

DWARFING IN ORNITHOPOD DINOSAURS FROM THE EARLY CRETACEOUS OF ROMANIA

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Abstract. Sediments in the Lower Cretaceous (Berriasian-Valanginian) Cornet basin, near Oradea, northwestern Romania were deposited on part of an island in the Tethys sea. The vertebrate fauna comprises the ornithopods *Camptosaurus* sp., dryosaurids, including *Valdosaurus* sp., and iguanodontids, as well as rare theropods, ankylosaurs, pterosaurs, and possible birds. The majority of ornithopod remains belong to adults or at least subadults. Insular adaptations are shown in *Camptosaurus* sp., the iguanodontids, and dryosaurids, which are smaller than their west European and North American counterparts, possible evidence of dwarfing because of resource limitation. The humerus of *Camptosaurus* sp. has proportions more similar to those of juvenile rather than adult *C. dispar*. Dwarfing is most likely to have occurred via progenetic paedomorphosis, i.e. retention of ancestral juvenile characteristics by earlier maturation in the descendant.

Key words. Dinosaur, dwarfing, island faunas, Cretaceous, Romania.

Rezumat. Sedimentele Cretacic inferioare (Berriasian-Valanginian) din regiunea Cornet, din apropierea localității Oradea, nord-vestul României, s-au acumulat pe o insulă a mării Tethys. Fauna de vertebrate a insulei cuprinde ornithopodele *Camptosaurus* sp., dryosauride (inclusiv *Valdosaurus* sp.) și iguanodontide, alături de mai rarele theropode, ankylosaurieni, pterosauri și, posibil, păsări. Cea mai mare parte a resturilor de ornithopode provin de la exemplare adulte, sau cel puțin sub-adulte. Atât *Camptosaurus* sp., cât și iguanodontidele și dryosauridele prezintă adaptări pentru un mod de viață insular, fiind de dimensiuni mai reduse decât reudele lor din vestul Europei și America de Nord. Micșorarea taliei este considerată ca posibilă adaptare la diminuarea resurselor disponibile. Humerusul de *Camptosaurus* sp. prezintă proporții ce amintesc de mai curând de juvenili, decât de adulții speciei *C. dispar*. Fenomenul de nanism s-a produs probabil printr-un proces de paedomorfoză progenetică, adică prin menținerea caracterelor ancestrale de juvenil la descendenți, prin maturare timpurie.

Cuvinte cheie. Dinosauri, nanism, faune insulare, Cretacic, România.

INTRODUCTION

The bauxite mine at Cornet, near Oradea, north-western Romania, has produced thousands of bones during excavations from 1978 to 1995. The 1978 collections include many reptile and supposed bird taxa, and a number of publications were produced (Jurcsák and Popa, 1978, 1979, 1983a, b, 1984; Jurcsák, 1982; Patrușiu *et al.*, 1983; Kessler and Jurcsák, 1984a, b, 1986; Kessler, 1984; Jurcsák and Kessler, 1986, 1987, 1991; Marinescu, 1989). Specimens are lodged in the Muzeul Țării Crișurilor, Oradea (MTCO). The dinosaurian material was reviewed by Benton *et al.* (1997), but the pterosaur and supposed bird remains still await revision.

The dinosaurs aroused interest from the beginning because they seemed to be small. Could it be that they represent another example of dwarfism, as is famously the case for the Late Cretaceous dinosaurs from the Hațeg basin of Romania, first identified as an island with insular fauna by Nopcsa (1914)? The postulated dwarfing in the Late Cretaceous

dinosaurs of Romania is analogous to dwarfing seen later in island mammals, most notably the dwarfed elephants from Sicily and Malta, dwarf hippos from Sumatra, and dwarf marsupials from Australia, all Pleistocene in age (Boekschoten and Sondaar 1972; Sondaar 1976; Marshall and Corruccini 1978; Roth 1992). On islands, competitive release is believed to promote gigantism, whereas resource limitation promotes dwarfism. The general trend on islands seems to include dwarfism in the larger species to gigantism in the smaller species (Lomolino, 1985).

Dwarfing has also been suggested for the island-living Early Cretaceous dinosaurs of Cornet, NW Romania. Benton *et al.* (1997) found two pieces of evidence for insular adaptations, (1) the dinosaur fauna was more depauperate than a typical Wealden assemblage, consisting of only four or five species, instead of ten or more, as well as other reptiles and mammals; and (2) the ornithopods were smaller on average than their European and North American counterparts.

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The aims of this study are to review the Cornet fauna and its age, and to present outline evidence for dwarfing in the ornithopods. The work stems from a long-term project between MJB and EP that was enabled in the early 1990s by Dan Grigorescu, in whose honour this paper is presented. EP has been studying the ornithopod dinosaurs for some time, and the identifications are all hers, while NJM visited Romania in 2002 to compare the ornithopods with close relatives from elsewhere and to carry out anatomical and morphometric studies to assess the dwarfism hypothesis.

Institutional abbreviations. AMNH American Museum of Natural History, New York; BMNH, British Museum of Natural History, London; CM, Carnegie Museum, Pittsburgh; HMN, Humboldt Museum für Naturkunde, Berlin; MNHM, Muséum National d'Histoire Naturelle, Paris; MTCO, Muzeul Tarii Crisurilor, Oradea; OXFUM, University Museum, Oxford; USNM, United States National Museum, Washington D.C.; UT, Universität Tübingen.

LOCATION AND GEOLOGY

Location

In 1978, vertebrate fossils were discovered in lens 204 of the Lower Cretaceous bauxite mine of the S.C. "Bauxita Min" S.A. Dobrești Company at Cornet in the Pădurea Craiului mountains approximately 40 km ESE of Oradea, northwestern Romania (Fig. 1). Bones were first noticed in the bauxite by miners. Palaeontologists Tiberiu Jurcsák and Elisabeta Popa, from the Muzeul Țării Crișurilor in Oradea, worked in the mine for three months in 1978 and extracted 10 tonnes of bauxite by blasting. The bone-bearing bauxite has since been prepared by Elisabeta Popa and has yielded around 10,000 bones. Small-scale hand excavations were undertaken between 1978 and 1983, after which the mine closed. Florian Marinescu from the Institute of Geology, Bucharest, excavated by hand between 1978 and 1979 and recently donated the collection of about 600 bones to the Muzeul Țării Crișurilor, Oradea. The mine reopened in 1994 and fieldwork was undertaken as a joint project between the Muzeul Țării Crișurilor, Oradea, and the Department of Earth Sciences, University of Bristol in 1995 and 1996. The mine is now flooded.

Geology

The fossiliferous continental bauxite deposit is underlain by marine limestones of mid

Tithonian to early Berriasian age, and is overlain by marine limestones of early Barremian (Patrulus *et al.* 1983) or late Berriasian to early Valanginian (Dragastan *et al.* 1988) age. The underlying Tithonian Cornet Limestone was uplifted during latest Jurassic tectonic movements, forming a complex archipelago of small islands (Bordea and Mantea 1991). The bauxite is detrital and was formed by humid tropical subaerial weathering of igneous and metamorphic rocks. Lens 204 was one of three sink holes on a small plateau at a height of 492 m on the southern slope of a low hill (Jurcsák and Kessler, 1991) into which bauxite and fossils drained from valleys and nearby ponds and lakes (Benton *et al.* 1997). Patrulus *et al.* (1983), Grigorescu (1993), Posmoșanu and Cook (2000) present sedimentary logs for lens 204 and Benton *et al.* (1997) have reviewed the sedimentology in detail.

The bones appear to have accumulated partially as a talus cone below the fissure opening, while some show evidence of water transport. The 1995 fieldwork identified eleven bone-bearing units and that the bones are concentrated towards the centre of the lens, which indicates that at least part of the deposit was a talus cone below the aperture of the sinkhole (Posmoșanu and Cook 2000). There was generally no preferred orientation of the bones, although large blocks of bauxite were found to have elongate bones in parallel alignment (Benton *et al.* 1997). This supports the observations of Jurcsák (1982) who noted that the bones occurred in greatest concentration, making up nearly 50% of the volume of the sediment, in a 0.6m thick band in the middle of lens 204, which has now been removed. Patrulus *et al.* (1983) describe the bones as occurring in mud-grade bauxites in the lower 1m of the section in the lens. Many of the bones in the collection in Oradea are associated with such a matrix, but the majority are in a fine-grained conglomerate (Benton *et al.* 1997).

The local palaeogeography suggests that the Cornet site was part of an island, approximately 30-40 km in diameter, in an extensive archipelago in the region that is now between northwestern Romania and eastern Hungary, with the nearest major land masses in Germany and Russia, several hundred kilometres away (Benton *et al.* 1997). The island formed during a regression between the early Tithonian and early Valanginian (Grigorescu 1993).



Fig. 1. Location of Cornet. A, Simplified map of Romania, showing the location of Oradea. B, Location of Oradea and Cornet. C, The Cornet area, showing the mining buildings, the site of lens 204, the access road, rivers, and streams. The outline geology is indicated – Jurassic and Cretaceous limestones blank and Quaternary sediments shaded; faults are marked with heavy lines. (After Benton *et al.*, 1997.)

Taphonomy

The Cornet bones are all disarticulated and the majority are incomplete, but in most cases only a small part of the bone is missing. The collection is dominated by cuboid-shaped bones, with vertebrae and vertebral centra making up 40% of the collection, and metapodials, metatarsals, and phalanges making up 24% (Posmoşanu and Cook 2000). Most of the bones show slight to moderate abrasion. Approximately half of the bones have been affected by post-depositional distortion, causing twisting about their axes, and others show evidence of cracking and crushing. Several of the vertebrae and phalanges show evidence of predator or scavenger activity with isolated and paired tooth marks in the form of rounded and oval depressions of various dimensions.

The small size and shape ranges of the bones and their abrasion states suggest that this is an attritional assemblage that accumulated over a considerable time through cycles of deposition and reworking in the cave system and surrounding landscape. The limited occurrence of *in situ* weathering and direct evidence of scavenging suggests that the bones were rapidly buried in waterlogged sediments, or washed into the sinkholes and caves soon after death of the animal (Benton *et al.* 1997; Posmoşanu and Cook 2000). The detrital bauxite and bones were probably washed into the cave by periodic high-energy flash floods and lower-energy gravitational and fluvial processes, which is indicated by bands of coarse- and fine-grained sediments in the cave (Posmoşanu and Cook 2000).

PALAEONTOLOGY

Previous interpretations

The Cornet fauna is dominated by ornithopod dinosaurs, with rare theropods and ankylosaurs, and also pterosaurs and possible birds. Patruşius *et al.* (1983) identified the ornithopods *Camptosaurus* and *Iguanodon*, which were later renamed by Marinescu (1989) as the iguanodontid *Bihariosaurus bauxiticus*. Note that this genus and species has never been widely accepted as unique, and indeed it is technically a *nomen nudum* since the description and illustrations are inadequate to distinguish it from any other ornithopod. Jurcsák and Kessler (1991) identified four ornithopod taxa belonging to the families Hypsilophodontidae and Iguanodontidae, with the former as the dominant group. Among hypsilophodontids they identified the dryosaurid *Valdosaurus canaliculatus* on the basis of the distal end of a femur (MTCO 33/14.295) and neurocranium (MTCO 7601/22.405), and *Hypsilophodon* sp. on the basis of the left humerus MTCO 6001/16.225. Two iguanodontids were noted, *Iguanodon* cf. *mantelli*, based on a left humerus (MTCO 5284/21.333), anterior caudal vertebrae, metatarsals and ungual phalanges, and *Vectisaurus valdensis*.

Jurcsák and Kessler (1991) also identified the ankylosaur *Hylaeosaurus* sp. on the basis of a dorsal armour spine (MTCO 297/21.369) and flattened metapodials. Jurcsák (1982) and Jurcsák and Popa (1983a) identified some vertebrae (MTCO 16.499 and 706/14.520) as cervicals and caudals of the theropod *Aristosuchus* sp. which, if correctly identified, would come from a species larger than that of the Wealden of England (Benton *et al.* 1997). There are also some theropod ungual phalanges (MTCO 1631/16.241) and the existence of theropods is also indicated by the bite marks on ornithopod phalanges and vertebrae.

Jurcsák and Popa (1983a, b, 1984) were the first to report pterosaur remains - limb bones of *Gallodactylus* sp., an ornithocheirid, and a partial snout (MTCO 9651/18262) assigned to *Dsungaripterus* sp., and noted as from "possibly a *Tapejara*-like animal" (E. Frey, pers. Comm., 2002). Birds from Cornet have been described in detail by Kessler and Jurcsák (1984a, b, 1986) and Jurcsák and Kessler (1986, 1987). They identified *Archaeopteryx* sp. on the basis of a partial left humerus (MTCO 1503/14.422), the flightless ratite (palaeognath) *Palaeocursornis biharicus* on the basis of the distal left femur MTCO 1637/14.909 (Kessler and Jurcsák 1986), and the grebe-like

(neognath) *Eurolimnornis corneti* on the basis of the distal right humerus MTCO 7896/17.642 (Kessler and Jurcsák 1984a, b; Kessler and Gall 1995). If the identifications of *P. biharicus* and *E. corneti* are correct, then they represent the earliest known examples of these families, making the Cornet avifauna very important, but the specimens could equally well be from a small theropod or pterosaur, which seems more likely (Benton *et al.* 1997).

Re-identifications of the ornithopod specimens

Most of the Cornet material is disarticulated and damaged, and so many of the bones are difficult to identify. The ornithopod fauna appears to comprise camptosaurids, iguanodontids, and dryosaurids. *Camptosaurus* sp. is identified on the basis of a neurocranium, a humerus, fused carpal bones, and teeth (Tallodi-Posmoşanu and Popa, 1997). An ulna and ungual phalanges are also attributed to a camptosaurid. The dryosaurid, *Valdosaurus* sp., is identified on the basis of the distal end of a femur. A humerus has been attributed to Dryosauridae, as well as a quadrate, ulna and ungual phalanges. These may belong to *Valdosaurus* sp., but the forelimb of this genus is unknown, so they are referred to Dryosauridae until further *Valdosaurus* material is discovered. Iguanodontids are represented by teeth and ungual phalanges. The metatarsals and first phalanges of the pes are probably those of a camptosaurid or iguanodontid, although some of the more slender first phalanges may be those of a dryosaurid. The distal phalanges are all those of a camptosaurid or iguanodontid. The vertebrae lack any real diagnostic features. These re-identifications are ongoing (Posmoşanu, 2002, 2003).

Ontogenetic age of the ornithopods

The majority of bones in the collection exhibit features used by previous authors to distinguish adult from juvenile dinosaurs. The long bones, such as the camptosaurid and dryosaurid humeri, have a surface of smooth lamellar bone as in adults (Callison and Quimby, 1984), and they have well developed surface structures for muscle and ligament attachment as in adults (Galton, 1981a, 1982a, b, 1983a; Coombs, 1986), whereas those of babies and juveniles are poorly developed (Carpenter and McIntosh, 1994). The long bones, such as humeri, ulnas, and the *Valdosaurus* femur, have well ossified articular ends unlike those of juveniles, babies, and

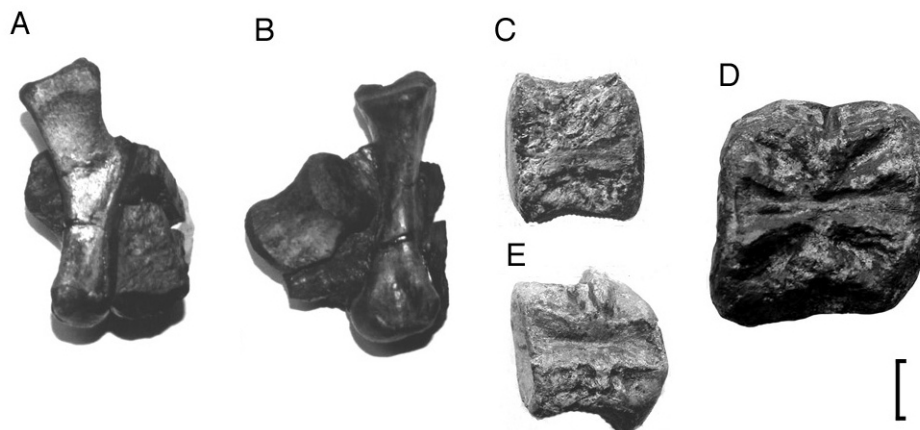


Figure 2. Elements of possible juvenile ornithopods. Metatarsal IV, MTCO 7561/21.371 (A, B) in ventral (A) and lateral (B) views. Vertebral centra in dorsal view: caudal centrum, MTCO 1750/14.624 (C), caudal centrum, MTCO 2435/15.047 (D), and sacral centrum, MTCO 496/16.481 (E). Scale bar is 20 mm.

embryos, which are poorly ossified or composed of cartilage, giving them a rough and pitted appearance (Callison and Quimby, 1984; Benton, 1988; Horner and Weishampel, 1988; Britt and Naylor, 1994; Carpenter, 1994; Carpenter and McIntosh, 1994; Chure *et al.* 1994; Jianu and Weishampel, 1999). The processes of the long bones are also well developed as in adults. The humeri also have curved shafts, and the coracoids a ventral ridge, which is characteristic of adult ornithopods (Carpenter, 1994).

The metatarsals and phalanges of the pes also have a surface of smooth lamellar bone with well-developed muscle and ligament scars and articular surfaces, indicating that they are also those of adults. There are two possible juvenile fourth metatarsals (Fig. 2a, b) that are much smaller than the other fourth metatarsals and have a very smooth surface texture without well developed surface structures, and shallow ligament grooves, all juvenile features (Galton, 1981a, 1982a, b, 1983a; Coombs, 1986; Carpenter and McIntosh, 1994).

The neural arches of the vertebrae are fused to the centra, unlike in embryos, babies and juveniles (Galton, 1981a, 1982a, b; Coombs, 1982, 1986; Weishampel *et al.*, 1993; Britt and Naylor, 1994; Chure *et al.*, 1994). There are also several juvenile vertebrae, represented by centra to which the neural arch was not fused (Fig. 2c-e). The majority of carpal bones are also fused together as in adult *Camptosaurus* (Tallodi-Posmoşanu and Popa, 1997).

The ontogenetic stages at which these features appear in dinosaurs are not known, and so the ontogenetic age of the Cornet specimens cannot be resolved. However, the majority of bones evidently come from adults or subadults.

Comparison of size with other ornithopods

Comparative data on ornithopods was obtained from examination of specimens in the BMNH and OXFUM, and from published studies on *Camptosaurus* (Gilmore, 1909; Dodson, 1980; Galton and Powell, 1980), *Dryosaurus* (Galton, 1975, 1981b), *Hypsilophodon* (Galton, 1974, 1975), *Iguanodon* (Norman, 1980, 1986), *Othnielia rex* (Galton, 1983b), *Tenontosaurus* (Dodson, 1980), and *Valdosaurus* (Galton and Taquet, 1982). There were insufficient well-preserved humeri, ulnas, femora, and coracoids in the Cornet collection to calculate population statistics, so bone dimensions were compared individually to those of other ornithopods. All measurements were taken with extensible callipers, accurate to 0.1 mm.

Gilmore (1909) recognised five species of *Camptosaurus*, *C. dispar*, *C. medius*, *C. browni*, and *C. nanus* from the same quarry in the Morrison Formation of the United States; but, given the range of individual variation shown in *Dryosaurus* and *Hypsilophodon foxii*, it is reasonable to refer all this material to one species of *Camptosaurus*, *C. dispar* (Galton and Powell, 1980). *C. medius* is perhaps a subadult female, *C. browni* an adult female, and *C. nanus* a juvenile *C. dispar*. The holotype of the other *Camptosaurus* identified by Gilmore (1909), *C. amplius*, is a pes of the theropod *Allosaurus fragilis*. The English *Camptosaurus prestwichii* appears to be a distinct species, comparable in size to *C. dispar* (Galton and Powell, 1980).

The Cornet *Camptosaurus* sp. was about two-thirds the linear dimensions of its typical relatives from elsewhere (Benton *et al.* 1997). The humerus (MTCO 5284/21.333, 208 mm) is

longer than that of a juvenile *C. dispar* (USNM 2210, 143 mm), but is shorter than the American and British adult *Camptosaurus* specimens (227-394 mm; mean 324 mm). At the low end of this size range, the coracoid of an American *Camptosaurus* specimen, a presumed subadult (CM 11337, 68 mm high), is comparable in size to the Cornet camptosaurid coracoids (MTCO 8384/21.372, 51 mm; MTCO 5296/14.611, 70.0 mm). Other American *Camptosaurus* have much larger coracoids (80-133 mm high).

The Cornet iguanodontid humerus (MTCO 2224) is damaged, but, with an estimated length of 210 mm, is considerably shorter than those of *Iguanodon* (430-820 mm). Scaling from this, the Cornet iguanodontid was then one-third of the linear dimensions of the mean western European *Iguanodon*. The Cornet iguanodontid coracoids (MTCO 5030/14.582, 51.0 mm; MTCO 292/14.315, 59.0 mm) are considerably smaller than those of *Iguanodon* (120-380 mm; mean 254 mm). The largest Cornet coracoid (MTCO 5296/14.611) is represented by a glenoid facet and so cannot be positively identified. Using the ratios of the other Cornet coracoids, it is estimated to have been 64 to 93 mm high, which is comparable to *C. prestwichii* (OXFUM J3303, 80-90 mm), but considerably smaller than *Iguanodon*. The Cornet coracoids, if those of an iguanodontid, indicate an animal that was one-quarter to one-third of the size of western European *Iguanodon*.

The camptosaurid or iguanodontid metatarsals from Cornet are larger than those of *Hypsilophodon foxii* and smaller than those of *Iguanodon*, *Tenontosaurus*, and *Camptosaurus*. There is no significant size difference between the Cornet metatarsals and *Dryosaurus*. The Cornet vertebrae are shorter than those of *C. prestwichii*, adult male and female *C. dispar*, and *Iguanodon*; and longer than those of juvenile *C. dispar*.

The Cornet dryosaurid is at the low end of the size range for this family. The humerus (MTCO 6001/16.225, 142 mm) is in the middle of the range for juvenile to adult *Dryosaurus* (68-190 mm) and *Hypsilophodon* (69-159 mm), and it is in proportion with the dryosaurid-like ulna (MTCO 8090/16.325, 112 mm). The Cornet dryosaurid would have been similar in size to *D. lettowvorbecki* (UT 1495/22), a juvenile or subadult, or the juvenile *C. dispar*, which was estimated to have been about 2 m long and 1.5 m tall (Gilmore, 1909). It is not possible to compare the distal fragment of the Cornet dryosaurid *Valdosaurus* sp. femur (MTCO 33/14.295), to *V. nigeriensis* (MNHN GDR 332, 230 mm long), but it is comparable in

dimensions to *D. altus* (AMNH 834), *D. lettowvorbecki* (UT 1523/15; UT 1495/14; HMN dy 37), *H. foxii*, and the possible juvenile *Tenontosaurus* (AMNH 3109). This would give it an estimated length of 190 to 225 mm, which is just less than that of *V. nigeriensis*.

The material from Cornet is an attritional assemblage, and is dominated by the smaller skeletal elements, suggesting some degree of size sorting; however, long bones are present, indicating that at least some large elements passed through the taphonomic filter, but there are no metatarsals or phalanges of comparable dimensions to adult individuals from Europe and North America. The Cornet ornithopods are generally smaller than their relatives from elsewhere, the dryosaurid being at the lower end of the size ranges of *Dryosaurus* and *Valdosaurus*, the camptosaurid being two-thirds the size of its American and British relatives, and the iguanodontid being one-quarter to one-third the size of western European *Iguanodon*. Scaling to weight, an animal that is half the overall length of another of identical shape and proportions, weighs one-eighth as much ($0.5 \times 0.5 \times 0.5 = 0.125$). So, if a large American *Camptosaurus* weighed 700 kg (Peczis, 1994), then the Cornet camptosaurid weighed only 87.5 kg. Likewise, if the range of body masses for different species of *Iguanodon* was 4 - 7 tonnes (Peczis, 1994), the Cornet iguanodontid, at say one-third the length, weighed only one-twentyseventh (0.037) as much, a mere 150 - 260 kg.

CONCLUSIONS

The vertebrate fauna preserved in bauxite deposited in caves at Cornet, NE Romania (Berriasian, Lower Cretaceous) comprises the ornithopods *Camptosaurus* sp., an iguanodontid, and dryosaurids, including *Valdosaurus* sp., as well as rare theropods and ankylosaurs, pterosaurs, and possible birds. The majority of ornithopod remains belong to adults or at least subadults, based on osteological criteria. The sediments were deposited on islands formed from uplifted Late Jurassic limestones on the north shore of Tethys.

The Cornet ornithopods are largely dwarfed. The dryosaurids are at the smaller end of the size range of relatives from Europe and Africa. Individual bones of the Cornet *Camptosaurus* sp. are about two-thirds of the linear dimensions of equivalent elements of its North American and British relatives, hence it was scaled to about one-twelfth (0.0833) of the body mass. Elements of the Cornet iguanodontid are one-quarter to one-third of the linear

dimensions of those of the western European *Iguanodon* species, hence one-thirtysecond to one-twentyfourth (0.03125-0.04167) of the body mass.

The small size of the Cornet ornithopods is almost certainly a result of dwarfing – the adults are the size of juveniles, sometimes very young juveniles, from other locations. Dwarfing implies that paedomorphosis rather than peramorphosis was the heterochronic mechanism, and this is supported by the limited evidence that bones of adult ornithopods from Cornet had the proportions of juveniles. There are several paedomorphic mechanisms, of which progenesis might be indicated here, the mechanism whereby adulthood is achieved in the body of a juvenile by earlier sexual maturation. Progenesis is linked to the evolution of precociality by r-selection in unpredictable environments such as islands with limited resources (Gould, 1977); the attainment of early sexual maturation enables individuals to survive and reproduce, in conditions where food supplies are reduced or unpredictable, thereby passing on these genes. The Cornet deposits come from an island, one of many in the area, and isolated from the nearest mainland, several hundred kilometres away in central Germany.

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REFERENCES

- Benton, M. J. (1988) Bringing up baby. *Nature*, 334, 566.
- Benton, M. J., Cook, E., Grigorescu, D., Popa, E., and Tallodi, E. (1997) Dinosaurs and other tetrapods in an Early Cretaceous bauxite-filled fissure, northwestern Romania. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 130, 275-292.
- Boekschoten, G. J. and Sondaar, P. Y. (1972) On the fossil mammals of Cyprus. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, 75, 306-338.
- Bordea, S. and Mantea, G. (1991) Stratigraphical position of the bauxite deposits in the Pădurea Craiului Mountains (Northern Apuseni Mountains). *Acta Geologica Hungarica*, 34, 351-374.
- Britt, B. B. and Naylor, B. G. (1994) An embryonic *Camarasaurus* (Dinosauria, Sauropoda) from the Upper Jurassic Morrison Formation (Dry Mesa Quarry, Colorado). In Carpenter, K., Hirsch, K. F., and Horner, J. F. (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York, pp. 256-264.
- Callison, G. and Quimby, H. M. (1984) Tiny dinosaurs, are they fully grown? *Journal of Vertebrate Paleontology*, 3, 200-209.
- Carpenter, K. (1994) Baby *Dryosaurus* from the Upper Jurassic Morrison Formation of Dinosaur National Monument. In Carpenter, K., Hirsch, K. F., and Horner, J. F. (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York, pp. 288-297.
- Carpenter, K. and McIntosh, J. (1994) Upper Jurassic sauropod babies from the Morrison Formation. In Carpenter, K., Hirsch, K. F., and Horner, J. F. (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York, pp. 265-278.
- Chure, D., Turner, C., and Peterson, F. (1994) An embryo of *Camptosaurus* from the Morrison Formation (Jurassic, Middle Tithonian) in Dinosaur National Monument, Utah. In Carpenter, K., Hirsch, K. F., and Horner, J. F. (eds.), *Dinosaur eggs and babies*. Cambridge University Press, New York, pp. 298-311.
- Coombs, W. P. (1982) Juvenile specimens of the ornithischian dinosaur *Psittacosaurus*. *Palaeontology*, 25, 89-107.
- Coombs, W. P. (1986) A juvenile ankylosaur referable to the genus *Euoplocephalus* (Reptilia, Ornithischia). *Journal of Vertebrate Paleontology*, 6, 162-173.
- Dodson, P. (1980) Comparative osteology of the American ornithopods *Camptosaurus* and *Tenontosaurus*. *Société Géologique de France, Mémoires*, 139, 81-85.
- Dragastan, O., Coman, O., and Știucă, E. (1988) Bauxite-bearing formations and facies in the Pădurea Craiului and Bihor Mountains (Northern Apuseni). *Revue Roumaine de Géologie, Géophysique et Géographie*, 32, 67-81.
- Galton, P. M. (1974) The ornithischian dinosaur *Hypsilophodon* from the Wealden of the Isle of Wight. *Bulletin of the British Museum (Natural History), Geology Series*, 25, 1-152.
- Galton, P. M. (1975) English hypsilophodontid dinosaurs (Reptilia, Ornithischia). *Palaeontology*, 18, 74(1-75(2))
- Galton, P. M. (1981a) A juvenile stegosaurian dinosaur, *Astrodon pusillus*, from the Upper Jurassic of Portugal, with comments on Upper Jurassic and Lower Cretaceous biogeography. *Journal of Vertebrate Paleontology*, 1, 245-256.
- Galton, P. M. (1981b) *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and Africa. Postcranial Skeleton. *Paläontologische Zeitschrift*, 55, 271-312.
- Galton, P. M. (1982) Juveniles of the stegosaurian dinosaur *Stegosaurus* from the Upper Jurassic of North America. *Journal of Vertebrate Paleontology*, 2, 47-62.
- Galton, P. M. (1982b) The postcranial anatomy of stegosaurian dinosaur *Kentrosaurus* from the Upper Jurassic of Tanzania, East Africa. *Geologica et Palaeontologica*, 15, 139-160.
- Galton, P. M. (1983a) A juvenile stegosaurian dinosaur, *Omosaurus phillipsi* Seeley from the Oxfordian (Upper Jurassic) of England. *Geobios*, 16, 95-101.

- Galton, P. M. (1983b) The cranial anatomy of *Dryosaurus*, a hypsilophodontid dinosaur from the Upper Jurassic of North America and East Africa, with a review of hypsilophodontids from the Upper Jurassic of North America. *Geologica et Palaeontologica*, 17, 207-243.
- Galton, P. M. and Powell, H. P. (1980) The ornithischian dinosaur *Camptosaurus prestwichii* from the Upper Jurassic of England. *Palaeontology*, 23, 411-443.
- Galton, P. M. and Taquet, P. (1982). *Valdosaurus*, a hypsilophodontid dinosaur from the Lower Cretaceous of Europe and Africa. *Geobios*, 15, 147-159.
- Gilmore, C.W. (1909) Osteology of the Jurassic reptile *Camptosaurus*, with a revision of the species of the genus, and descriptions of two new species. *Proceedings of the U. S. National Museum*, 36, 197-332.
- Gould, S. J. (1966) *Ontogeny and Phylogeny*. Belknap Press, Cambridge, Massachusetts, 501 pp.
- Grigorescu, D. (1993) Nonmarine Cretaceous formations of Romania. In Mateer, N. J. and Chen, P.-J. (eds.), *Aspects of Nonmarine Cretaceous Geology*. Academia Sinica, Beijing, pp. 142-164.
- Horner, J. R. and Weismhampel, D. B. (1988) A comparative embryological study of two ornithischian dinosaurs. *Nature*, 332, 256-257.
- Jianu, C. M. and Weishampel, D. B. (1999) The smallest of the largest, a new look at possible dwarfing in sauropod dinosaurs. *Geologie en Mijnbouw*, 78, 335-343.
- Jurcsák, T. (1982) Occurrences nouvelles des sauriens mésozoïques de Roumanie. *Vertebrata Hungarica*, 21, 175-184.
- Jurcsák, T. and Kessler, E. (1986) Evoluția avifaunei pe teritoriul României. I. *Nymphaea*, 16, 577-615.
- Jurcsák, T. and Kessler, E. (1987) Evoluția avifaunei pe teritoriul României. II. Morfologia speciilor fosile. *Nymphaea*, 17, 583-609.
- Jurcsák, T. and Kessler, E. (1991) The Lower Cretaceous fauna from Cornet, Bihor County, Romania. *Nymphaea*, 21, 5-32.
- Jurcsák, T. and Popa, E. (1978) Resturi de dinozaurieni în bauxitele de la Cornet (Bihor). *Nymphaea*, 6, 61-64.
- Jurcsák, T. and Popa, E. (1979) Dinozaurieni ornitopozii din bauxitele de la Cornet (Munții Pădurea Craiului). *Nymphaea*, 10, 7-15.
- Jurcsák, T. and Popa, E. (1983a) La faune de dinosaures du Bihor (Roumaine). In Buffetaut, E., Mazin, J.-M., and Salmon, E. (eds), *Actes du Symposium Paléontologique G. Cuvier*. Montbéliard, Ville de Montbéliard, pp. 325-335.
- Jurcsák, T. and Popa, E. (1983b) Reptile zburătoare în bauxitele de la Cornet, notă preliminară. *Nymphaea*, 10, 7-15.
- Jurcsák, T. and Popa, E. (1984) Pterosaurians from the Cretaceous of Cornet, Romania. In Reif, W.-E., and Westphal, F. (eds), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Attempto, Tübingen, pp. 117-118.
- Kessler, E. (1984) Lower Cretaceous birds from Cornet (Romania). In Reif, W.-E., and Westphal, F. (eds), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*. Attempto, Tübingen, pp. 119-121.
- Kessler, E. and Gall, E. (1995) A new theory concerning the origin and evolution of birds. In Sun, A. and Wang, Y.-Q. (eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers*. China Ocean Press, Beijing, pp. 215-216.
- Kessler, E. and Jurcsák, T. (1984a) Fossil bird remains in the bauxite from Cornet (Pădurea Craiului Mountains – Romania). In *75 Years Laboratory of Palaeontology Special Volume*. Universitatea Bucharest, Bucharest, pp. 129-134.
- Kessler, E. and Jurcsák, T. (1984b) Fossil bird remains in the bauxite from Cornet (Romania, Bihor county). *Travaux du Muséum d'Histoire Naturelle, Grigore Antipa*, 25, 393-401.
- Kessler, E. and Jurcsák, T. (1986) New contributions to the knowledge of Lower Cretaceous bird remains from Cornet (Romania). *Travaux du Muséum d'Histoire Naturelle, Grigore Antipa*, 28, 290-295.
- Lomolino, M.V. (1985) Body size of mammals on islands, the island rule re-examined. *American Naturalist*, 125, 310-316.
- Marinescu, F. (1989) Lentila de bauxită 204 de la Brusturi – Cornet (Jud. Bihor), zăcământ fosilifer cu dinozauri. *Ocotirea Naturale Mediului Inconjur*, 33, 125-133.
- Marshall, L. G. and Corruccini, R. S. (1978) Variability, evolutionary rates, and allometry in dwarfing lineages. *Palaeobiology*, 4, 101-119.
- Nopcsa, F. (1914) Ueber das Vorkommen der Dinosaurier in Siebenbürgen. Verhandlungen des zoologische-botanische Gesellschaft, Vienna, 64, 12-14.
- Norman, D. B. (1980) On the ornithischian dinosaur *Iguanodon bernissartensis* of Bernissart (Belgium). *Institut Royal des Sciences Naturelles de Belgique*, 178, 1-103.
- Norman, D. B. (1986) On the anatomy of *Iguanodon atherfieldensis* (Ornithischia, Ornithopoda). *Bulletin Institut Royal Sciences Naturelle Belgique Sciences de la Terre*, 56, 281-372.
- Patrușiu, D., Marinescu, F., and Bălteș, A. (1983) Dinosaures ornithopodes dans les bauxites Néocomiennes de l'Unité de Bihor (Monts Apuseni). *Anuarul Institutului de Geologie și Geofizică*, 59, 109-117.
- Peczki, J. (1994) Implications of body-mass estimates for dinosaurs. *Journal of Vertebrate Paleontology*, 14, 520-533.
- Posmoșanu, E. (2002) Preliminary report on the revision of the dinosaur (Ornithopoda) collection from the Lower Cretaceous bauxite deposits, Cornet – Romania. In *The 7th European Workshop of Vertebrate Palaeontology, Sibiu, Romania, Abstract Volume and Excursions Field Guide*, p. 36.
- Posmoșanu, E. (2003) The palaeoecology of the dinosaur fauna from a Lower Cretaceous bauxite deposit from Bihor (Romania). In A. Petculescu & E. Stiuca (eds.), *Advances in Vertebrate Paleontology: Hen to Panta. Romanian Academy, "Emil Racoviță" Institute of Speleology, Bucarest*, pp. 121-124

- Posmoşanu, E. and Cook, E. (2000) Vertebrate taphonomy and dinosaur palaeopathology from a Lower Cretaceous bauxite lens, northwest Romania. *Oryctos*, 3, 39-51.
- Roth, V. L. (1992) Inferences from allometry and fossils, dwarfing of elephants on islands. *Oxford Surveys in Evolutionary Biology* 8, 259-288.
- Sondaar, P. Y. (1976) Insularity and its effect on mammal evolution. In Hecht, M. K., Goody, P. C. and Hecht, B. M. (eds.), *Major patterns in vertebrate evolution*. Plenum, New York, pp. 671-707.
- Tallodi-Posmoşanu, E. and Popa, E. (1997) Notes on a camptosaurid dinosaur from the Lower Cretaceous bauxite, Cornet – Romania. *Nymphaea*, 23-25, 35-44.
- Weishampel, D.B., Norman, D.B., and Grigorescu, D. (1993) *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania, the most basal hadrosaurid dinosaur. *Palaeontology*, 36, 361-385.