Journal of Vertebrate Paleontology 25(2):343–353, June 2005

A NEW SPECIES OF *DORATODON* (CROCODYLIFORMES: ZIPHOSUCHIA) FROM THE LATE CRETACEOUS OF SPAIN

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ABSTRACT—A new species of a ziphodont crocodyliform is described on the basis of newly-discovered material from the Late Cretaceous (Campanian) Sierra Perenchiza Formation of Valencia, Spain. It is referred to the genus *Doratodon* as *D. ibericus* sp. nov. To date, *Doratodon* (type-species *D. carcharidens*) was only known by fragmentary cranial remains from the Campanian of Muthmannsdorf (Austria). This genus was previously regarded either as a goniopholid or as a hsisosuchid within the Mesoeucrocodylia, but a phylogenetic analysis suggests that *Doratodon* is a member of Ziphosuchia, placing it as the sister taxon of Sebecosuchia. *Doratodon* shares with Sebecosuchia (including *Bergisuchus*) features concerning the shape and implantation of teeth (margins of tooth crowns with denticulate carinae; tip of tooth crowns caudally curved; tooth implantation in isolated alveoli). Its inclusion in Ziphosuchia is based also on mandibular traits (splenials broad and robust behind symphysis, sculpturing of lateral surface of dentary based on development of longitudinal depression). The absence of the external mandibular fenestra is an autopomorphy of *Doratodon* in the context of Ziphosuchia. *Doratodon* is characterized by: short and narrow rostrum with reduced dentition (11 to 13 dentary teeth); dorsal profile of lower jaw showing two vertical waves. The most distinctive characteristic of the new species relative to *D. carcharidens* is the heterodonty in size of teeth, especially in the caudal part of the dental series. From a palaeobiogeographical point of view, *Doratodon* represents the first occurrence of a sebecosuchian-like crocodyliform in the Late Cretaceous of Europe.

INTRODUCTION

The crocodyliform continental fauna from the Late Cretaceous (Campanian-Maastrichtian) of Europe is mainly composed of eusuchians such as the short-snouted alligatorid *Acynodon*, the basal alligatoroid *Musturzabalsuchus*, and *Allodaposuchus*, the sister-taxon of Crocodylia. These three eusuchians are known in several localities of southern France, Spain, and Romania (Buscalioni et al., 1997, 1999, 2001; Buscalioni and Ortega, 2002). Non-eusuchian crocodyliforms are represented by the huge *Ischyrochampsa* from southern France and Spain (Vasse, 1995; Buscalioni et al., 1999) and by the enigmatic ziphodont *Doratodon* from Austria (Buffetaut, 1979). An isolated crocodyliform tooth from the Late Maastrichtian of Romania has been assigned to cf. *Doratodon* as well (Grigorescu et al., 1999).

Recently, an incomplete lower jaw with dentition of a ziphodont crocodyliform was collected from a largely fossiliferous bed of the Late Cretaceous (Campanian) continental deposits of the Sierra Perenchiza Formation, about 2 Km south of the village of Chera, Valencia province, eastern Spain (Fig. 1). The Sierra Perenchiza Formation is a carbonate unit discontinuously exposed along the southeastern margin of the Iberian Range (Vilas et al., 1982), and represents the beginning of the continental sedimentation which took place in shallow, lacustrine basins during the final Cretaceous marine regression, in the southwestern Iberian domain (Alonso et al., 1991). In the Chera area, the lacustrine and palustrine sediments of this formation overlie the lagunal deposits of the Sierra de Utiel Formation (Santonian-lower Campanian), and they are unconformably overlain by alluvial sequences that are probably Maastrichtian and Paleocene in age (Alonso et al., 1987; Floquet, 1991). The vertebrate-bearing beds of Chera consist mostly of shallow-water carbonate deposits containing the charophyte species *Peckicara pectinata* (M. Feist, pers. comm.), a biostratigraphical marker of the middle to late Campanian (Riveline et al., 1996).

The vertebrate fauna of Chera is dominated by dinosaurs. In addition, crocodylian remains, including isolated bones and teeth of *Acynodon* and *Musturzabalsuchus*, turtle, and pterosaur remains comprise this fossil assemblage together with freshwater microvertebrates (Company et al., 1999). The Chera fauna shares many taxa with other Campanian localities of southern Europe, mainly Laño, in the Iberian Peninsula (Pereda Suberbiola et al., 2000), and Villeveyrac in southern France (Buffetaut et al., 1996; Garcia and Pereda-Suberbiola, 2003).

Institutional abbreviations—IPUW, Institut fur Paläontologie, Universität Wien; **HLMD**, Museum Darmstadt, Darmstadt; **MGUV**, Museo del Departamento de Geología, Universidad de Valencia, Burjassot.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970
CROCODYLIFORMES Hay, 1930
ZIPHOSUCHIA Ortega et al., 2000
DORATODON Seeley, 1881

Type Species—*Doratodon carcharidens* (Bunzel, 1871).

Revised Diagnosis—Small-sized crocodyliform with a narrow rostrum and deep vertical maxillae with straight alveolar edges, and an anteorbital fenestra. The mandible has a pair of occlusal

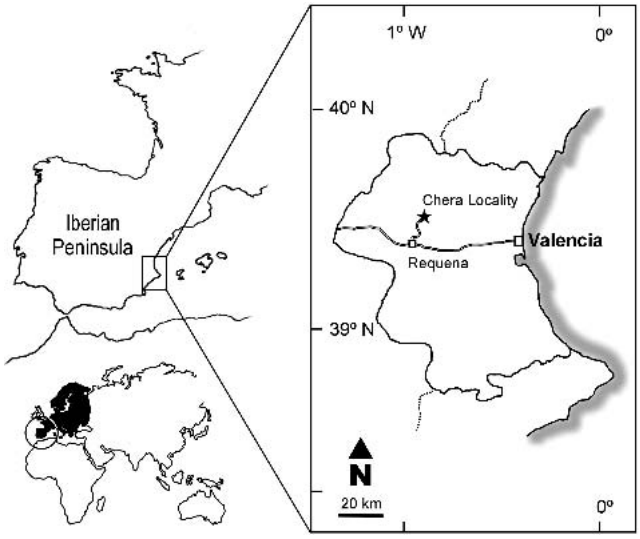

FIGURE 1. Location map of the Chera locality, Valencia province, eastern Spain.

pits of the premaxillary teeth medial to the dental series at the level of the fourth and fifth alveoli.

Doratodon shares with Sebecosuchia the following synapomorphies: teeth serrated; crowns curved caudally; splenials robust and convex in transverse section; lateroventral margin of lateral surface of dentary with longitudinal groove. It can be diagnosed by a set of primitive and derived features as well: mandible bearing procumbent teeth (first one larger than second); reduced number of teeth (11 to 13); fourth dentary tooth not hypertrophied, as large as tenth; dorsal profile of lower jaw showing two vertical waves. (Although most ziphosuchians show a unique anterior wave, this feature is also observed in the sebecid from Itaborai, Paleocene of Brazil.); closed external mandibular fenestra (among crocodiles with ziphodont dentition, shared by *Wanosuchus*); surangular lacking caudal extension; angular with external ventral rim (similar to condition in *Baurusuchus*).

DORATODON CARCHARIDENS Bunzel, 1871
(Fig. 6)

Holotype—IPUW 2349/57, an almost complete mandible with teeth (Bunzel, 1871:pl. 1, figs. 29–32; Buffetaut, 1979:pl. 1, figs. 1–3).

Type Locality and Horizon—Muthmannsdorf, near Wiener Neustadt, Lower Austria; continental coal-bearing series of the Gosau Formation, Grünbach Basin; Late Cretaceous, early Campanian (Brix and Plochinger, 1988).

Referred Material from the Same Beds—IPUW 2349/52, a fragment of maxilla (Bunzel, 1871:pl. 1, figs. 3–5; Buffetaut, 1979:pl. 2, figs. 7–9); IPUW 2349/58–61, isolated teeth (Buffetaut, 1979:pl. 1, figs. 4–7). An isolated parietal (IPUW 2349/54) was provisionally referred to *D. carcharidens* by Buffetaut (1979:pl. 3, fig. 6; see also Bunzel, 1871:pl. 1, figs. 1–2). This bone will not be taken into account in the present work.

Revised Diagnosis—Mandibular tooth row homodont in size (alveolar length ranging from 3 to 5 mm); slope of symphyseal area not abrupt; single diastema (between second and third alveoli).

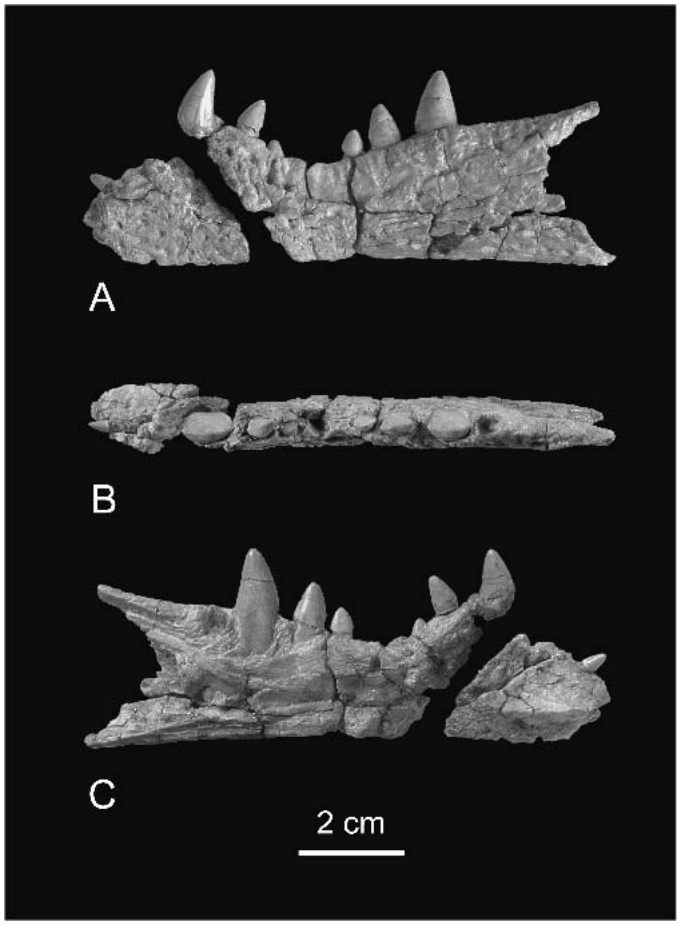

FIGURE 2. *Doratodon ibericus* sp. nov., Late Cretaceous of Valencia (Campanian), Spain. Left dentary in lateral (**A**), dorsal (**B**), and medial (**C**) views.

DORATODON IBERICUS, sp. nov.
(Figs. 2–5)

Holotype—MGUV 3201, incomplete left mandible with dentition.

Etymology—The term 'ibericus' (Latin) refers to the Iberian Peninsula, concerning the provenance of the type specimen.

Type Locality and Horizon—About 2 km south-east of the village of Chera, Valencia province, Spain (exact location on file at DGPA, Generalitat Valenciana); Sierra Perenchiza Formation, Late Cretaceous, Campanian.

Diagnosis—Dentary tall dorsoventrally; teeth heterodont in size and shape increasing in length from eighth to tenth; fourth and tenth largest of dental series; two diastemata at mandible (between second and third and between seventh and eighth).

DESCRIPTION

The specimen MGUV 3201 (Figs. 2, 3) consists of a nearly complete left dentary (preserved length of about 105 mm). The dentary contains at least eleven alveoli, with nine teeth in situ. It is preserved in two fragments found in anatomical connection, but separated by a narrow portion that was badly damaged by root action (Fig. 2). It has been reconstructed according to the images taken in the field. The posterior end of the mandible is broken away.

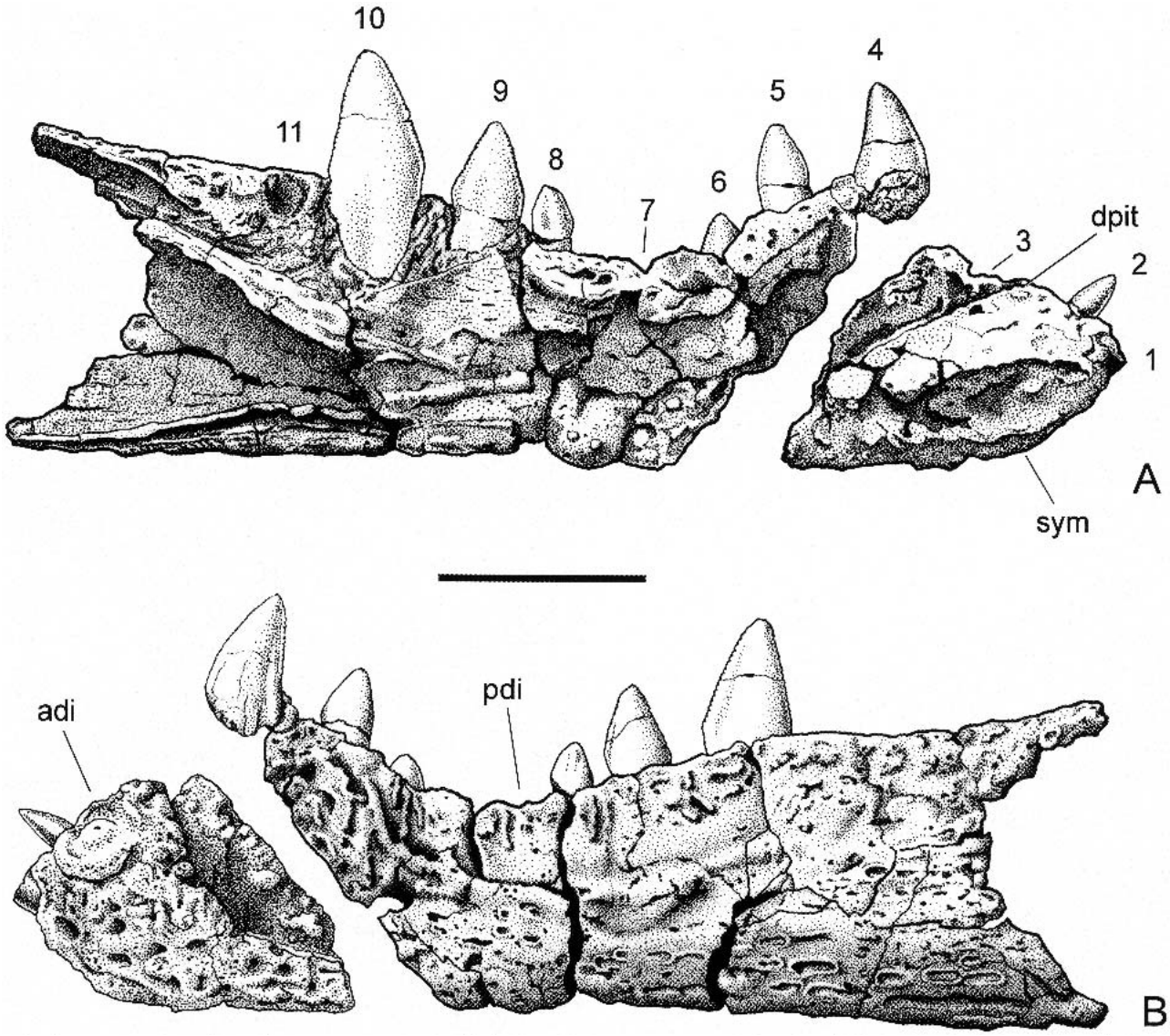

FIGURE 3. *Doratodon ibericus* sp. nov., Late Cretaceous of Valencia (Campanian), Spain. Left dentary in lateral (**A**), and medial (**B**) views. **Abbreviations**: **adi**, anterior diastema; **dpit**, premaxilary dental pits; **pdi**, posterior diastema; **sym**, symphyseal area; **1** to **11**, number of dentary teeth and alveoli. Scale bar equals 20 mm.

Dentary

The dentary is strongly lateromedially compressed, with a dorsal profile gently festooned vertically, showing two vertical waves. The first concave arch is delimited by the second and fourth alveoli, and the second, by the fourth to ninth. The mandibular rami diverge posteriorly at an acute angle of about 15 to 20 degrees. The rostral tip of the mandible is blunt and wide. The external surface is ornamented with grooves and pits. Round pits are confined to the rostralmost portion of the ramus. Elongated, longitudinal grooves are best developed on the ventrolateral margin. Laterally, a well-marked groove runs parallel to the dorsal edge of the dentary. Atop the groove, the bone surface displays a pattern of vertical crests lateral to the alveolar border. This lateral groove diverges caudoventrally and extends almost parallel to the ventral mandibular margin. The dentary extends beyond the tooth row forming a dorsal ascending process, on which part of the contact with the surangular is preserved on its medial surface. The lateral dentary surface is vertical and is almost perpendicular to its ventral margin.

Part of the dorsal and ventral sutural surfaces for the splenial are preserved, and thus, the splenial bone would be involved in the mandibular symphysis. The symphysis extends back to the level between the fourth and fifth alveoli. The dorsal surface of the symphysis is concave, with its maximum width and height at the fourth tooth. The symphyseal suture is eroded, but it expands rostrocaudally in a horizontal plane. The dorsal surface of the symphysis is somewhat weathered, although a pair of large, oval dental pits is observed. They have an oblique longitudinal axis rostromedially to caudolaterally directed. Both pits are placed medial to the third alveolus. The first pit is the smallest, and it is placed close to the diastema. The second pit is disposed caudomedially to the first one. The position of the pits implies that at least two large, premaxillary teeth have a medial occlusion relative to the rostral part of the dentary tooth row. The Meckelian fossa is greatly developed caudally, and tapers anteriorly forming a narrow Meckelian canal. The Meckelian canal appears to extend rostrally up to the fourth alveolus.

The splenial is not preserved in the specimen, but the sutures

on the dentary show that the splenial would reach its dorsal margin caudal to the eighth tooth, constituting the medial wall of the last three individual alveoli. The splenial symphyseal area could start at the mesial margin of the seventh alveolus, although the specimen is badly damaged at that level. The ventromedial suture of the dentary for the splenial shows a longitudinal groove, indicating that the latter bone would be thick transversely. In contrast, its caudalmost suture with the dentary suggests that the splenial becomes a thin lamina.

There are preserved 11 alveoli in the dentary, with nine teeth in situ (Fig. 3). The rostralmost part of the dental row lies near the midline of the dentary. Then it twists very slightly towards the labial margin, and posterior to the second diastema, it deviates slightly lingually, the last three alveoli being placed on the lingual margin of the dentary.

The symphyseal fragment comprises the first three alveoli plus the mesial wall of the fourth one. There is a short diastema between the second and third tooth positions. The caudal fragment contains eight tooth positions. Behind the fourth tooth, the dorsal edge of the dentary deflects into a concavity. In dorsal view, the caudal tooth row is approximately straight. Alveoli seven and eight are separated from each other by a short diastema, 4 mm long. Caudal to the diastema the teeth vary in size, the tenth (or penultimate) tooth being the largest of the dental series (see Table 1 for measurements of the alveoli). A gentle interlocking pit lies lateral to the posterior diastema, and thus, a medial occlusion of the mandible is expected. This feature suggests that the maxillary walls would expand laterally more than those of the premaxillae.

Dentition

Nine complete or fragmentary ziphodont teeth (i.e., serrated and labiolingually compressed) are preserved in the specimen (Figs. 3–5). Teeth are set in individual sockets. Dentition is heterodont in size and shape, with waves of size variation along the tooth row (Table 1). The first and third teeth have broken crowns. The first and second are procumbent, with the second being the smallest. The anterior crowns are subconical and slightly curved lingually, whilst middle to posterior teeth become gradually straight and laterally compressed (i.e., subtriangular to lanceolate in shape). Posteriormost and largest teeth have curved mesial margins but relatively straight distal margins, almost perpendicular to the base of the crown. All teeth exhibit finely serrated mesial and distal margins, placed along the longitudinal midline of the crown. There is no constriction at the base of the crown; therefore, the crown-root junction is marked only by the sudden disappearance of the medial carina. The distal carina diminishes more gradually. The tooth enamel is smooth. There are no wear facets in the crown enamel.

Doratodon ibericus is a true ziphodont crocodyliform (Langston, 1975; Legasa et al., 1994; Prasad and Lapparent de Broin, 2002), because the serrations of the carina are formed by clearly individualized denticles, not by crenulations of the enamel. The serrations run down from the tip up to the basal region of the crown (Fig. 4A). Except in the lowermost part of the carinae, both the mesial and distal denticles point toward the apex of the tooth. Denticles are minute and closely spaced. Denticle size does not vary significantly on either the mesial or the distal carinae, but scales to tooth size. There are about three denticles per millimeter on the large teeth and up to five denticles per millimeter on the small ones, measured half way along the length of the carinae. Each denticle is relatively straight, chisel-like in form, and has slightly pointed or rounded distal margins (Figs. 4B, 5A). Basal denticles are minute and progressively increase in size toward the tip of the tooth (Figs. 4A and 4Ba). Middle and apical denticles display a wide range of variability in shape and size. Some of them are eventually bicusped (Fig. 4Bc). Measurements of serration size are specified in Table 2.

DISCUSSION

The mandible of the Chera crocodile shows a close resemblance with that of *Doratodon carcharidens*, a ziphodont crocodyliform from the Late Cretaceous of Austria. Bunzel (1871:pl. 1, figs. 29–30) erected *Crocodilus carcharidens* as a new species on the basis of a lower jaw from the continental coal-bearing beds of the Gosau Formation at Muthmannsdorf, Lower Austria, and referred other cranial remains (maxilla, parietal) from the same beds to *Crocodilus* sp. (1871:pl. 1, figs. 1–5). Seeley (1881)

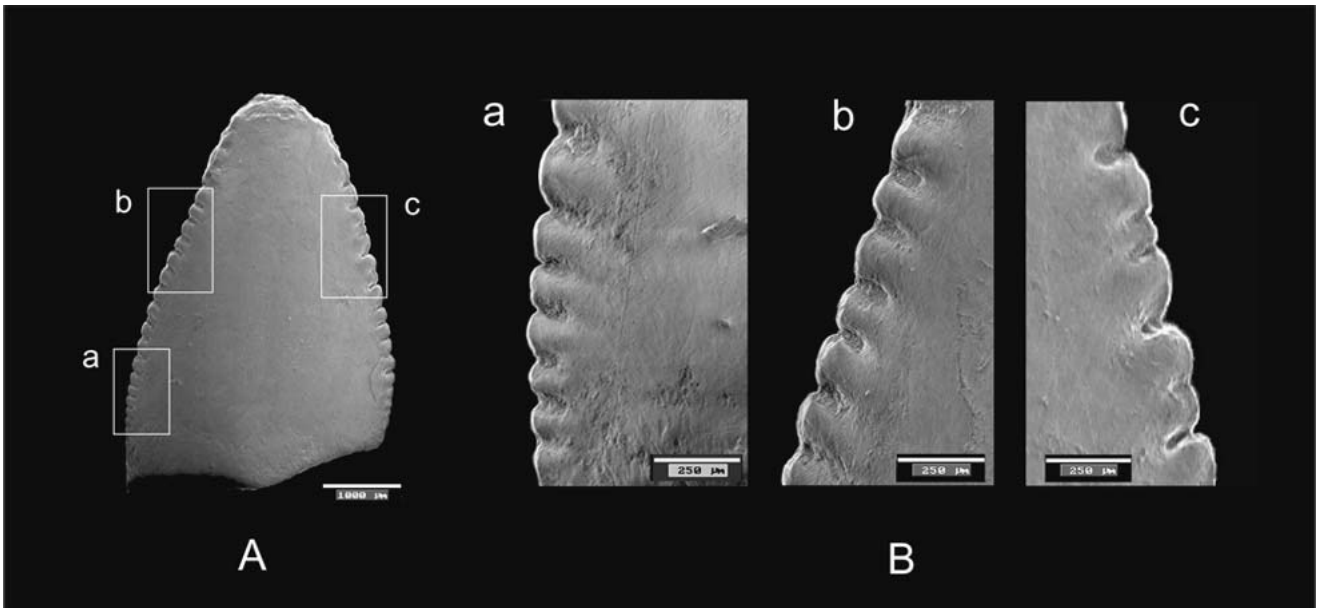

FIGURE 4. *Doratodon ibericus* sp. nov., Late Cretaceous of Valencia (Campanian), Spain. **A**, second tooth in lingual view; **B**, details of the serrations on the mesial (**a**, lower; **b**, upper) and proximal carina (**c**). Note the disparity in size and shape of the denticles. Scale in A equals 1 mm. Scale in B equals 0.25 mm.

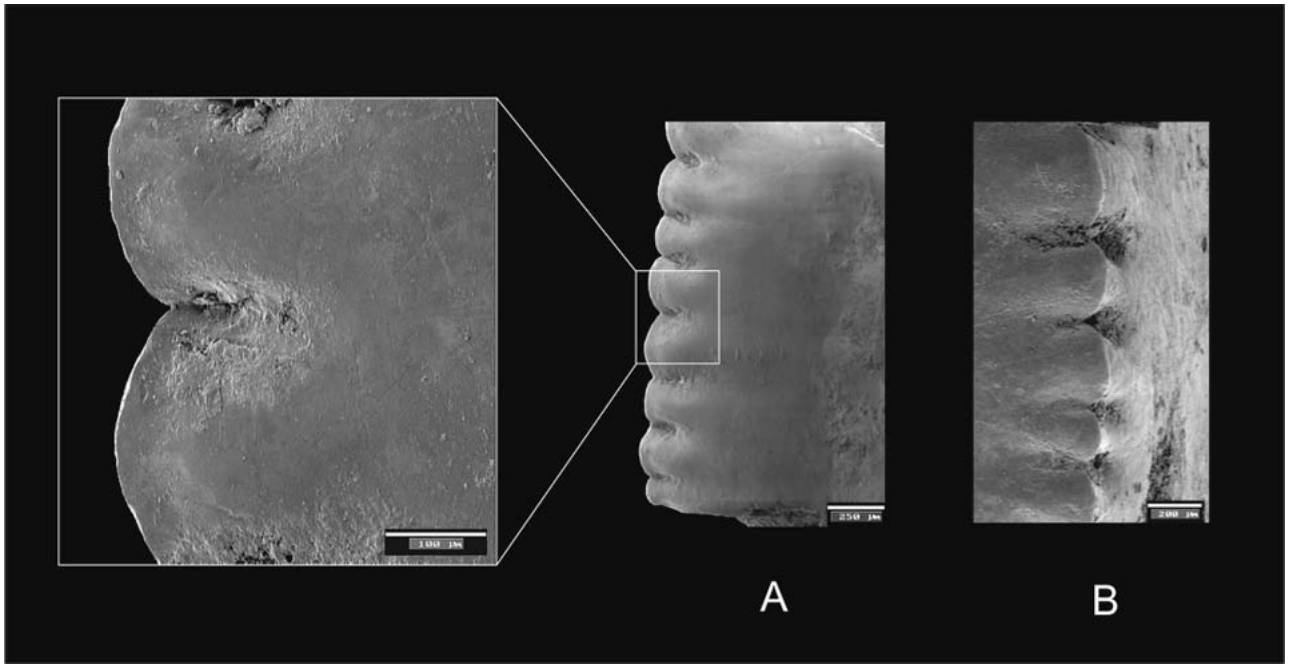

FIGURE 5. *Doratodon ibericus* sp. nov., Late Cretaceous of Valencia (Campanian), Spain. **A**, labial view of the serrations placed near the base of the crown. Inset shows an enlargement of denticles. Note the circular shape of the tips of the denticles and the narrow interdenticle spaces. **B**, fragmentary tooth. Distal? view of the carina showing increase in size of basal denticles. Scale in close-up view equals 0.1 mm. Scale bar in lower magnification figures equals 0.25 and 0.2 mm respectively.

cast doubt on Bunzel's generic determination and tentatively referred all the material, including a few other fragments, chiefly from a lower jaw, to a dinosaur, as *Doratodon*. Later, Nopcsa (1926) considered *Doratodon carcharidens* as crocodyliform, an interpretation followed by Mook (1934) and subsequent authors, although the affinity of *Doratodon* remains controversial (see below). Buffetaut (1979) reviewed the crocodylian remains from the Gosau Beds of Austria and described *D. carcharidens*. He listed the material of this taxon as follows: lower jaw, with complete right ramus and incomplete left ramus (holotype, IPUW 2349/57), fragmentary right maxilla (IPUW 2349/52), isolated teeth (IPUW 2349/58–61), and a parietal fragment (IPUW 2349/54). Buffetaut (1979) noted that the maxillary teeth were similar in size to those of the mandible. Thus he considered that the maxilla could belong to the same individual. The parietal was tentatively referred to *D. carcharidens*, but no argument was given to justify this attribution.

A revision of the material of *Doratodon carcharidens* allows us to reevaluate some anatomical characters. Firstly, the number of alveoli in the type specimen has been overestimated. Seeley (1881:672) pointed out that "it is difficult to count the exact number of sockets…but there were not fewer than fifteen." Buffetaut (1979) noted that the alveoli were not well preserved and gave an estimate of twenty tooth positions. In fact, the tooth row of *D. carcharidens* consists of twelve or, more probably, thirteen alveoli. This ambiguity is probably due to the singular preservation of the specimen. The right ramus of the mandible is almost complete, but the left one is broken caudally and has a number of aligned oval marks on the caudal region. Furthermore, these marks are located on the dorsal surface of the surangular and splenial. This excludes the possibility that they are alveoli. Comparison of the Austrian mandible with that from Spain permits an accurate estimation of the number and disposition of teeth along the tooth row (Fig. 6). Both share a reduced dentition, with

TABLE 1. Alveolar measurements for *Doratodon ibericus* sp. nov. and *Doratodon charcaridens.* Length: mesiodistal diameter of the alveoli; width: labiolingual diameter of the alveoli (asterisk indicates estimated width); distance: distance between two adjacent alveoli (always to the posteriorly following one); tooth: **E**, empty; **N**, not preserved; **R**, root only; **T**, complete tooth; **T-**, broken tooth; **T'**, partially erupted tooth. All measurements are in mm. (Following Rossmann et al., 2000).

Tooth position	1	2	3	4	5	6	7	8	9	10	11	12	13
Doratodon ibericus sp. nov. (left dentary)													
Preservation	T-	T	R	T	T	T'	E	T	T	T	E	———	———
Length	5.8	3.8	~4	9*	5.5	5.9	4.3	5.3	7.2	9.5	5.3	———	———
Width	4.6	3.2	?	5*	4.7	4.0	5.0	4.0	5.0	6.0	4*	———	———
Distance	1.5	3.1	?	1.5	<1	<1	4.4	1.0	2.5	1.1	———	———	———
Doratodon carcharidens (left dentary)													
Preservation	N	N	E	E	E	E	E	E	E	E	T-	E	N
Length	———	———	3.5	5	4.5	4	4	4	~3	4	5	~5	———
Doratodon carcharidens (right dentary)													
Preservation	N	R	N	T-	T-	E	E	E	N	T-	N	T-	E
Length	———	3	———	5	4	3.5	~3	4	———	5	———	4.5	~4

TABLE 2. Tooth and serration size measurements (in mm) of *Doratodon ibericus* sp. nov. Crowns of 3rd, 7th, and 11th teeth not preserved; crown of 6th tooth not totally erupted. **Abbreviations**: **Ac**, anterior (mesial) carina; **BW**, tooth basal width (Farlow et al., 1991); **DSDI**, dentical size difference index (Rauhut and Werner, 1995); **FABL**, fore-aft basal length (Currie et al., 1990); **Pc**, posterior (distal) carina; **SD**, serration density defined as number of serrations per 5 mm measured approximately halfway along the carina (Farlow and Brinkmann, 1987); **TCH**, tooth crown height (Farlow et al., 1991). Measurements in mm. Asterisk indicates estimated measurement.

Tooth	1	2	4	5	8	9	10
FABL	5.4	3.4	8*	5.2	4.7	6.5	9
BW	4.6	2.9	5	4.5	3.4	4.6	5.5
TCH	———	5	13*	8.5	5.7	9.2	12.7
FABL/BW	1.17	1.17	1.60	1.16	1.38	1.41	1.64
SD Ac	———	5	3	4	5.5	3	3
SD Ac	———	4.5	3	5	4	3	3
DSDI	———	1.1	1	0.8	1.4	1	1

11 teeth in the Chera dentary, and 12 or, more probably, 13, in *D. carcharidens*. The presence of a diastema between the second and third alveoli was not taken into account in previous works. The third alveolus of the right mandibular ramus is compressed.

The mandible of *Doratodon carcharidens* (dentary length from the rostral tip up to the dorsal suture with the surangular about 72 mm) is smaller than that of *D. ibericus* (105 mm, as reconstructed). When proportions between length and height of the dentaries are compared, it can be noticed that the Muthmannsdorf specimen has a more slender mandible than that of Chera (Table 3). In addition, the concavity of the dentary is more extreme in *D. carcharidens* than in *D. ibericus*. Size and shape might be indicative of a different ontogenetic stage of the Austrian specimen. Nevertheless, the bones are too profusely ornamented to be a juvenile. A relative decrease in the length of the alveolar ridge is common in larger individuals of *Alligator sinensis* (Cong et al., 1998). The relative length of each mandibular element changes during ontogeny. Thus, the proposal of a new species for the Spanish material is based on the overall morphology, size heterodonty, especially the caudal series, and, tentatively, a different number of teeth. An increase in crown height from the eighth to the tenth teeth is a diagnostic feature of the new species. In contrast, *D. carcharidens* shows alveoli similar in size, with the fourth, tenth, and eleventh alveoli slightly larger than the others (see Table 1). It should be noted that *Wanosuchus atresus*, a small crocodyliform from the ?Paleocene of China, has a mandible equivalent in size to that of *D. carcharidens* (mandibular total length 149 mm, and tooth row length up 62 mm), but the teeth differ notably in size and shape (Zhang, 1981).

A closer revision of *Wanosuchus atresus* should be made since it also exhibits a set of common features with *Doratodon*: the serrated and compressed dental crowns; the reduced number of teeth (13); the absence of the external mandibular fenestra and of a surangular caudal extension along the retroarticular process. *Wanosuchus* shows, furthermore, a double wave in the dentary tooth row, the fourth and eleventh teeth being the largest. However, the proportions of the mandibles of both species of *Doratodon*, regarding the relative length of the alveolar wave at the middle of the dentary, are more similar to each other than to those of *Wanosuchus* (Table 3 and Fig. 7).

As noted by Buffetaut (1979), the symphyseal area of *Doratodon carcharidens* reaches up to the eighth tooth. The splenial is not preserved in the Chera specimen, preventing the confirmation of this feature. The symphyseal area of both mandibles of *Doratodon* shows a similar contour and an analogous pattern of pits for the occlusion of premaxillary teeth. The symphyseal plane slopes slightly dorsorostrally and presents a concave subequal (as wide as long) surface. In *Bretesuchus* and *Bergisuchus*,

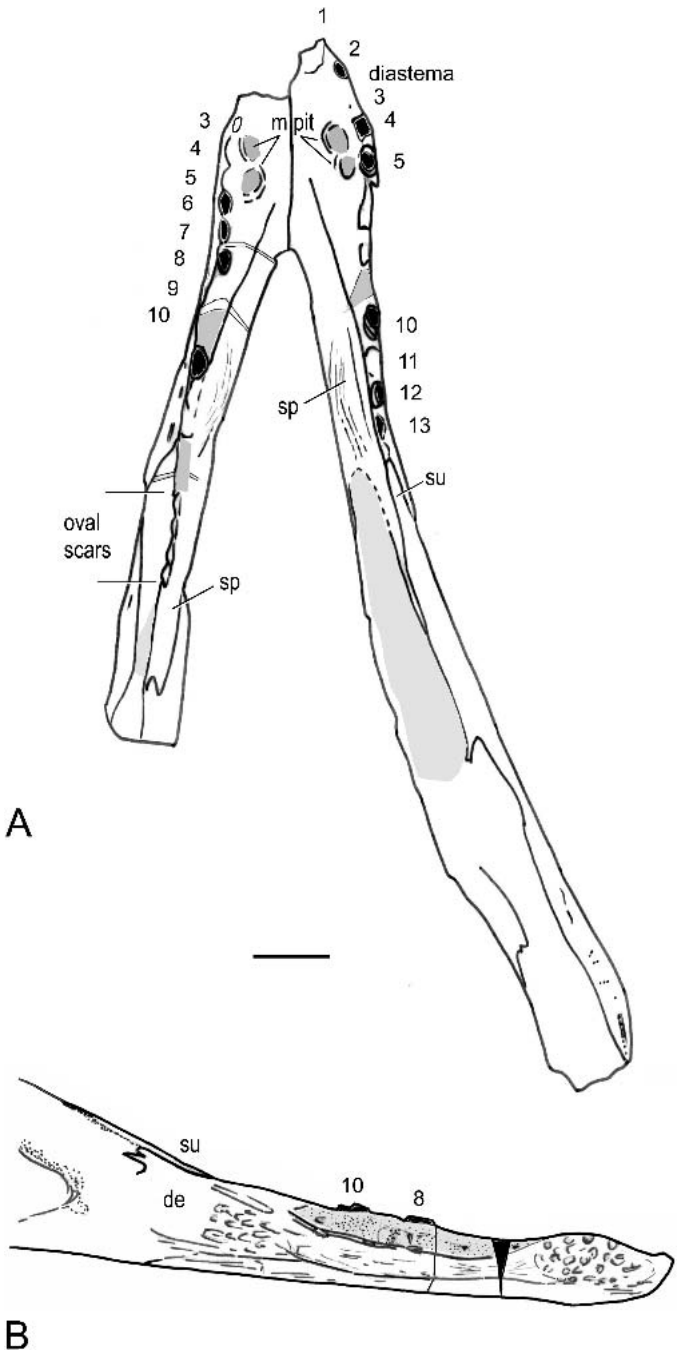

FIGURE 6. *Doratodon carcharidens* (IPUW 2349/57) from the Late Cretaceous (Early Campanian) of Muthmannsdorf, Austria. Mandible in dorsal (**A**) and right lateral (**B**) views. **Abbreviations**: **de**, dentary; **m. pit**, premaxillary dental pits; **sp**, splenial; **su**, surangular; **1** to **13**, number of teeth. Scale line equals 1 cm.

the symphyseal plane slopes abruptly dorsorostrally. Nonetheless, the slope is lesser in the Austrian specimen, the anterior margin is rather pointed, and the fourth and fifth alveoli are about the same size. The striking feature concerns the size of the pits, especially the caudal one (maximum diameter 6 mm) in both specimens. These pits are oval, and their major axes tend to converge medially. When these two traits (the symphyseal sloping and the pattern of occlusal pits) are considered together, a narrow but tall premaxilla may be inferred, recalling that of *Bergisuchus* (figured in Rossman et al., 2000:figs. 3, 6). Because

TABLE 3. Measurements of the dentaries of *Doratodon carcharidens, D. ibericus,* and *Wanosuchus atresus.* **Abbreviations**: **a**, maximum height in symphyseal area (distal edge of 4th alveolus); **b**, minimum height; **c**, height posterior to last alveolus; **d**, length of tooth row (rostral tip-distal edge of last alveolus); **e**, distance between maximum and minimum height in symphyseal area; **f**, distance between minimum height and distal edge of last alveolus. All measurements are in mm. Data for *Wanosuchus* taken from Zhang (1981:fig. 1).

	a	b	c	d	e	f	c/d	e/f
Doratodon carcharidens	11	8.2	11.1	50.3	9.3	27.1	0.22	0.34
Doratodon ibericus sp. nov.	25	18.5	27.5	79	17.3	40	0.35	0.43
Wanosuchus atresus	12.5	10.5	17.6	62.7	17.6	24	0.28	0.73

of the medial occlusion of the premaxillary teeth on the symphysis, the distance between the premaxillary teeth is very short (about 24 mm in the Chera mandible). Moreover, the trace of occlusal pits suggests the presence of an enlarged third or fourth premaxillary tooth. Occlusal pits at the symphyseal region are uncommon; the only other ziphosuchian showing this particular condition is *Baurusuchus*. In this taxon, a set of deep and long parasagittal grooves extend medial to the dental series from the third to the fifth teeth (Riff and Kellner, 2001).

The presence of two pairs of procumbent teeth (the first and second of the tooth row) is another common character of both the Muthmannsdorf and Chera specimens. Procumbent, anteriorly projected teeth occur in other ziphosuchians (e.g., in *Bretesuchus* and *Bergisuchus*, as well as in the Itaborai sebecid housed at the Earth Science Museum in Rio de Janeiro) and in *Wanosuchus*.

The maxilla IPUW 2349/52 of *Doratodon carcharidens* consists of a small fragment containing five teeth plus two small caudalmost alveoli. It includes the basal part of the serrated, laterally compressed crowns (Bunzel, 1871; Buffetaut, 1979). This is the only trait used to suggest that this specimen belongs to *D. carcharidens*. However, a combination of character states can be suggested to designate the maxilla to the same taxon, including the bone surface ornamentation and the deepness of the maxillary wall.

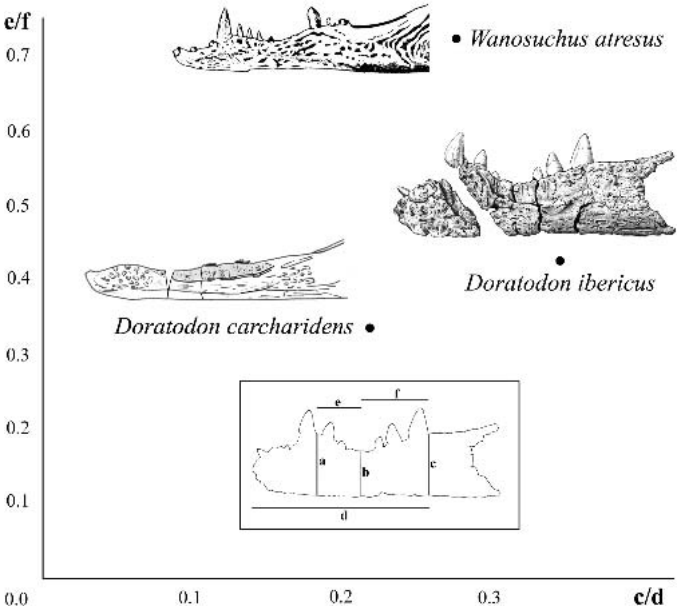

FIGURE 7. Metric description of the mandibles of *Doratodon carcharidens* (right ramus, reversed), *Doratodon ibericus* sp. nov. (left ramus), and *Wanosuchus atresus* (left ramus, taken from Zhang, 1981:fig. 1). All mandibles in lateral view. Drawings not to scale. Note differences in relative height and relative size of tooth-waves. The c/d index (height posterior to the last alveolus/length of the tooth row) tends to increase in adult individuals (Cong et al., 1998). Values of c/d index strengthen the proposal that *Doratodon carcharidens* represents an earlier ontogenetic stage than the Spanish specimen. Inset shows the measurements taken from dentaries (Table 3). Definitions of measurements are found in caption of Table 3.

PHYLOGENETIC RELATIONSHIPS

Nopcsa (1926) regarded *Doratodon carcharidens* as a short-snouted crocodyliform and suggested affinities with *Notosuchus*. Mook (1934) referred *Doratodon* to the Goniopholidae, an interpretation followed by subsequent authors (Huene, 1956; Steel, 1973). Kühn (1968) noted similarities in the tooth form between *Doratodon* and sebecosuchians. Buffetaut (1979) regarded *Doratodon* as closely allied to *Hsisosuchus* from the Late Jurassic of China and referred it to the Hsisosuchidae. Nevertheless, Wu et al. (1994) cast doubt on the close affinities between *Doratodon* and *Hsisosuchus*, and concluded that the latter is a primitive mesoeucrocodylian not closely related to the Sebecidae. The type species of *Doratodon* clearly differs from *Hsisosuchus* in the presence of a suborbital fenestra (closed in the Chinese crocodile) and in the participation of the lacrimal in the antorbital fenestra (Li et al., 1994). Furthermore, the external mandibular fenestra of *Hsisosuchus* is opened, and the surface of the dentary is not ornamented.

Phylogenetic relationships among crocodyliforms were analyzed by Benton and Clark (1988) and Clark (1994). The results of those analyses show that the monophyly of Sebecosuchia is debatable. However, recent phylogenetic analyses including more taxa (Ortega et al., 2000; Sereno et al., 2001; Pol, 2003) support the hypothesis that the Sebecosuchia seem to be a monophyletic clade.

The phylogenetic relationships of *Doratodon* are discussed here in the context of a recent cladistic analysis of Crocodylomorpha (Ortega et al., 2000). The position of *Doratodon* was evaluated according to the character matrix, including mandibular and maxillary characters of *D. carcharidens* and *D. ibericus* (see Appendix). The list of characters and the distribution of character states are summarized by Ortega et al. (2000:appendices 1–2). The data set includes 184 characters in 32 crocodylomorph taxa. Two new genera (*Doratodon* and the monospecific genus *Bergisuchus* from the middle Eocene of Germany) and two new characters (see Appendix) were added to the original matrix. Using the branch and bound method of PAUP 3.1.1 (Swofford, 1993), the phylogenetic analysis yielded four most-parsimonious trees (see strict consensus in Fig. 8).

The result of the analysis shows that *Doratodon* is a member of the Ziphosuchia, a clade which involves *Notosuchus*, *Libycosuchus,* and Sebecosuchia (sensu Ortega et al., 2000). This latter clade is defined as (*Baurusuchus* + (*Iberosuchus* + (*Sebecus* + (Itaborai crocodile + *Bretesuchus*)))). As determined in the result, the node Ziphosuchia shows the same topology and is diagnosed by the same unambiguous synapomorphic characters as in the work of Ortega et al. (2000). The fragmentary nature of the material of *Doratodon* makes difficult its comparison with other members of Ziphosuchia. Only two unambiguous characters from those used by Ortega et al. (2000) to diagnose Ziphosuchia could be checked in *Doratodon carcharidens*, and even those have a certain degree of homoplasy within this clade.

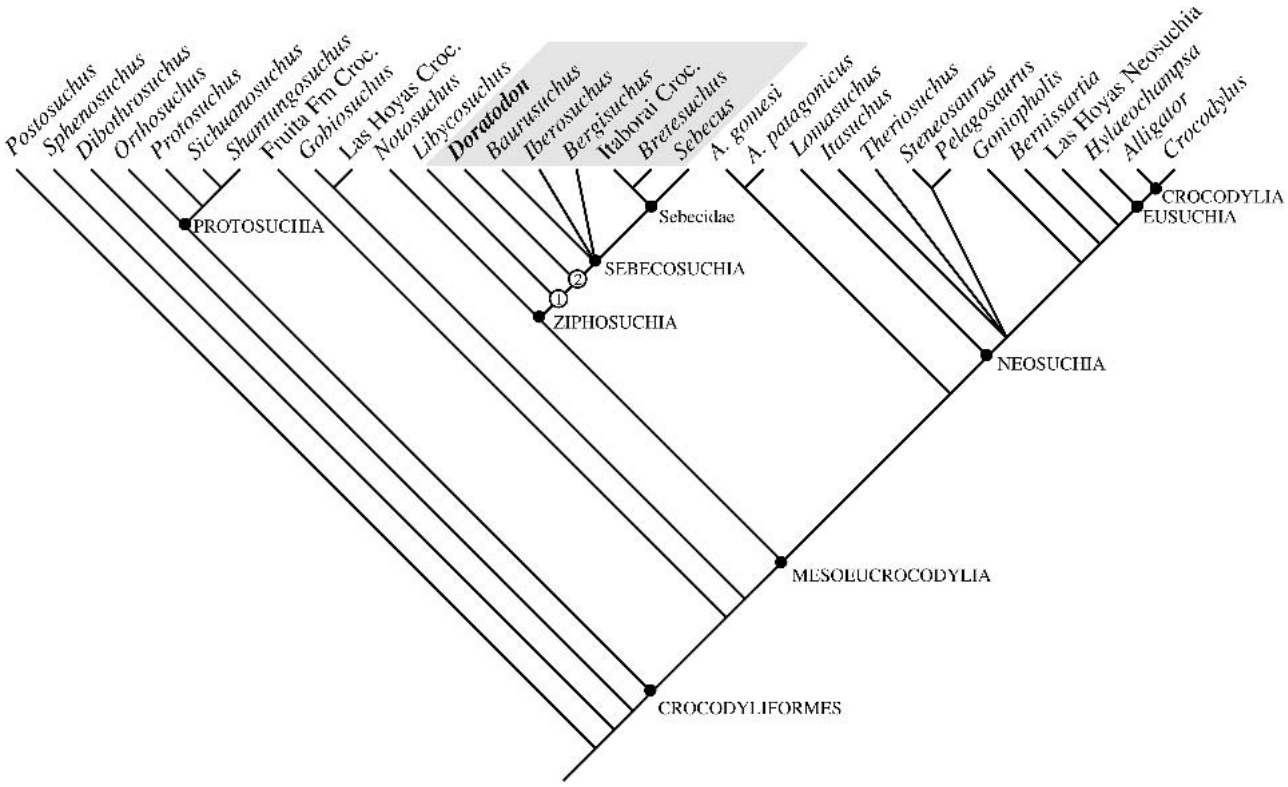

FIGURE 8. Cladogram showing the phylogenetic position of *Doratodon*. The depicted cladogram shows a strict consensus tree among four equally parsimonious trees (with a tree length of 419 steps, consistency index 0.461, and retention index 0.741), using branch and bound method (TBR with 80 replicates) of PAUP 3.1.1. Five outgroups were considered: *Postosuchus*, *Sphenosuchus*, *Dibothrosuchus*, *Protosuchus* and *Alligator*. Strict consensus tree shows unresolved internal relationships of Sebecosuchia. *Bergisuchus* is placed either as the sister taxon of Sebecosuchia or as the sister taxon of Sebecidae. (*Pelagosaurus* + *Steneosaurus*) appear also as a conflicting clade within Neosuchia. The phylogenetic result places *Doratodon* as the sister group of Sebecosuchia (sensu Ortega et al., 2000).

These are as follows: the reversion of character #18, in which the last maxillary tooth is placed behind the palatal fenestra, and character #92, convex transversal section of splenial.

The high number of missing data coded in *Doratodon* probably affects its basalmost position within the less inclusive clade Sebecosuchia. *Doratodon* shares with Sebecosuchia (including *Bergisuchus*) several features concerning the shape and implantation of teeth (i.e., character #100, mesial and distal margins of tooth crowns with denticulate carinae; character #106, tip of dentary tooth crowns caudally curved; character #19, tooth implantation in isolated alveoli; see Fig. 8). The maxillary fragment of *Doratodon* does not provide much phylogenetic information (except for character #156, enlargement of second or third maxillary tooth); rather, its position on the cladogram is based on mandibular traits (i.e., character #89, splenials broad and robust behind symphysis; and character #184, sculpturing of lateral surface of dentary based on development of longitudinal depression). The absence of the mandibular fenestra externa is an autapomorphy of *Doratodon* in the context of Ziphosuchia.

The fragmentary information of *Doratodon* conditions its phylogenetic position. The small portion of maxilla, as preserved, prevents the evaluation of other traits. For instance, along the maxillary dental series, the first preserved tooth is the largest of the series, double the size of the rest. Buffetaut (1979:fig. 2) interpreted this tooth as the fifth (regarding the potential preservation of an orbital rim). Although an accurate position of the maxillary fragment within the snout is difficult, this large tooth should occupy an anterior position (at least the anterior third of the snout). It is not rejected that further analysis and discoveries would place *Doratodon* within Sebecosuchia, due to the resemblance of the maxilla to that of *Sebecus* (Colbert, 1946:fig. 2), with a straight alveolar edge and a deep vertical wall.

Two alternative solutions place *Bergisuchus* either as the sister taxon of Sebecosuchia or as the sister taxon of Sebecidae (sensu Ortega et al., 2000). In the first solution, the clade is diagnosed by character #183, presence of hypertrophied mandibular tooth. *Bergisuchus* as a member of Sebecosuchia is shown by the presence of a premaxillo-maxillary notch (character #14), and enlargement of the second or third maxillary tooth (character #156). The other most-parsimonious solution shows *Bergisuchus* as the sister taxon of the Sebecidae, based on the existence of a ventral edge of the premaxilla associated with a strongly concave anterior dorsal contour of the dentary (character #10). This character will support the reiterated suggestions assessing *Bergisuchus* as a close relative of *Sebecus* (see Rossmann et al., 2000 for a historical summary).

BIOGEOGRAPHICAL IMPLICATIONS

Sebecosuchians are fairly well-known in the Late Cretaceous (*Baurusuchus*) and the Tertiary of South America (*Sebecus*, *Bretesuchus*, Itaborai form) and Africa (*Eremosuchus*). In the Tertiary of Europe there is also good evidence of bizarre sebecosuchians such as *Iberosuchus macrodon* (Ortega et al., 1996) and *Bergisuchus dietrichbergi* (Rossman et al., 2000). Although *Doratodon* is too fragmentary to ascertain its relationship with Sebecosuchia, it confirms the presence of Ziphosuchia in the Late Cretaceous of Europe. This suggests a greater diversity within this clade than expected previously, and a wider distribution in time and space as well. Therefore, the presence of new

ziphosuchian species in other continents during the Late Cretaceous is not unlikely. This could be the case for *Ricardoestesia isosceles*, a tooth-based species from the Late Cretaceous of the United States (Sankey, 2001; Sankey et al., 2002). Although described originally as a theropod, the teeth of *R. isosceles* seem more crocodyliform than dinosaurian (see Legasa et al., 1994), and their identification as a sebecosuchian should not be excluded.

ACKNOWLEDGMENTS

We thank Prof. Dr. G. Rabeder and Mag. Dr. K. L. Rauscher (IPUW, Vienna) for access to specimens in their care. We are also grateful to F. Ortega (Madrid) for useful suggestions and Dr. M. Feist (Montpellier) for providing the age of the Chera locality based on charophytes. Financial support for research and field work was provided by the following institutions: The Jurassic Foundation, Generalitat Valenciana, Ministerio de Ciencia y Tecnología (project BTE2001–0185-C02–01) and Ministerio de Asuntos Exteriores (project HU2000–0004). Financial support for the research project of the second author (X.P.S.) has been provided by the Ramon y Cajal Program from the Ministerio de Ciencia y Tecnología of Spain. We would also like to thank all the students, colleagues, and friends who have accompanied us in field seasons, collecting a large number of fossil specimens. The quality of the manuscript benefited from scientific and linguistic comments from two anonymous reviewers.

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Submitted 20 October 2003; accepted 27 July 2004.

APPENDIX 1

Data matrix is founded on the one provided by Ortega et al. (2000), with 182 characters and 30 taxa. Values in data matrix: missing data (?); primitive (0); derived (1). For the present analysis, two new taxa and characters have been incorporated. Character score for the genus *Doratodon* includes separate information for *Doratodon carcharidens* and *D. ibericus.* The holotype of *D. carcharidens* was revised by A. D. Buscalioni. *Bergisuchus dietrichbergi* (middle Eocene from Messel, Germany) has been coded according to specimen HLMD-Me-7003.

New characters—Character #183 as defined by Tykosky et al. (2002): Anterior dentary teeth opposite premaxilla-maxilla contact no more than twice length of other dentary teeth (0) or more than twice length (1). Character #184 as defined by Ortega et al. (1996): Lateral surface of dentary: without longitudinal depression (0), with longitudinal depression (1). This character does not concern the sculpture of the bone.

Conflicting Characters in *Doratodon carcharidens*—This species is an enigmatic Late Cretaceous crocodyliform. As a matter of fact, its phylogenetic relationships have never been clear because of its incompleteness and its singular combination of character states, "a mixture of primitive and specialized" (Buffetaut, 1979:94). Some authors view *D. carcharidens* as a putative member of Neosuchia. The phylogenetic position of this crocodile depends on how character states are interpreted, combining the information provided by mandible and maxilla. In the present study it is shown that a different combination of states placed *D. carcharidens* within Ziphosuchia. Below are summarized those features in order to justify their character score.

Doratodon carcharidens possesses a thick dentary, orthogonal in section, with a planar and wide ventral surface. The dentary lateral surface is flat and even slightly concave. Character #81 (mandibular compression: compressed, 0; dentary transversely expanded, and with convex lateroventral surface, 1) has been coded as primitive because the type lacks a curved convex surface of the dentary. The number of teeth has been long debated; up to 20 has been suggested. This character is important because a lesser number of teeth would imply the extension of the dentary beyond the tooth row, with a dorsal ascending projection (the derived condition of character #83 shared by ziphosuchians). Figure 6 schematizes the interpretation of the above characters. With the maxilla, the main character concerns the position of the enlarged teeth at the anterior part of the maxilla (character #156, prominent second or third alveoli: 1; fourth or fifth alveoli: 2). The first preserved tooth in the maxilla IPUW 2349/52 is the largest (5.2 mm versus 4.2 mm the second). The score in *D. carcharidens* proposed in our data matrix (1) is based on the straight alveolar edge of the maxilla, and the increasing deepness of the lingual alveolar wall toward the anterior preserved alveoli.

APPENDIX 2

Character-taxon matrix used for phylogenetic analysis.

Doratodon
0???0?????????0??0000??????1?????????????????????????????????????
?????01???????1?2001010?11001?000???00000?0?????????????????????
???000?????????????????????1???01??????????????0??????????01

B e r g i s u c h u s
0???0010?1??01???000?00????10?????????????????????????????????????
?????011??????1??001100?11??1??00???0?0001?????????????????????
???000?????????????????????1???01?????0?00???2?10??0???????11

Postosuchus (only characters 183 and 184; see Ortega et al., 2000:appendix 2).
0?

Sphenosuchus
??

Dibothrosuchus
??

Protosuchus
10

Orthosuchus
00

Sichuanosuchus
1?

Shantungosuchus
??

Gobiosuchus
10

Las Hoyas Croc
00

Fruita Fm Croc
10

Notosuchus
00

Baurusuchus
11

Itaborai Croc
01?

Bretesuchus
1?

Sebecus
01

Iberosuchus
11

Libycosuchus
00

Araripesuchus gomesi
00

Araripesuchus patagonicus
00

Lomasuchus
1?

Itasuchus
00

Theriosuchus
00

Pelagosaurus
00

Steneosaurus
0?

Goniopholis
00

Bernissartia
00

Las Hoyas Neosuchian
00

Hylaeochampsa
??

Alligator
00

Crocodylus
00

Unambigous synapormorphies diagnosing Ziphosuchia and its inclusive clades are:
Ziphosuchia. Characters: #18, last maxillary tooth cranial to anterior edge of palatine fenestra (reversed in *Doratodon carcharidens*); #53, medial quadrate condyle expanded ventrally; #92, convex transverse section of splenial; #127, radiale as long as wide; #148, coracoidal shaft rod-like; and #177, primary pterygoidean palate with deep parasagittal depressions.

Node 1. (*Libycosuchus* + (*Doratodon* + (*Bergisuchus*, Sebecosuchia))). Characters: #42, outer surface of squamosal dorsally oriented; #171, lacrimal descending lateral process laminar; #173, anterior jugal branch much deeper than caudal one. None of the proposed synapomorphies can be checked in *Doratodon*.

Node 2: (*Doratodon* + (*Bergisuchus*, Sebecosuchia)). Characters: #89, splenials broad and robust behind symphysis; #100, mesial and distal margins of tooth crowns with denticulate carinae; #106, tips of dentary tooth crowns caudally curved (these traits are unknown in *Libycosuchus*); #19, tooth implantation in isolated alveoli; # 156, enlargement of second or third maxillary teeth; and #184, sculpturing of lateral surface of dentary based on development of longitudinal depression.

Sebecosuchia. Characters: #14, presence of premaxillo-maxillary notch (unknown in *Doratodon*); #156, enlargement of second or third maxillary tooth; and #90, big, slot-like foramen intramandibularis oralis (unknown in *Bergisuchus*).

Solution 1:
(*Bergisuchus* + Sebecosuchia). Character #183, hypertrophied mandibular tooth.
Sebecosuchia. Characters: #8, premaxilla-maxillary suture in lateral view zig-zag shaped; #24, caudal tip of nasals separated by anterior sagittal projection of frontal.

Solution 2:
(*Baurusuchus* + (*Iberosuchus* + (*Bergisuchus* + Sebecidae))).
Characters: #90, foramen intermandibularis oralis big, slot-like (not observed in *Bergisuchus*); #183, hypertrophied mandibular tooth.
(*Iberosuchus* + (*Bergisuchus* + Sebecidae)). Characters: #44, quadrate inclination less than 45 degrees; #85, postcaniniform dentary teeth almost homodont in size; and #135, caudal branch of quadrate at least as long as broad.

(*Bergisuchus* + Sebecidae). Characters: #10, ventral edge of premaxilla deep, and anterior dorsal contour of dentary strongly concave.