Paläontologische Zeitschrift | 72 (1/2) | 179–189 | 8 Abb., 1 Tab. | Stuttgart, April 1998

Small theropod teeth from the Upper Jurassic coal mine of Guimarota (Portugal)

JENS ZINKE, Berlin

With 8 figures and 1 table

Kurzfassung: Isolierte Zähne theropoder Dinosaurier aus dem Oberen Jura der Kohlengrube Guimarota (bei Leiria, Portugal) werden beschrieben und abgebildet. Die häufigsten Zahnfunde ähneln morphologisch den Bezahnungen der oberjurassischen Theropoden *Archaeopteryx* und *Compsognathus*. Ein Morphotyp deutet auf das Vorhandensein eines Allosauriden hin. Sechs weitere Morphotypen von Theropoden-Zähnen zeigen große Ähnlichkeiten mit kreidezeitlichen Formen, wie Dromaeosauriden, Troodontiden, Tyrannosauriden, *Richardoestesia* und *Paronychodon*. Für diese Gruppen wird ein spätjurassischer Ursprung diskutiert, wie er von einigen Autoren bereits vermutet wurde.

Abstract: Isolated teeth of small theropod dinosaurs from the Upper Jurassic lignite coal mine of Guimarota (near Leiria, Portugal) are described and illustrated. The well known Upper Jurassic theropods from Europe, *Archaeopteryx* and *Compsognathus*, are the most common taxa in the Guimarota assemblage. One morphotype is closely related to an allosaurid theropod. Six further morphotypes of theropod teeth are also described, which are closely related to Cretaceous theropods such as dromaeosaurids, troodontids, tyrannosaurids, *Richardoestesia* and *Paronychodon*. A Late Jurassic origin of these groups of theropods, which is very often postulated, is discussed.

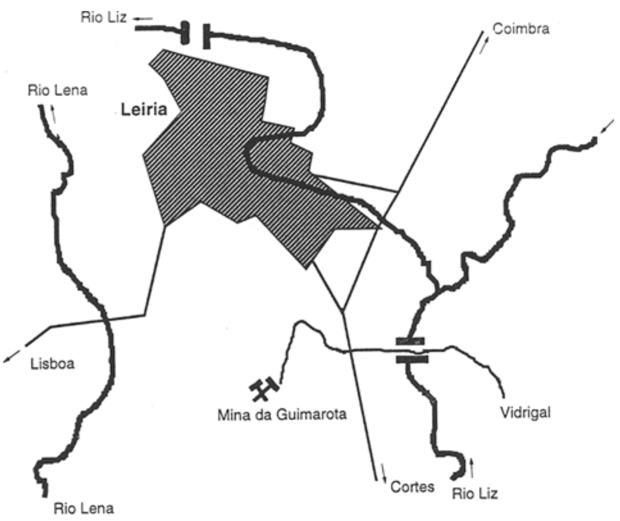

Fig. 1. Geographical position of the coal mine Guimarota, near Leiria (from SCHUDACK 1993).

Introduction

The screen washing activities of the Free University of Berlin, searching for early mammals in many parts of Europe, also yielded dinosaur material, which has been briefly described (THULBORN 1973; ZINKE & RAUHUT 1994). The coal mine of Guimarota (near Leiria, Portugal, Fig. 1) is one of the most important Upper Jurassic microvertebrate localities, being especially famous for early mammals (detailed publication list in KREBS 1991). Dinosaur remains, mainly teeth, are also quite common. The locality was dated as early Kimmeridgian by HELMDACH (1971) and this was confirmed by SCHUDACK (1993) on the basis of ostracods. The vertebrate-bearing strata are two lignite coal layers within marly limestone. The lower coal layer yielded more vertebrate remains, and was the subject of a systematic dig from 1972-1982. Of the dinosaur fauna, only the Ornithischians were examined by THULBORN (1973), who described a new hypsilophodontid ornithopod, *Phyllodon henkeli*, on the basis of isolated teeth. Further studies in the collection of the Free University Berlin will provide new information about the Ornithischians in Guimarota (RAUHUT in prep.). MILNER & EVANS (1991) described a maxilla of *Lisboasaurus estesi* as a maniraptoran theropod, which was reexaminated and interpreted as a notosuchian crocodile by BUSCALIONI et al. (1996). Teeth and a fragmentary dentary of a small theropod dinosaur were described by ZINKE & RAUHUT (1994). WEIGERT (1995) described isolated teeth of cf. *Archaeopteryx* sp.

Since new research in the Upper Jurassic Morrison Formation (USA) has revealed small dinosaur teeth, as well (CHURE et al. 1993; CHURE 1994, 1995), the description of the small theropod teeth from the coal mine of Guimarota in this paper will give new information about the diversity of tooth morphologies in Upper Jurassic theropod dinosaurs for a comparison with the American forms.

Address of the author: JENS ZINKE, Institut für Paläontologie, Freie Universität Berlin, Malteserstraße 74-100, Haus D, D-12249 Berlin, Germany.

0031–0220/98/0072–0179 $ 3.00

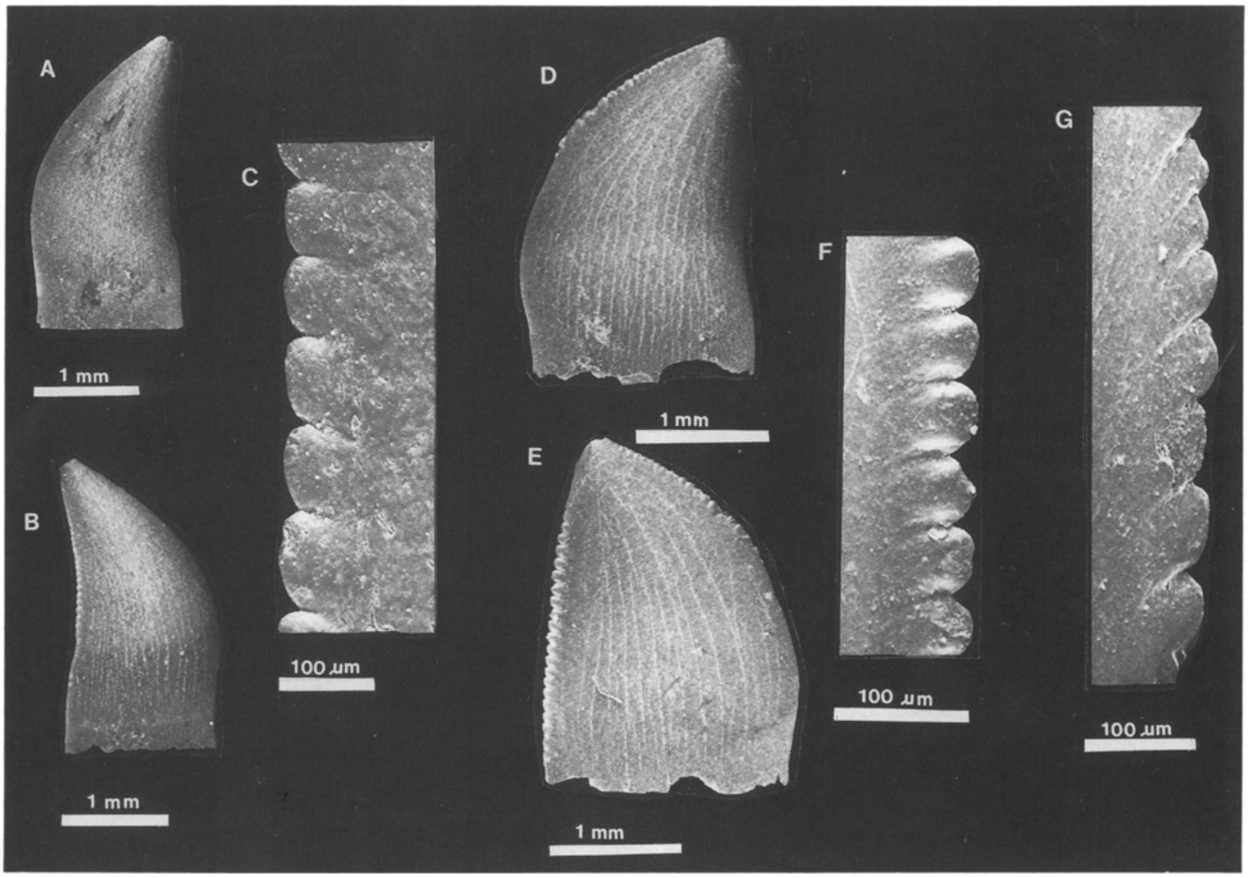

Fig. 2. cf. *Compsognathus* sp.; **A:** lingual view, **B:** labial view, **C:** posterior denticles; IPFUB GUI D 64. – **D:** lingual view, **E:** labial view, **F:** posterior denticles, **G:** anterior denticles; IPFUB GUI D 65.

Tab. 1. Mean value of measurements taken from all Guimarota-specimens referred to known genera and variation range of DSDI.

Guimarota genera	number of teeth	TCH (mm)	FABL (mm)	BW (mm)	anterior denticles per 1 mm	posterior denticles per 1 mm	DSDI
cf. *Compsognathus* sp.	49	1.71	1.01	0.75	10-17	10-15	0.79-1.33
velociraptorine dromaeosaurids	28	2.26	1.65	0.79	8-16	5-10	1.0-2.4
cf. *Dromaeosaurus* sp.	1	8.05	4.47	4.05	5	5	1.0
cf. *Paronychodon* sp.	29	1.67	1.12	0.65	(18)	6-13	(1.63)
cf. *Richardoestesia* sp.	40	3.42	2.08	1.02	8-14	9-14	0.8-1.33
probable troodontids	14	1.02	0.92	0.51	8-16	6-14	0.8-1.5
large morphotaxa	13	10.15	3.71	2.5	6-8.5	5.5-8	1.09-1.33
probable allosaurids	4	8.75	5.12	2.75	6-10	5.5-8	1.0-1.18
probable tyrannosaurids	3	6.19	3.02	2.99	5-7	5-7	1.0

Materials and methods

From the first two years of screen washing (05.06.1974-30.04.1976), the author recognized 440 isolated theropod teeth, which are described in this paper. 296 of these theropod teeth were identified and measured (Tab. 1) using SEM (Cambridge Stereoscan 360) or a Leitz-Microscope.

The theropod teeth are characterized by the following features: TCH = tooth-crown-height; FABL = fore-aft-basal-length; BW = basal width (these terms have been defined by CURRIE et al. 1990 and FARLOW et al. 1991); number of denticles per 1 mm on the anterior and posterior carina; DSDI = denticle size difference index (defined by RAUHUT & WERNER 1995); cross-section of the base. All systematic terms are used following HOLTZ (1994).

The abbreviation IPFUB GUI D (Number) means: IPFUB = Institute for Paleontology of the Freie Universität Berlin, GUI = Guimarota, D = Dinosauria.

Description

Class Dinosauria OWEN 1841
Superorder Saurischia SEELEY 1888
Order Theropoda MARSH 1881
Suborder Coelurosauria (sensu HOLTZ 1994)
Family Compsognathidae

cf. *Compsognathus* sp.
Fig. 2 A-G

Referred material: 49 isolated teeth; IPFUB GUI D 28-65, 98, 103, 105-110, 112-113.

Description: These teeth are represented by three morphotypes which correspond with different positions in the jaw. The first morphotype is characterised by very slender, cone-shaped crowns, which are only recurved at the apex and lack serrations, approximately from the anterior part of the jaw. The second morphotype is less recurved apically, and the posterior carina is only slightly concave and shows serrations (Fig. 2A-C). The anterior carina lacks serrations, but is sharp-edged. These teeth are from a middle position of the jaw. The third morphotype shows nearly the same TCH as FABL, which results in a compact shape (Fig. 2D-E). Usually both carinae are serrated, with the anterior denticles smaller and more strongly hooked apically than the posterior ones (Fig. 2F-G). The anterior denticles are found only at the very tip of the crown (Fig. 2D). Like the teeth of the second morphotype these teeth show a slight constriction between crown and root. The DSDI varies from 0.79-1.33.

Discussion: The three morphotypes described above can be correlated very well with different tooth positions in the jaw of the Upper Jurassic genus *Compsognathus*, which have been described and illustrated by STROMER (1934). In *Compsognathus* there are cone-shaped teeth from the anterior part of the dentary, slightly recurved teeth with only posterior serrations from the middle of the dentary and compact-shaped teeth with fine serrations on the posterior carina from the back of the mouth. The variation of TCH and FABL in the Guimarota specimens is nearly the same as in *Compsognathus*. Since some Guimarota specimens show serrations on both carinae, the teeth from Guimarota belong to a closely related form, but not to *Compsognathus* itself.

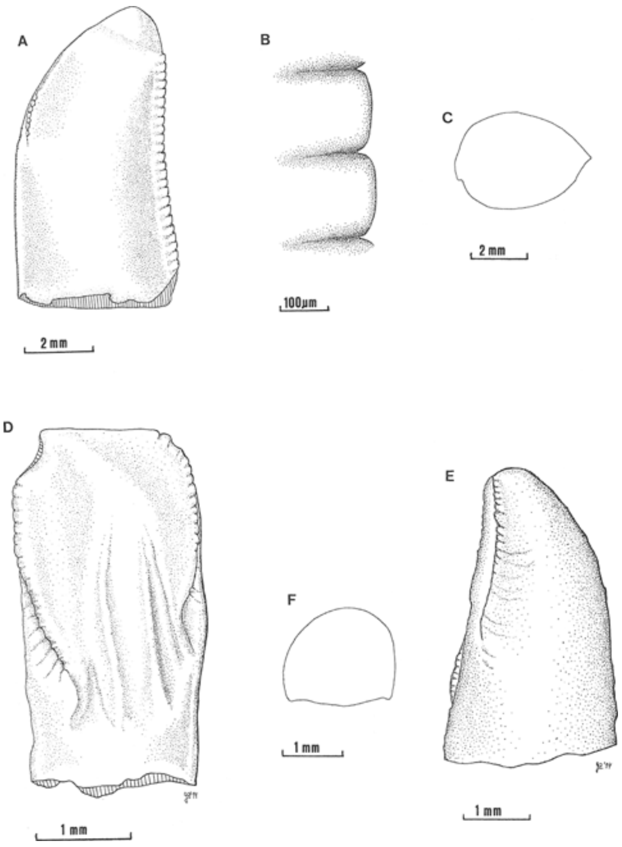

Fig. 3. Premaxillary tooth from cf. *Dromaeosaurus* sp.; **A:** lingual view, **B:** enlargement of posterior denticles, **C:** cross-section of the base; IPFUB GUI D 77. – A premaxillary tooth of a probable tyrannosaurid; **D:** lingual view, **E:** anterior view, **F:** cross-section of the base; IPFUB GUI D 89.

Family Dromaeosauridae
Subfamily Dromaeosaurinae
cf. *Dromaeosaurus* sp.
Fig. 3A-C

Referred material: 1 premaxillary tooth; IPFUB GUI D 77.

Description: The tooth IPFUB GUI D 77 shows the typical crown shape of a premaxillary tooth (Fig. 3A). The serrated anterior carina appears on the upper half of the crown and bends inward to the lingual surface at its lower part (Fig. 3 A). All denticles are heavily worn down. The posterior carina is also serrated and the denticles, which are well preserved, are orientated perpendicularly to the edge and only slightly hooked apically

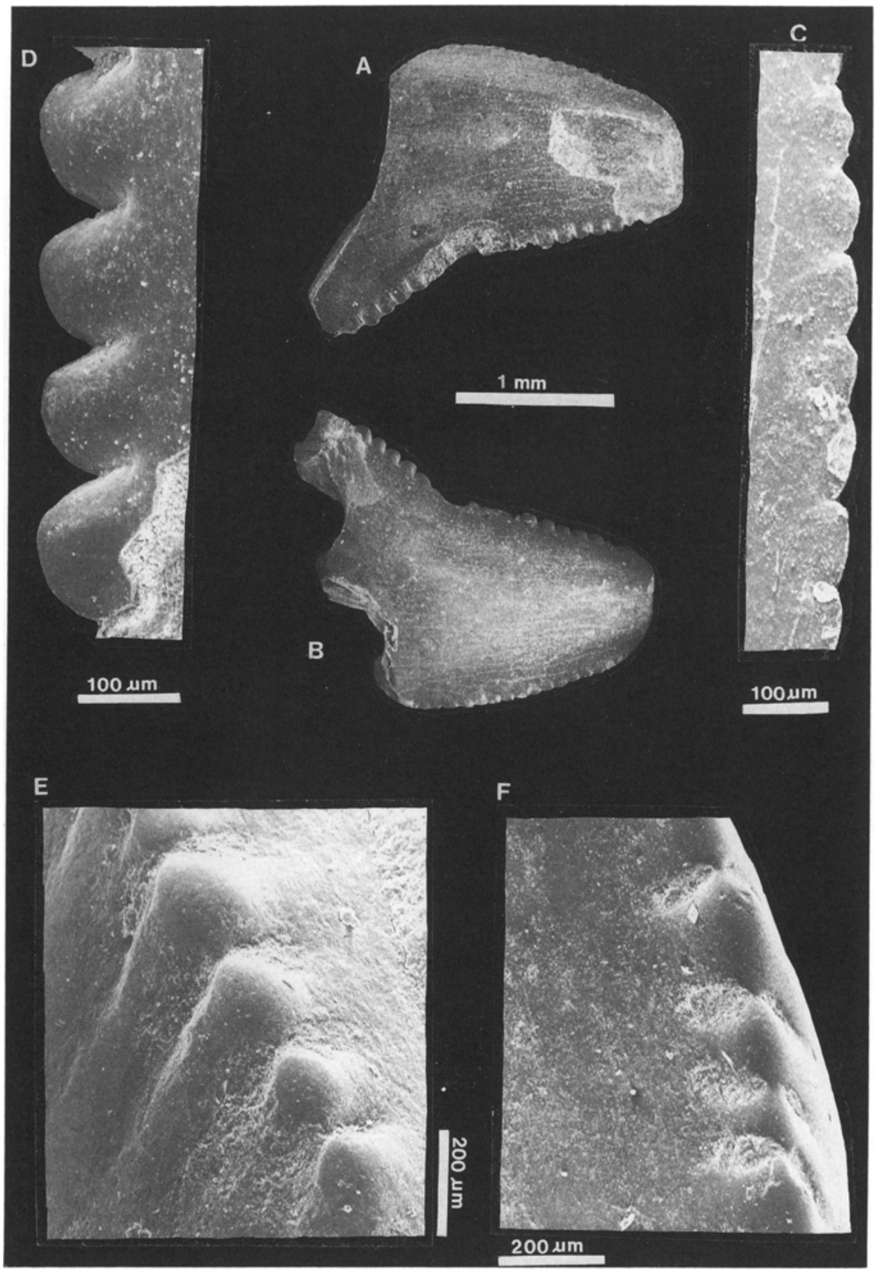

Fig. 4. A velociraptorine dromaeosaurid; **A:** labial view, **B:** lingual view, **C:** anterior denticle, **D:** posterior denticles; IPFUB GUI D 75. – A probable tyrannosaurid premaxillary tooth; **E:** posterior denticles, **F:** anterior denticles; IPFUB GUI D 89.

(Fig. 3B). The blood grooves do not reach the surface of the tooth. The cross-section appears rounded and not D-shaped, because of the appearance of the carinae (Fig. 3C).

Discussion: IPFUB GUI D 77 is closely related to the premaxillary teeth of the Late Cretaceous genus *Dromaeosaurus* for the following reasons: 1. The anterior and posterior carinae are on the lingual side of the tooth; 2. the cross-section of the base is rounded and not D-shaped; and 3. the DSDI is 1.0 and lies within the range for *Dromaeosaurus* (RAUHUT & WERNER 1995). The posterior denticles may have been longer than those from the anterior carina, as proposed for *Dromaeosaurus* (CURRIE et al. 1990), but due to intensive wear this cannot be determined.

Subfamily Velociraptorinae

Gen. et spec. indet.
Fig. 4A-D

Referred material: 28 isolated teeth; IPFUB GUI D 66-88, 99, 101, 157, 158, 170.

Description: These teeth are strongly laterally compressed and recurved (Fig. 4A-B). The serrated carinae show a significant difference in denticle size on the anterior and posterior serrations. The posterior denticles are twice as high as those from the anterior carina (Fig. 4C-D). The posterior serrations are slightly hooked apically, while those from the anterior carina are orientated perpendicularly to the edge (Fig. 4C-D). The cross-section of the base is rectangular. The DSDI varies from 1.0-2.4.

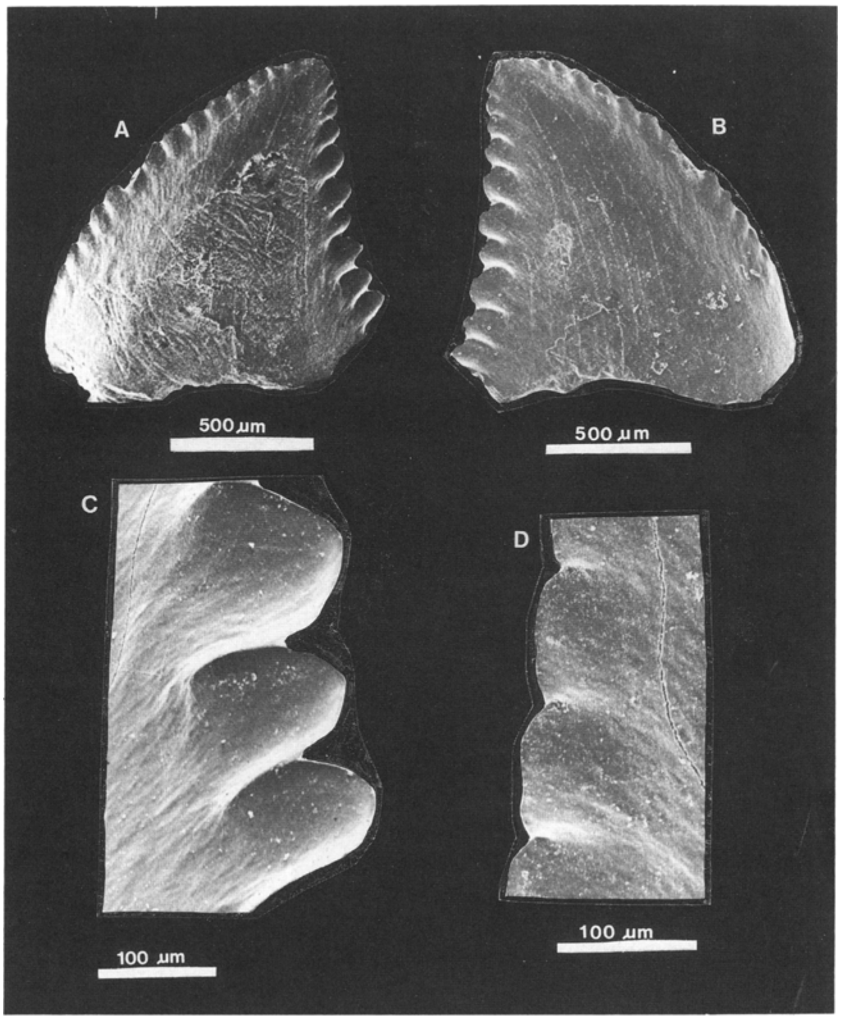

Fig. 5. A possible troodontid; **A:** labial view, **B:** lingual view, **C:** posterior denticles, **D:** anterior denticles; IPFUB GUI D 94.

Discussion: A significant difference in the size of denticles from the anterior and posterior serrations, in combination with the tooth shape described above, is only found in velociraptorine dromaeosaurids (Currie et al. 1990; Rauhut & Werner 1995). Usually the denticles of velociraptorine dromaeosaurids are strongly hooked toward the tip of the crown, but the Guimarota specimens differ in this character. Since strongly hooked denticles are the advanced character, the Guimarota specimens may belong to a primitive velociraptorine dromaeosaur. The variation range of the DSDI in the Guimarota specimens lies within the range of the Cretaceous velociraptorines *Saurornitholestes*, *Deinonychus* and *Velociraptor* (Rauhut & Werner 1995).

Family Tyrannosauridae

Gen. et spec. indet.
Figs. 3D-F, Figs. 4E-F

Referred material: 3 premaxillary teeth; IPFUB GUI D 89-91.

Description: These teeth show a D-shaped, basal cross-section with the anterior and posterior carina situated on the lingual side of the tooth (Fig. 3D-F). Both carinae are serrated, but the denticles are heavily worn down (Fig. 4E-F). Blood grooves between adjacent denticles extend onto the surface of the tooth (Fig. 4E). Both carinae bend inwards to the lingual surface antapically (Fig. 3D). A well defined median ridge is found on the lingual surface of the tooth near the posterior carina, which becomes more shallow and less pronounced apically. Smaller ridges can be found on both sides of the median ridge (Fig. 3D). IPFUB GUI D 90 possesses a broken lingual surface which has been worn down to a smooth surface probably through mastication. IPFUB GUI D 89 and D 91 have a DSDI of 1.0.

Discussion: The occurrence of two characteristic features of tyrannosaurids – a D-shaped cross-section at the base, and a typical wear surface – means that it is likely that these teeth represent a closely related form. A well developed median ridge on the lingual surface of D-shaped teeth is found only in the Upper Cretaceous genus *Aublysodon*, which could represent a juvenile morph of a tyrannosaurid (Molnar & Carpenter 1989; Currie et al. 1990). The variation of the DSDI lies within the range of *Tyrannosaurus* and *Aublysodon* (Rauhut & Werner 1995).

Family Troodontidae

Gen. et spec. indet.

Fig. 5A-D

Referred material: 14 isolated teeth; IPFUB GUI D 93-97, 100, 102, 104, 111, 114-116, 156, 190.

Description: These teeth are laterally compressed with a triangular cross-section at the base (Fig. 5A-B). In the majority of specimens, both carinae are serrated, with the anterior denticles being broader and less high than those of the posterior carina, which are strongly hooked apically (this is also true for teeth with only posterior serrations). The anterior denticles (where they exist), and posterior denticles are very large in relation to the TCH; therefore they are reduced to a number of 8-9 denticles per 1 mm (Fig. 5C-D). The blood grooves between adjacent denticles do not reach the surface of the crown. In some of the Guimarota specimens the anterior denticles are found only at the apex. A constriction between crown and root is found in all the Guimarota specimens. The DSDI varies from 0.8-1.5.

Discussion: These Guimarota specimens are closely related to the Upper Cretaceous troodontids on the basis of the following features: 1. constriction between crown and root is found in all teeth; 2. the triangular cross-section of the base; 3. they possess large denticles in relation to the TCH. Usually these features are seen as autapomorphies of troodontids (Barsbold 1974; Currie 1987; Currie et al. 1990). Besides these features, the number of denticles per 1 mm is nearly the same as that in troodontids, but this feature is not very useful for diagnostic purposes (Farlow et al. 1991). The arrangement of the denticles, and the difference in the shape of the anterior and posterior denticles in the Guimarota specimens is very similar to the pattern known in troodontids. The variation range of the DSDI in the Guimarota specimens is higher than in troodontids, but this may be due to a position within the jaw.

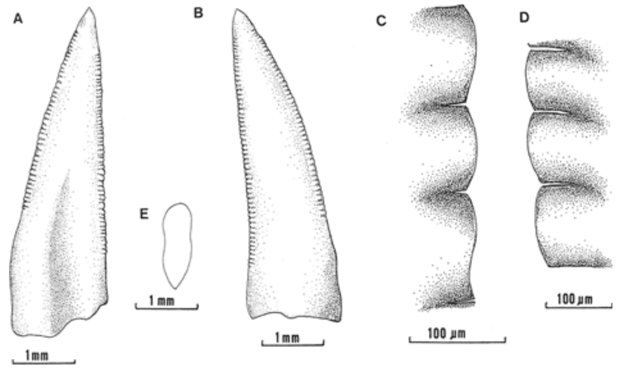

Fig. 6. cf. *Richardoestesia* sp.; **A:** lingual view, **B:** labial view, **C:** enlargement of posterior denticles, **D:** enlargement of anterior denticles, **E:** cross-section of the base; IPFUB GUI D 128.

Theropoda incertae sedis

cf. *Richardoestesia* sp.

Fig. 6A-E

Referred material: 40 isolated teeth; IPFUB GUI D 118-155.

Description: These teeth are laterally compressed, strongly elongated and recurved only toward the apex (Fig. 6A-B). Both carinae are serrated, but the denticles are very small in relation to tooth size. There is only a slight difference in the size of the denticles on the anterior and posterior carina; therefore the variation range of the DSDI is rather low and varies from 0.8-1.33 (Fig. 6C-D). On both the lingual and labial sides of the teeth, a longitudinal groove is found. This groove, which becomes more shallow and narrow toward the tip of the crown, is more pronounced on the lingual side (Fig. 6A). The cross-section of the base is rectangular (Fig. 6E).

Discussion: The teeth of *Richardoestesia gilmori* from the Upper Cretaceous deposits of the Judith River Formation (USA) are the only well described theropod teeth which also show a lanceolate shape, very small denticles in relation to tooth size and a longitudinal groove on the sides (Currie et al. 1990). The teeth of the type species *Richardoestesia* show a greater difference in the size of the denticles of the anterior and posterior serrations than the specimens from Guimarota, but our specimens are nearly the same as *Richardoestesia*-like teeth from the Lower Cretaceous Spanish locality Uña (Rauhut & Zinke 1995). Similarities with the teeth of the Upper Triassic theropod *Coelophysis* (Colbert 1989) and the temporal distance to *Richardoestesia* might indicate that the combination of characters found in the specimens from Guimarota is a result of convergent development. The variation of the DSDI in the specimens from Guimarota lies within the range of *Richardoestesia* and *Coelophysis* (Rauhut & Werner 1995).

cf. *Paronychodon* sp.

Referred material: A fragmentary left dentary and 29 isolated teeth; IPFUB GUI D 1-27.

Description: The dentary fragment and the isolated teeth are described in detail by Zinke & Rauhut (1994). So far, the most interesting feature on the teeth in the jaw and the isolated teeth are the longitudinal grooves and ridges found on both sides of the tooth. All *Parony-*

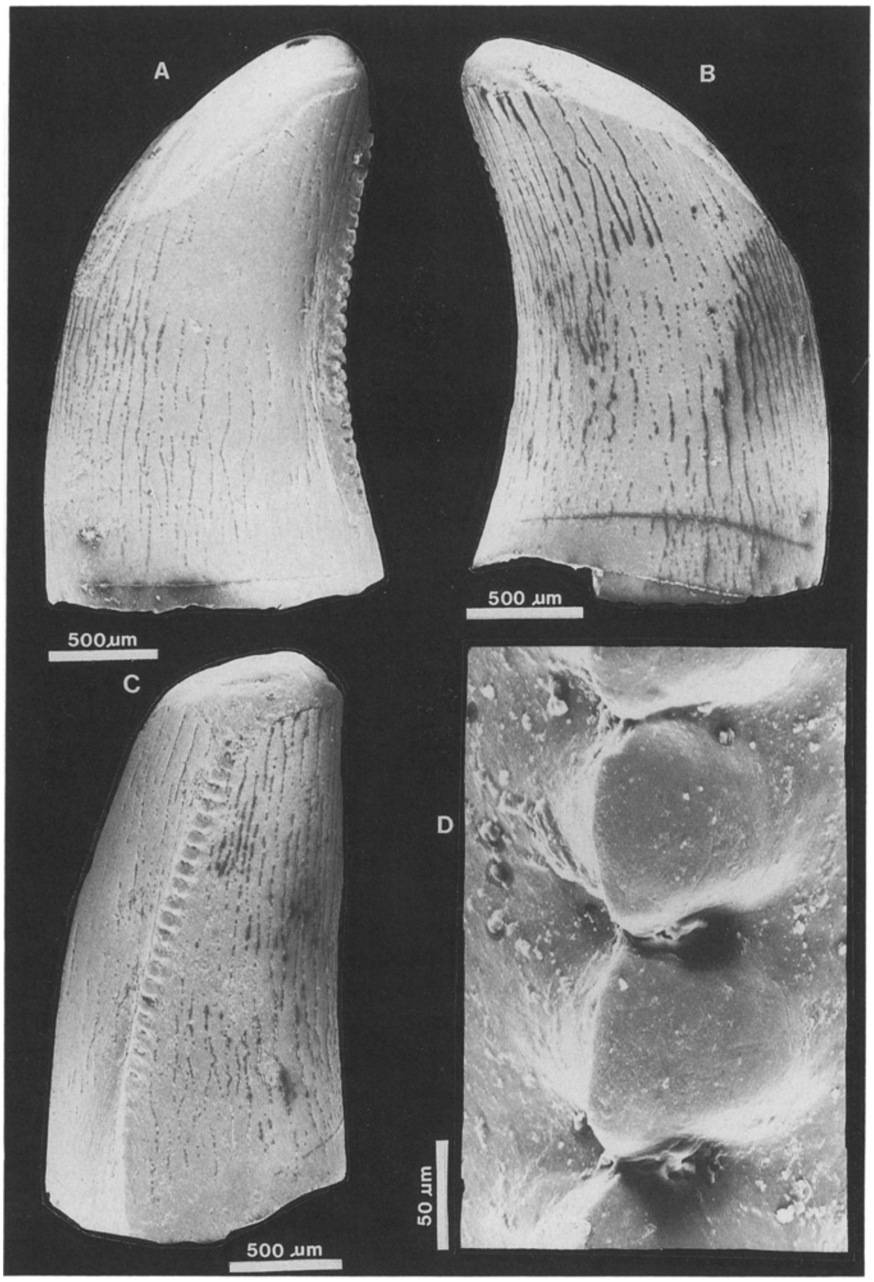

Fig. 7. A peculiar theropod tooth; **A:** labial view, **B:** lingual view, **C:** posterior view, **D:** posterior denticles in occlusal view; IPFUB GUI D 159.

chodon-like teeth from Guimarota show serrations on the posterior carina, and sometimes on both carinae.

Discussion: Since the holotype of *Paronychodon* (Cope 1876) is known from the Upper Cretaceous, again the temporal distance might suggest, that the reference of the specimens from Guimarota to the same genus is wrong. It is very difficult to do systematic work with the teeth of *Paronychodon*, as the holotype has only been described tentatively and a lot of teeth bearing longitudinal grooves on their faces, from different localities and of different times, have been ascribed to this genus, but their taxonomic position is still uncertain. As mentioned by Currie et al. (1990), the name *Paronychodon lacustris* should be restricted to non-serrate forms. For the specimens from Guimarota it is important to mention that similar teeth have been found in the Lower Cretaceous Spanish locality Galve (Rauhut & Zinke 1995). So far, the occurrence of this tooth morphotype is certain on the Iberian Peninsula from the Upper Jurassic until the Lower Cretaceous. Since the Iberian Peninsula was a consolidated landmass during these periods, the specimens from Spain and Portugal may belong to closely related forms. The exact taxonomic position is difficult to determine, but a few features of the dentary fragment and the isolated teeth indicate a relationship to the maniraptorans, and above all to the troodontids (Zinke & Rauhut 1994).

Indeterminate small theropod teeth
Fig. 7A-D

Referred material: 11 isolated teeth; IPFUB GUI D 159-169.

Description: These teeth are slightly recurved with a rounded cross-section at the base. The arrangement of the serrated posterior carina is very peculiar, because they are mostly in a labial position (Fig. 7A-B). Four teeth show serrations, which are chisel-like in appearence. Serrations are missing from the other teeth, but on most of them a row of rounded pits can be found, which represents the remains of worn denticles. The shape of the denticles on the posterior carina is very peculiar too, since they are asymmetric. The lingual side of each denticle is higher and more oblique than the labial side (Fig. 7C-D). The posterior carina bends antapically toward the labial side. A deep groove is developed labially to the entire serration.

Discussion: This morphotype has never been described before, and its taxonomic position remains uncertain. The only comparison could be to a peculiar tooth morphotype mentioned by MOLNAR & CARPENTER (1989) in their description of *Aublysodon mirandus*. Since asymmetrical carinae are known from tyrannosaurid teeth, it is possible that our teeth may represent a member of this family. However, as such teeth have not been described in detail, this is only a conjecture. Some of the larger teeth from Guimarota (TCH more than 1 cm) show asymmetrical carinae, as well as a rounded basal cross-section, and it is possible that these large teeth are closely related to the teeth described above.

Larger theropod teeth with a rounded cross-section
Fig. 8A-D

Referred material: 13 isolated teeth; IPFUB GUI D 174-186.

Description: These teeth are strongly elongated and recurved only apically (Fig. 8A). In half of the sample, both carinae are serrated with denticles orientated perpendicularly to the edges. The posterior denticles are higher than the anterior ones (Fig. 8B-C). The denticles are relatively small in relation to tooth size. Blood grooves between adjacent denticles reach the surface of the tooth, but they are not orientated toward the base of the crown. The posterior carina shows a twist toward the labial side of the tooth in the middle of the crown. The most striking feature is the nearly rounded cross-section of the base, which gives these teeth a compact basal shape (Fig. 8D), whereas apically these teeth show a lenticular cross-section. The DSDI is rather low and varies from 1.0-1.33.

Discussion: Strongly elongated teeth with a rounded, basal cross-section have been described and illustrated for maxillary and dentary teeth of *Aublysodon mirandus* (MOLNAR & CARPENTER 1989). The rounded sockets of the alveoli known in tyrannosaurid jaws, which were illustrated for *Gorgosaurus* (LAMBE 1917), suggest that tyrannosaurid lateral teeth possessed a rounded cross-section at the base, above all the anterior teeth (CURRIE pers. com. 1996). However, this has not been described before. The Guimarota specimens differ from tyrannosaurid teeth in the appearance of the blood grooves, which are not orientated toward the base (FIORILLO & CURRIE 1994), and also in the slightly higher variation range of DSDI (RAUHUT & WERNER 1995).

Probable allosaurid teeth
Fig. 8E-I

Referred material: 4 lateral teeth; IPFUB GUI D 191-194.

Description: The lateral teeth are laterally compressed and recurved at the apex (Fig. 8E). They show a FABL/BW ratio of two to one, which gives them a very broad appearance in anterior-posterior direction (Fig. 8I). On three of these teeth both carinae are serrated. The basal length of the anterior and posterior denticles is the same, but the posterior denticles tend to be longer than those from the anterior carina (Fig. 8F-G). The blood grooves extend onto the surface of the tooth, but they are not orientated toward the base of the tooth. On the lingual side a well developed median ridge follows the midline of the crown, becoming narrower toward the tip (Fig. 8E). This ridge shows the appearance of two longitudinal grooves between the carinae and the median ridge, mainly in the upper half of the tooth (Fig. 8E). The cross-section of the base is rectangular, while apically the cross-section is rather lenticular (Fig. 8I). The DSDI varies from 1.0-1.18.

Discussion: Lateral teeth of *Allosaurus* are characterised by a middle FABL/BW ratio of two to one (pers. obs.), which is found in all the Guimarota specimens. A well-pronounced median ridge on the lingual side of the tooth, showing the appearance of two longitudinal grooves between the carinae and the median ridge, is also developed in these lateral teeth of *Allosaurus* (pers. obs.). The anterior and posterior denticles of *Allosaurus* lateral teeth show the same basal length apically-antapically, but the posterior denticles tend to be longer than those from the anterior carina (pers. obs.). The same is found in all the Guimarota specimens. Therefore the variation range of the DSDI in *Allosaurus* (1.0) and in the Guimarota specimens is rather small. While downpointing blood grooves have been found in *Allosaurus* lateral teeth, the Guimarota specimens differ in this respect (pers. obs.). However, this may be due to the ontogenetic stage of the Guimarota teeth and so cannot be stated for certain.

Distribution of isolated teeth

440 theropod teeth were collected from the screen washing between the years 1972-1974 (including the isolated

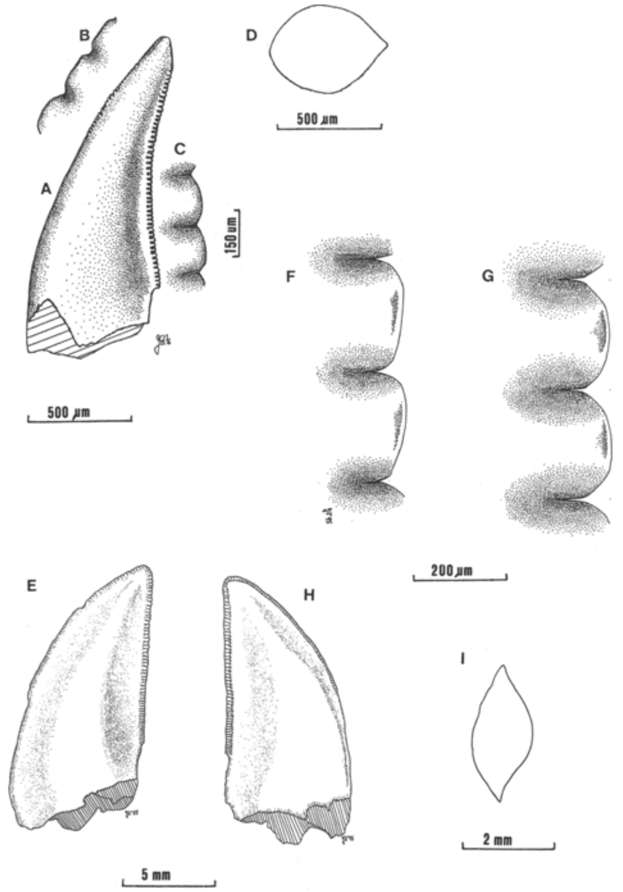

Fig. 8. A side tooth from a larger theropod with a rounded cross-section; **A:** labial view, **B:** enlargement of anterior denticles, **C:** enlargement of posterior denticles, **D:** cross-section of the base; IPFUB GUI D 178. – A side tooth of a probable allosaurid; **E:** lingual view, **F:** enlargement of anterior denticles, **G:** enlargement of posterior denticles, **H:** labial view, **I:** cross-section of the base; IPFUB GUI D 191.

teeth of cf. *Archaeopteryx* sp. described by Weigert 1995). 67.3 % of these have been identified, and the rest remains unidentified, because they lack taxonomically-valid features. The most common theropod teeth at Guimarota are those of cf. *Archaeopteryx* sp. (23.4 %), followed by cf. *Compsognathus* sp. (11.1 %), cf. *Richardoestesia* sp. (9.1 %), cf. *Paronychodon* sp. (6.6 %), velociraptorine dromaeosaurids (6.4 %), probable troodontids (3.2 %), larger theropod teeth (2.9 %), the small indeterminate theropod teeth (2.5 %), probable allosaurids (1.1 %), probable tyrannosaurids (0.7 %) and cf. *Dromaeosaurus* sp. (0.2 %).

The significance of the number of tooth positions in the mouth of theropod dinosaurs in relation to their distribution in the Guimarota coal mine is extremely hard to determine. Fiorillo & Currie (1994) argued that the relative abundance of teeth can only give a rough idea of the relative abundance of the animals from which they are derived. Also taphonomic sorting may have occurred. In that case, the following palaeoecological informations about the Guimarota specimens cannot be given without difficulties and inaccuracies.

Since *Archaeopteryx* shows the smallest number of tooth positions of all theropods described in this paper, this taxon may represent the most common theropod in this locality. The teeth of cf. *Compsognathus* sp. and cf. *Richardoestesia* sp. are represented by nearly the same number in the Guimarota fauna, which can be correlated with their similar number of tooth positions. The velociraptorine theropods are more common than the probable troodontids and tyrannosaurids, although the latter usually show a larger number of tooth positions.

In relation to the distribution of herbivore dinosaurs in Guimarota, which are represented by 45 isolated teeth (39 hypsilophodontid teeth [Thulborn 1973], 4 sauropod teeth [pers. obs.], 2 iguanodontid teeth [pers. obs.]), theropod teeth form the dominant component.

Systematic and paleobiogeographic significance

From the theropod teeth described in this paper, only two genera are well known from Upper Jurassic localities of Europe: *Compsognathus* (Solnhofen, Germany [Stromer 1934; Ostrom 1978], Canjuers, France [Bidar et al. 1972]) and *Archaeopteryx* (Solnhofen, Germany [Wellnhofer 1993]). These genera are also the most common theropods in the Guimarota assemblage, forming 34.5 % of the teeth studied. With their proposed palaeoecological habits as small predators perhaps specializing on a diet of insects and tiny vertebrates, they would have been perfectly adapted for the swampy environment proposed for Guimarota (Schudack 1993). So far, the occurrence of these theropods in the fauna is supported by morphological, paleobiogeographical and temporal aspects.

The occurrence of allosaurid teeth is also not surprising, since *Allosaurus* has been found in the Upper Jurassic Morrison Formation (USA; Madsen 1976).

According to the systematic studies of Holtz (1994) *Archaeopteryx* is proposed as a sister taxon of the Dromaeosauridae. If this is correct, the occurrence of dromaeosaurids at Guimarota is not surprising. 'Dromaeosaur'-like teeth were also found in Middle Jurassic deposits of England (Metcalf & Walker 1994). Since teeth similar to dromaeosaurids, troodontids, tyrannosaurids and ornithomimids have also been found in the Upper Jurassic beds of the Morrison Formation, a Middle to Late Jurassic origin of these theropods may be assumed (Chure & Madsen 1993; Chure 1995). This argument is especially supported by the worldwide diversification of dromaeosaurids in the Lower Cretaceous (Ostrom 1969; Kirkland et al. 1993; Azuma & Currie 1995; Rauhut & Werner 1995), and from their presence in the Barremian of the Iberian Peninsula (Zinke & Rauhut 1994; Rauhut & Zinke 1995). Since the Iberian Peninsula was more or less a consolidated landmass during Late Jurassic and Lower Cretaceous times, and as there is good evidence for a faunal interchange between Europe, North America and Africa in the Late Jurassic (ZIEGLER 1988; GALTON 1972; GALTON & TAQUET 1982), the dispersal of early dromaeosaurids and other maniraptorans could have taken place during this period.

Besides dromaeosaurids, isolated teeth from cf. *Richardoestesia* sp. and cf. *Paronychodon* sp. are also known from the Barremian of Spain (ZINKE & RAUHUT 1994; RAUHUT & ZINKE 1995) and the Lower Cretaceous of Utah (KIRKLAND & PARRISH 1995). The temporal distance to the Upper Cretaceous finds of *Richardoestesia* and *Paronychodon* (CURRIE et al. 1990) and slight morphological differences, may indicate that the teeth from Guimarota, as well as those from Spain and Utah, belong to closely-related forms, but not to *Richardoestesia* and *Paronychodon* themselves, or that they are a result of convergent development.

Finally, the significance of theropod teeth to systematic and paleobiogeographic studies is always questionable, because the morphology of teeth underlies functional aspects, and convergent development could have taken place at many points in the evolutionary history of the Theropoda. However, in poorly-known dinosaur localities, theropod teeth can show an approximate insight into the composition of the theropod fauna, especially if they show a large morphological diversity like those at Guimarota. Hopefully, the comparison of the teeth studied in this paper with other Middle and Upper Jurassic localities, like Hornsleasow Quarry in the British Midlands and the Morrison Formation (USA), will help to settle the problems surrounding the early origin of maniraptoran theropods during Jurassic times.

Acknowledgements

I would like to thank SARA J. METCALF, ANTHONY R. FIORILLO and PHILIPP J. CURRIE for reviewing this manuscript and OLIVER RAUHUT for useful discussions while this paper was written. I also thank Prof. Dr. BERNHARD KREBS, who gave me the opportunity to study this material.

References

AZUMA, Y. & CURRIE, P.J. 1995. A new giant dromaeosaurid from Japan. – Journal of Vertebrate Paleontology **15** (suppl. to No. 3): 17 A, Lawrence/Kansas.

BARSBOLD, R. 1974. Saurornithoididae, a new family of small theropod dinosaurs from central Asia and North America. – Palaeontologica Polonica **30**: 5-22, Warsaw.

BIDAR, A.; DEMAY, L. & THOMEL, G. 1972. *Compsognathus corallestris*, nouvelle espèce de dinosaurien théropode du Portlandien de Canjuers (Sud-Est de la France). – Musée d'Histoire Naturelle de Nice, Annales **1**: 1-34, Nice.

BUSCALIONI, A. D.; ORTEGA, F.; PÉREZ-MORENO, B.P. & EVANS, S.E. 1996. The Upper Jurassic maniraptoran theropod *Lisboasaurus estesi* (Guimarota, Portugal) re-interpreted as a crocodylomorph. – Journal of Vertebrate Paleontology **16** (2): 358-362 Lawrence/Kansas.

CHURE, D.J. 1994. *Koparion douglassi*, a new dinosaur from the Morrison Formation (Upper Jurassic) of the Dinosaur National Monument: the oldest troodontid (Theropoda: Maniraptora). – BYU Geology Studies **40**: 11-15, Provo/ Utah.

— 1995. The teeth of small theropods from the Morrison Formation (Upper Jurassic: Kimmeridgian), UT. – Journal of Vertebrate Paleontology **15** (suppl. to No. 3): 23 A, Lawrence/Kansas.

CHURE, D.J.; KIRKLAND, J.I. & SCHEETZ, R.D. 1993. Embryos, hatchlings, juveniles and adults of the ornithopod dinosaur *Dryosaurus* from the Late Jurassic Morrison Formation. – Journal of Vertebrate Paleontology **13** (suppl. to No. 3): 29 A, Lawrence/Kansas.

CHURE, D.J. & MADSEN, J.H. jr. 1993. A tyrannosaurid-like braincase from the Cleveland-Lloyd Dinosaur Quarry (CLDQ), Emery County, UT (Morrison Formation, Late Jurassic). – Journal of Vertebrate Paleontology **13** (suppl. to No. 3): 30 A, Lawrence/Kansas.

COLBERT, E.H. 1989. The Triassic dinosaur *Coelophysis*. – Museum of Northern Arizona Bulletin **57**: 1-160, Flagstaff/ Arizona.

COPE, E.D. 1876. Description of some vertebrate remains from the Fort Union Beds of Montana. – Academy Natural Sciences Philadelphia, Proceedings **1876**: 248-261, Philadelphia.

CURRIE, P.J. 1987. Bird-like characteristics in the jaws and teeth of troodontid theropods (Dinosauria: Saurischia). – Journal of Vertebrate Paleontology **7** (1): 72-81, Lawrence/ Kansas.

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. [eds.] Dinosaur Systematics. Approaches and Perspectives: 107-125, Cambridge (Cambridge University Press).

FARLOW, J.O.; BRINKMANN, D.L.; ABLER, W.L. & CURRIE, P.J. 1991. Size, shape and serration density of theropod dinosaur lateral teeth. – Modern Geology **16**: 161-198, New York.

FIORILLO, A.R. & CURRIE, P.J. 1994. Theropod teeth from the Judith River Formation (Cretaceous) of South-Central Montana. – Journal of Vertebrate Paleontology **14**: 74-80 Lawrence/Kansas.

GALTON, P.M. 1977. The ornithopod dinosaur *Dryosaurus* and a Laurasia-Gondwanaland connection in the Upper Jurassic. – Nature **268**: 230-232, London.

GALTON, P.M. & TAQUET, P. 1982. *Valdosaurus*, a hypsilophodontid dinosaur from the Lower Cretaceous of Europe and Africa. – Géobios **15** (2): 147-159, Lyon.

HELMDACH, F.F. 1971. Stratigraphy and ostracod-fauna from the coalmine Guimarota (Upper Jurassic). – Mémoire Services Géologiques du Portugal, (nova Sér.) **17**: 41-88, Lisboa.

HOLTZ, T.R. jr. 1994. The phylogenetic position of the Tyrannosauridae: Implications for theropod systematics. – Journal of Paleontology **68** (5): 1100-1117, Lawrence/Kansas.

KIRKLAND, J.I.; BURGE, D. & GASTON, R. 1993. A large dromaeosaur (Theropoda) from the Lower Cretaceous of eastern Utah. – Hunteria **2** (10): 1-16, Boulder/Colorado.

KIRKLAND, J.I. & PARRISH, J.M. 1995. Theropod teeth from the Lower and Middle Cretaceous of Utah. – Journal of Vertebrate Paleontology **15** (suppl. to No. 3): 39 A, Lawrence/ Kansas.

KREBS, B. 1991. Das Skelett von *Henkelotherium guimarotae* gen. et sp. nov. (Eupanthotheria, Mammalia) aus dem Oberen Jura von Portugal. – Berliner geowissenschaftliche Abhandlungen, (A) **133**: 1-121, Berlin.

LAMBE, L.M. 1917. The Cretaceous Theropodous dinosaur *Gorgosaurus*. – Department of Mines, Geological Series, Memoir **100** (83): 1-85.

MADSEN, J.H. jr. 1976. *Allosaurus fragilis*, a revised osteology. – Utah Geological and Mineral Survey Bulletin **109**: 1-163, Salt Lake City.

METCALF, S.J. & WALKER, R.J. 1994. A new Bathonian microvertebrate locality in the English Midlands. - [In:] FRASER, N.C. & SUES, H.-D. [eds.] In the Shadow of the Dinosaurs - Mesozoic Small Tetrapods, Cambridge (Cambridge University Press).

MILNER, A.R. & EVANS, S.E. 1991. The Upper Jurassic diapsid *Lisboasaurus estesi* - a maniraptoran theropod. - Paleontology **34** (3): 503-513, London.

MOLNAR, R.E. & CARPENTER, K. 1989. The Jordan theropod (Maastrichtian, Montana, USA) referred to the genus *Aublysodon*. - Géobios **22** (4): 445-454, Lyon.

OSTROM, J.H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. - Bulletin Peabody Museum of Natural History **30**: 1-165, New Haven.

— 1978. The osteology of *Compsognathus longipes* WAGNER. - Zitteliana **4**: 73-118, München.

RAUHUT, O.W.M. & WERNER, CH. 1995. First record of the family Dromaeosauridae (Dinosauria: Theropoda) in the Cretaceous of Gondwana (Wadi Milk Formation, northern Sudan). - Paläontologische Zeitschrift **69** (3/4): 475-489, Stuttgart.

RAUHUT, O.W.M. & ZINKE, J. 1995. A description of the Barremian dinosaur fauna from Uña with a comparison of that of Las Hoyas. - II. International Symposium of Lithographic Limestone, Extended Abstracts: 123-126, Cuenca.

SCHUDACK, M.E. 1993. Charophyten aus dem Kimmeridgium der Kohlengrube Guimarota (Portugal). Mit einer eingehenden Diskussion zur Datierung der Fundstelle. - Berliner geowissenschaftliche Abhandlungen, (E) **9**: 211-231, Berlin.

STROMER, E. 1934. Die Zähne des *Compsognathus* und Bemerkungen über das Gebiß der Theropoda. - Centralblatt für Mineralogie, Geologie und Paläontologie, (B) **1934**: 74-85, Stuttgart.

THULBORN, R.A. 1973. Teeth of ornithischian dinosaurs from the Upper Jurassic of Portugal. - Memoire Services Géologiques du Portugal **22**: 89-134, Lisboa.

WEIGERT, A. 1995. Isolierte Zähne von cf. *Archaeopteryx* sp. aus dem Oberen Jura der Kohlengrube Guimarota (Portugal). - Neues Jahrbuch für Geologie und Paläontologie, Monatshefte **1995** (9): 562-576, Stuttgart.

WELLNHOFER, P. 1993. Das siebte Exemplar von *Archaeopteryx* aus den Solnhofener Schichten. - Archaeopteryx **11**: 1-47, Eichstätt.

ZIEGLER, P.A. 1988. Evolution of the Arctic-North Atlantic and Western Tethys. - American Association of Petroleum Geologists, Memoir **43**: 63-82, Tulsa/Oklahoma.

ZINKE, J. & RAUHUT, O.W.M. 1994. Small theropods (Dinosauria, Saurischia) from the Upper Jurassic and Lower Cretaceous of the Iberian Peninsula. - Berliner geowissenschaftliche Abhandlungen, (E) **13**: 163-177, Berlin.

Eingang des Manuskriptes am 10. September 1996;
Annahme durch die Schriftleitung am 3. Juni 1997.