilmore, 1920); B: *Tarbosaurus* (after Molnar et al., 1990); C: *Sinraptor* (after Currie and Zhao, 1993); D: *Allosaurus* (after Gilmore, 1920); E: *Bahariasaurus* (after Stromer, 1934). Not drawn to the same scale.

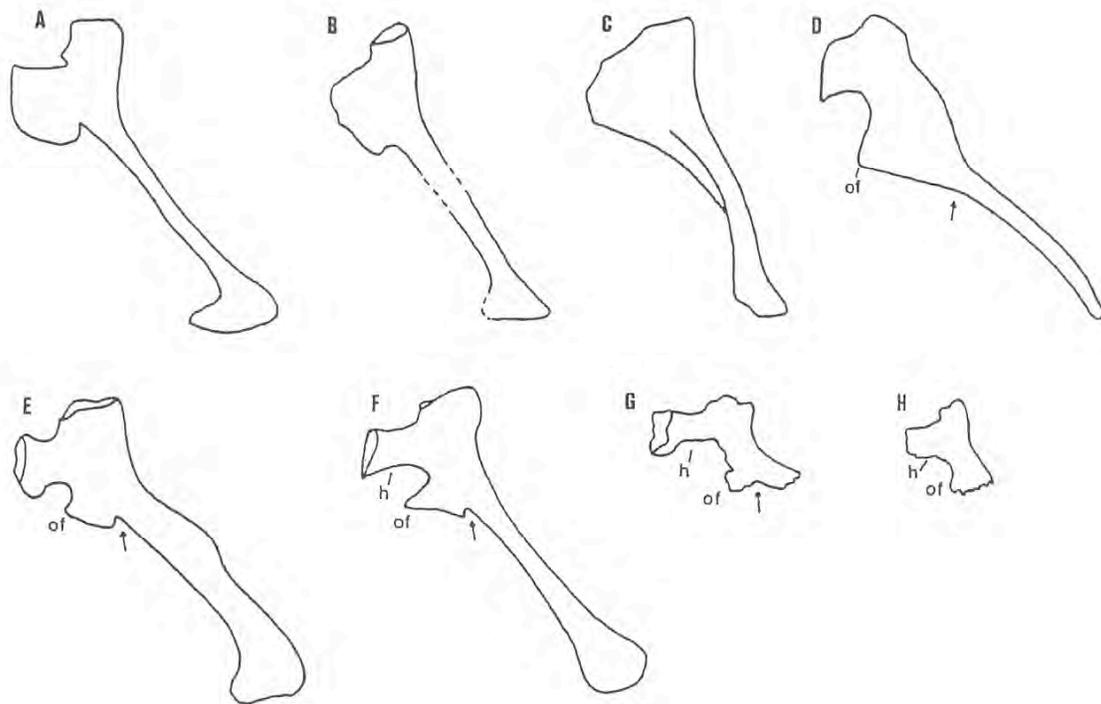


Fig. 4. Left ischium of several theropods in lateral view. A: *Ceratosaurus* (after Gilmore, 1920); B: *Carnotaurus* (reversed right ischium, after Bonaparte et al., 1990); C: *Torvosaurus* (reversed right ischium, after Galton and Jensen, 1979); D: *Tyrannosaurus* (reversed right ischium, after Osborn, 1916); E: *Sinraptor* (after Currie and Zhao, 1993); F: *Allosaurus* (after Madsen, 1976); G: *Carcharodontosaurus* (after Stromer, 1931); H: *Bahariasaurus* (after Stromer, 1934).

h: “neck” at the pubic process of the ischium; of: obturator process; Arrows point to the confluent distal contact between obturator process and ischium shaft in *Tyrannosaurus* in contrast to the small notch in *Sinraptor*, *Allosaurus* and *Carcharodontosaurus*. Not drawn to the same scale.

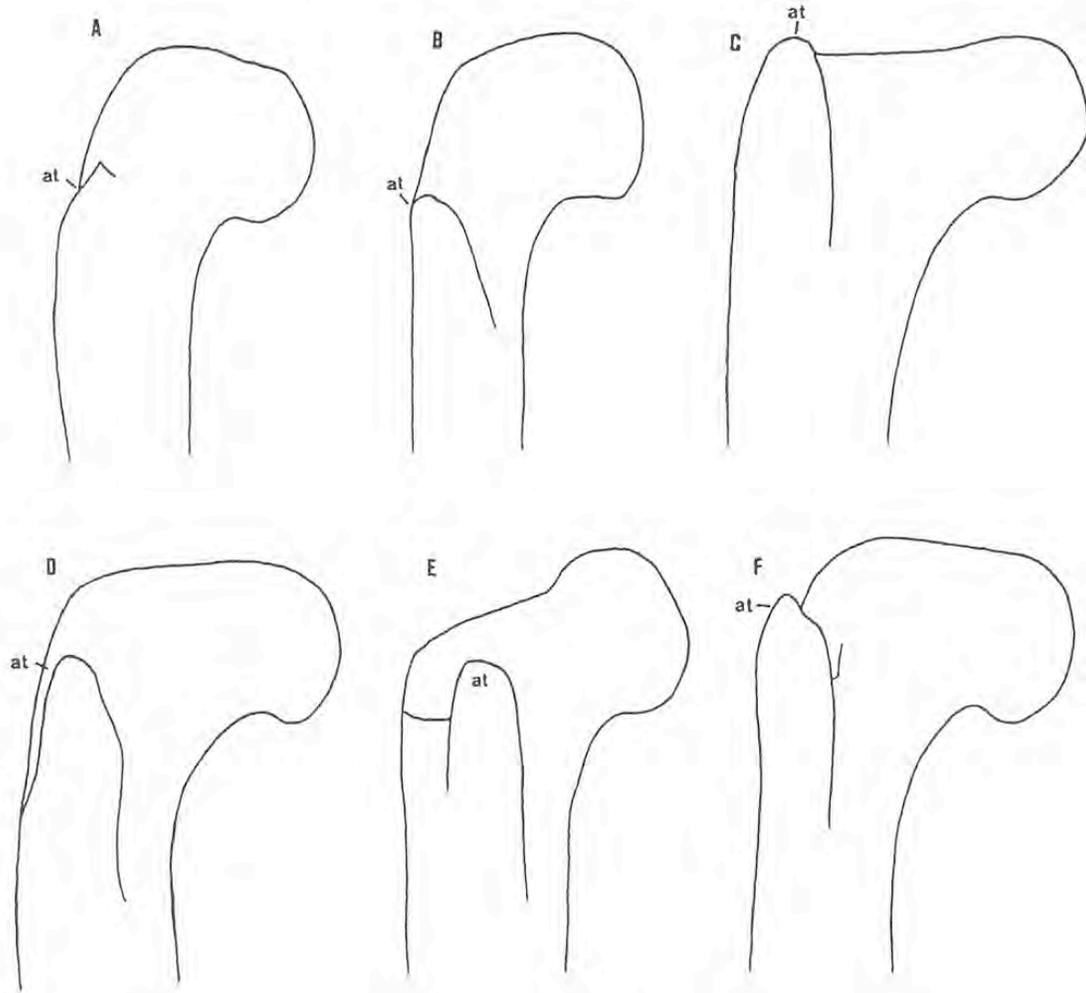


Fig. 5. Proximal ends of right femora of several theropods in cranial view, to show differences in the development of the lesser trochanter. A: *Ceratosaurus* (after Gilmore, 1920); B: *Carnotaurus* (after Bonaparte et al., 1990); C: *Tyrannosaurus* (after Osborn, 1916); D: *Allosaurus* (reversed left femur, after Madsen, 1976); E: *Carcharodontosaurus* (reversed left femur, after Stromer, 1931); F: *Bahariasaurus* (after Stromer, 1934).

at: lesser trochanter. The differences in the position of the lesser trochanter in *Allosaurus*, *Carcharodontosaurus*, and *Bahariasaurus* are most probably due to diagenetic stresses altering the femora from the Bahariya-Oasis. Not drawn to the same scale.

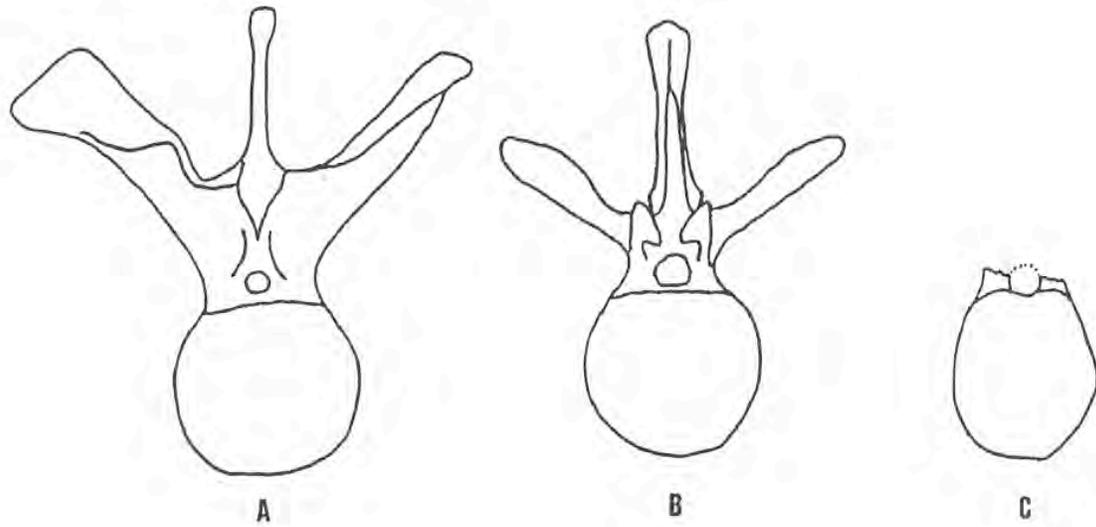


Fig. 6. Proximal caudal vertebrae of A: *Carnotaurus* (after Bonaparte et al., 1990), B: *Allosaurus* (after Madsen, 1976), and C: cf. *Bahariasaurus* (from the Wadi Milk Formation, Sudan; Rauhut, in prep.) in cranial view to show differences in the proportions of the neural canal and the vertebral centrum. Not drawn to the same scale.

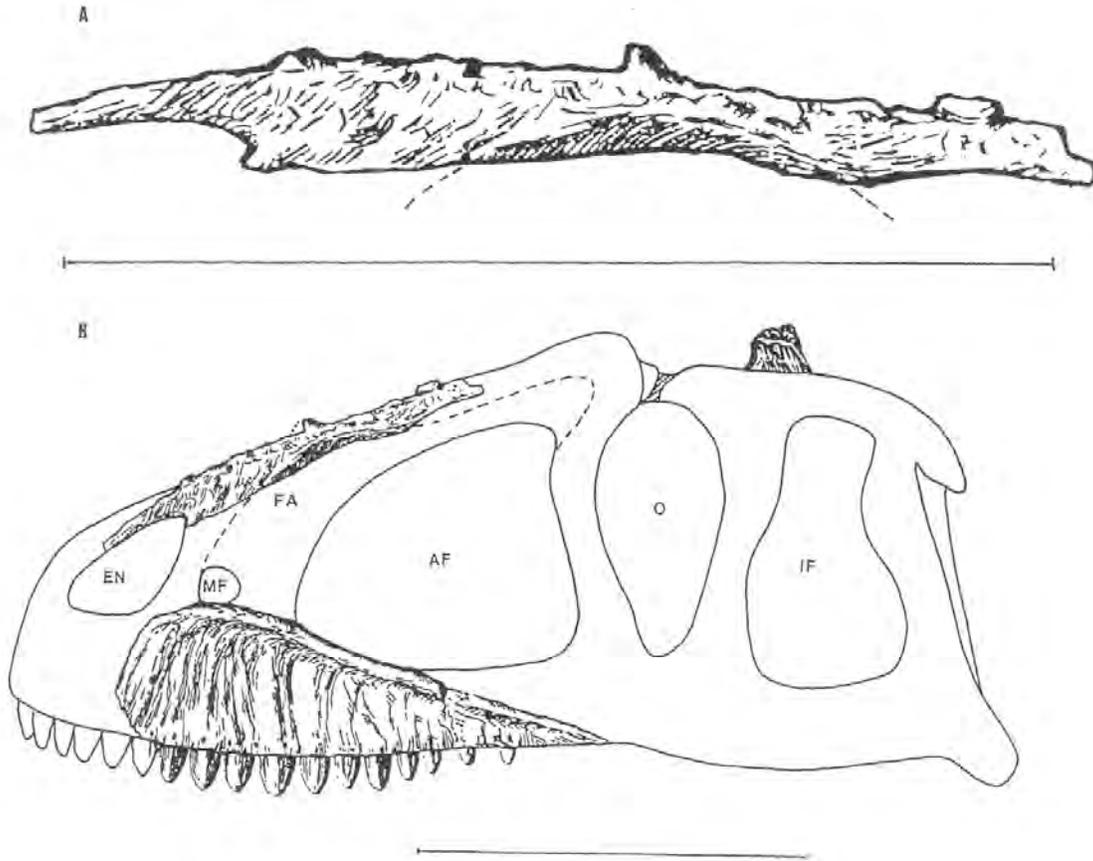


Fig. 7. A: Left nasal of *Carcharodontosaurus* in lateral view. Dotted lines indicate the shape of the antorbital fossa (modified from Stromer, 1936). B: Reconstruction of the skull of *Carcharodontosaurus*, with the probably shape of the antorbital fossa. AF: antorbital fenestra; EN: external nares; FA: antorbital fossa; IF: infratemporal fenestra; MF: maxillary fenestra; O: orbit. To do the reconstruction, the parts figured by Stromer (1936) were arranged in their approximate relations to each other, and the rest of the skull was completed by comparisons with *Sinraptor* and *Allosaurus*. The number of teeth in the premaxillary (4) is hypothetical; *Sinraptor* has 4 (which is the primitive count within theropods; Currie and Zhao, 1993), but in *Allosaurus* 5 teeth are found in the premaxillary (Strongly modified from Stromer, 1936). Both scale bars indicate 50 cm.

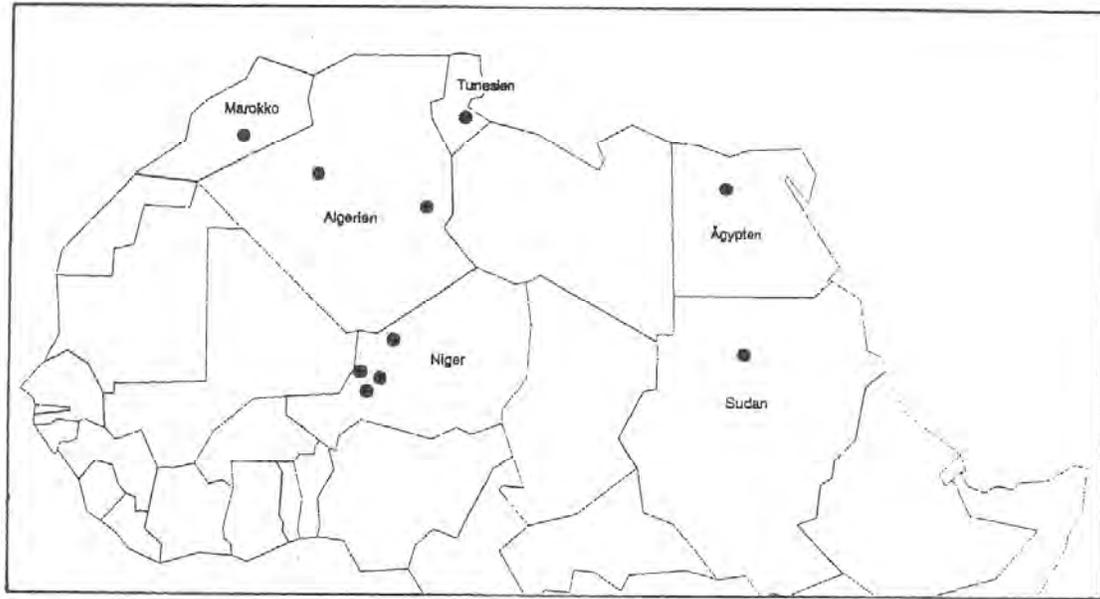


Fig. 8. Map of North Africa with localities where carcharodontosaurids were found (modified after data from Weishampel, 1990).