

**REINTERPRETATION AND NEW DENOMINATION
OF *ATACISAURUS CRASSIPRORATUS*
(MIDDLE EOCENE ; ISSEL, FRANCE)
AS CF. *IBEROSUCHUS*
(CROCODYLOROMORPHA, METASUCHIA)**

FRANCISCO ORTEGA, ANGELA D. BUSCALIONI & ZULMA GASPARINI

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ABSTRACT - The holotype of *Atacisaurus crassiproratus* ASTRE, 1931 (Middle Eocene ; Issel, France) is herein reinterpreted and attributed to cf. *Iberosuchus*. The holotype of *A. crassiproratus* consists of a fragment of a mandible that Astre (1931) assigned to an eusuchian crocodile. However, the combination of characters that we have recognized in this mandible allows to consider it as a member of the Metasuchia clade (*sensu* Benton & Clark 1988). Furthermore, the specimen from Issel shows a similar morphology and the same combination of character states than those of several specimens from the middle Eocene site of Caenes (Duero basin, Salamanca province, Spain). We consider that both the Issel and Caenes mandibles belong to the same taxon. The mandibles of all these specimens, attributed to cf. *Iberosuchus*, share with other metasuchians the following combination of apomorphic traits : a dorsal prolongation of the dentary ascending behind the tooth row ; the presence of a lateral depression on the dentary ; robust splenials ; the presence of a big slot-like *foramen intramandibularis oralis* ; and an anteroposteriorly elongated glenoid fossa of the articular. These specimens are also compared with the Eocene African species *Eremosuchus elkoholicus* BUFFETAUT, 1989. The phylogenetic relationships, based on mandibular characters, of cf. *Iberosuchus* with other taxa previously associated to this genus, such as the *Sebecosuchia* SIMPSON, 1937 (*sensu* Gasparini *et al.* 1991) and the Trematochampsidae Buffetaut, 1974 (*sensu* Buffetaut 1986, 1988, 1989), as well as with other members of the Metasuchia and Neosuchia clade, are discussed.

KEYWORDS : CROCODYLOROMORPHA, METASUCHIA, EOCENE, FRANCE, SPAIN, EUROPE.

RÉSUMÉ - L'holotype de *Atacisaurus crassiproratus* ASTRE, 1931 (Éocène moyen ; Issel, département de l'Aude, France) est réinterprété et son rapprochement de cf. *Iberosuchus* est proposé. L'exemplaire type de *Atacisaurus crassiproratus* est un fragment de mandibule que Astre (1931) a attribué à un crocodile eusuchien. L'ensemble des caractères relevés sur cette mandibule permet cependant de la considérer comme appartenant au clade Metasuchia (*sensu* Benton & Clark 1988). Le spécimen d'Issel est morphologiquement comparable et présente la même combinaison d'états de caractères que certains restes de mandibules provenant du gisement de l'Éocène moyen de Caenes (Bassin du Duero, Salamanca, Espagne). Nous considérons donc qu'ils appartiennent tous au même taxon. La mandibule de *A. crassiproratus* partage avec les autres Metasuchia la combinaison suivante d'apomorphies : la présence d'un prolongement dorsal du dentaire s'élevant en arrière de la rangée dentaire, de spléniaux élargis, d'un *foramen intramandibularis oralis* grand et allongé et d'une fosse glénoïde allongée antéro-postérieurement. Cf. *Iberosuchus* est aussi comparé à l'espèce africaine de l'Éocène *Eremosuchus elkoholicus* BUFFETAUT, 1989. Les relations phylogénétiques de cf. *Iberosuchus* avec des taxons précédemment associés à *Iberosuchus* tels que les *Sebecosuchia* SIMPSON, 1937 (*sensu* Gasparini *et al.* 1991), et les Trematochampsidés Buffetaut, 1974 (*sensu* Buffetaut 1986, 1988, 1989) et avec des crocodiles faisant partie des clades Metasuchia et Neosuchia sont discutées.

MOTS-CLÉS : CROCODYLOROMORPHA, METASUCHIA, ÉOCÈNE, FRANCE, ESPAGNE, EUROPE.

RESUMEN - Se propone una reinterpretación del holotipo de *Atacisaurus crassiproratus* ASTRE, 1931 (Eoceno medio; Issel, Departamento de Aude, Francia) y su nueva asignación como cf. *Iberosuchus*. El ejemplar tipo de *A. crassiproratus* está constituido por un fragmento de mandíbula que fue atribuido por Astre (1931) a un cocodrilo eusuquiano. Sin embargo, el conjunto de caracteres que pueden reconocerse sobre esta mandíbula permiten considerarla como perteneciente a un miembro del clado Metasuchia (*sensu* Benton & Clark, 1988). El ejemplar de Issel es morfológicamente similar y muestra la misma combinación de caracteres que algunos otros ejemplares del yacimiento del Eoceno medio de Caenes (Cuenca del Duero, Salamanca, España). La mandíbula de *A. crassiproratus* comparte con otros Metasuchia algunos caracteres apomórficos como : la prolongación postero dorsal del dentario elevándose por encima de la serie dentaria, un esplenial robusto, un *foramen intramandibularis oralis* grande y alargado y la fosa glenoidea del articular alargada antero posteriormente. Se comparan dichos ejemplares con la especie del Eoceno africano *Eremosuchus elkoholicus* BUFFETAUT, 1989. Se discuten las relaciones filogenéticas de estos especímenes con otros taxones con los que fue previamente asociado *Iberosuchus*, como los *Sebecosuchia* SIMPSON, 1937 (*sensu* Gasparini *et al.* 1991) y los Trematochampsidae Buffetaut 1974 (*sensu* Buffetaut 1986, 1988, 1989), y con otros miembros de los clados Metasuchia y Neosuchia.

PALABRAS CLAVE : CROCODYLOMORPHA, METASUCHIA, EOCENO, FRANCIA, ESPAÑA EUROPA.

INTRODUCTION

The classic middle Eocene locality of Issel (Aude Department, France) (Fig. 1) has yielded abundant fossil crocodiles. The taxonomic status of these crocodiles were largely discussed by several XIX century French paleontologists (see Astre, 1931). These crocodiles were listed as *Crocodylus Dodunii* GRAY, 1831 and as an *incertae sedis* reptile *Isselosaurus Doduni* FILHOL, 1888. Astre (1931) examined specimens from the Issel and other related sites, gathering them into two species of a new genus : *Atacisaurus glareae* and *Atacisaurus crassiproratus*, and referring them to the Crocodylidae.

The type species of *Atacisaurus*, *A. glareae*, was based on the anterior portion of a mandible from Laure (Aude Department) (Fig. 1) that, unfortunately, seems to be lost (Sudre, personal communication). Astre also assigned to *A. glareae* an unprepared skull from Issel, housed in the Muséum d'Histoire Naturelle de Toulouse, and labelled as : ["*Crocodylus dodunii* (*nomen nudum* : Astre 1931) ; Issel (Aude) ; Henri de Séverac 1873 ; *Atacisaurus glareae* Astre ; Lutétien supérieur ; Issel (Aude) ; Coll. Noulet"]. Hence, the latter specimen could be designated as the species lectotype if, after preparation, reveals new information to compare it with the Astre (1931) diagnosis based on the type.

The second species of *Atacisaurus*, *A. crassiproratus*, is founded on an anterior portion of mandible. Astre (1931) proposed its inclusion in this genus on: the enlargement of the mandibular symphysis, and the variation of the tooth morphology along the dentary. However, the original description is not totally accurate, and relevant features were omitted. Later revisions considered *A. crassiproratus* as a synonymous of *Asiatosuchus germanicus* BERG, 1966 (Berg & Crusafont 1970 ; Vasse 1992), founding the synonymy just on a similar mandibular symphysis length. However, there is no other feature shared to support the synonymy.



FIGURE 1 - Main western European Eocene localities with non eusuchian ziphodont crocodiles record : 1) "Canteras de Corrales", Zamora province, Spain ; 2) "Caenes"-Cabrerizos, Salamanca province, Spain ; 3) Mazaterón, Soria province, Spain ; 4) Prepyrenean sites : "Capella", and "Torsalet del Morral" (Huesca province) ; "Les Saleres" and "Les Badies" (Lérida province), Spain ; 5) Southern France sites: La Livinière, and Issel, Laure, Castrais, Massalle and Lautrec (Aude Department, France) ; A) "Vale Furado"-Nazaré, Leiria Province, Portugal ; B) Messel, Hesse, Germany. *Principaux gisements éocènes d'Europe occidentale ayant fourni des restes de crocodiles ziphodontes non eusuchiens* : 1) "Canteras de Corrales", Zamora, Espagne ; 2) "Caenes"-Cabrerizos, Salamanca, Espagne ; 3) Mazaterón, Soria, Espagne ; 4) Gisements prépyrénéens : "Capella" et "Torsalet del Morral" -Huesca, Espagne ; "Les Saleres" et "Les Badies" -Lérida, Espagne ; 5) Gisements du sud de la France : La Livinière et Issel, Laure, Castrais, Massalle et Lautrec (Aude, France) ; A) "Vale Furado"-Nazaré, Leiria, Portugal ; B) Messel, Hesse, Allemagne.



FIGURE 2 - Cf. *Iberosuchus* (holotype of "*Atacisaurus crassiproratus*"). Lateral view. (Negatives from Muséum d'Histoire Naturelle, Toulouse). Scale bar = 10 cm. *Vue latérale.*

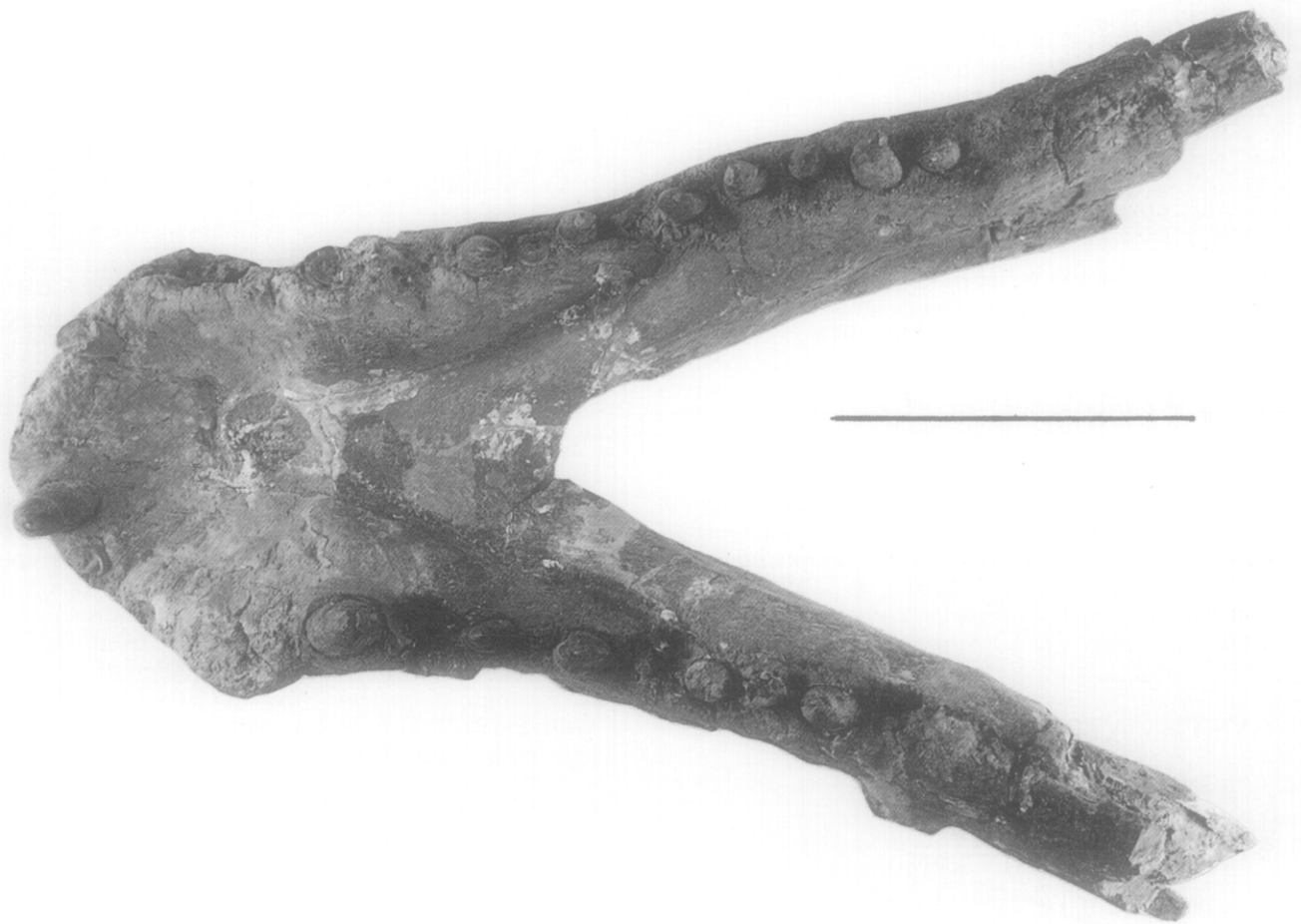


FIGURE 3 - Cf. *Iberosuchus* (holotype of "*Atacisaurus crassiproratus*"). Dorsal view. (Negatives from Muséum d'Histoire Naturelle, Toulouse). Scale bar = 10 cm. *Vue dorsale.*

After a preliminary preparation, we have revised the holotype of *A. crassiproratus*. The specimen exhibits a combination of interesting features that are comparable to those of several specimens previously assigned to the Iberian crocodile *Iberosuchus macrodon* ANTUNES, 1975 (Martín de Jesús *et al.* 1987 ; Ortega & Buscalioni 1992) (Fig. 1), and this is the reason to describe them together. *Iberosuchus*, from the middle Eocene site of Vale Furado (Nazaré, Portugal), was originally associated to the South American *Sebecosuchia* SIMPSON, 1937, because of its primitiveness (Antunes 1975). *Iberosuchus* was certainly treated as an uncommon form of the European Tertiary, and the subsequent literature (Molnar 1981 ; Gasparini 1984) has considered it as an *incertae sedis* genus, due to the scarcity of the available material. Buffetaut (1988) has contemplated *Iberosuchus* as a Trematochampsidae Buffetaut 1974, but this family is also a debatable taxon with an uncertain phylogenetic position (Gasparini *et al.* 1991). The trematochampsids as defined by Buffetaut (1986, 1988, 1989) include the African genera and species *Trematochampsia* (*T. taqueti* BUFFETAUT, 1974 and *T. oblita* BUFFETAUT & TAQUET, 1979), *Eremosuchus elkoholicus* BUFFETAUT, 1989, the South American *Peirosaurus torminii* PRICE, 1955, *Itasuchus jesuinoi* PRICE, 1955, and the European *Bergisuchus dietrichbergi* KUHN, 1968 and *Iberosuchus*.

The holotype of *Atacisaurus crassiproratus* is herein redescribed in comparison with two fragmentary mandibles from the Spanish Eocene, discussing their taxonomic status. An evaluation of mandibular characters provides a first approach to the phylogenetic relationships of the here considered cf. *Iberosuchus* from Issel and Spain within the Metasuchia clade. This analysis includes some putative relatives such as the trematochampsids (*Itasuchus* and *Amargasuchus* CHIAPPE, 1988 excluded) and the Peirosauridae Gasparini, 1982 (*sensu* Gasparini *et al.* 1991), as well as some *Sebecosuchia* such as *Baurusuchus pachecoi* PRICE, 1945 and *Sebecus icaeorhinus* SIMPSON, 1937.

SYSTEMATIC PALEONTOLOGY

CROCODYLOMORPHA Walker, 1970 (*sensu* Benton & Clark, 1988).

METASUCHIA BENTON & CLARK, 1988.

?SEBECOSUCHIA SIMPSON, 1937 (*sensu* Gasparini *et al.* 1991)

cf. *Iberosuchus* ANTUNES, 1975.

Referred specimens - The mandible (dentaries + splenials) lacking its posterior part, described by Astre (1931) as the holotype of *Atacisaurus crassiproratus* (Figs 2, 3). It is housed in the MHNT and labelled as : ["*Atacisaurus crassiproratus* (= *Isselosaurus dodunii*, Gray propose). Pièce figure Bulletin de la Société d'Histoire naturelle de Toulouse, 1931. Mandibule décou-

verte par E. Cuguillère, 1893"]. The specimen comes from the classic "Lutetian" fossil site of Issel (Aude Department, France) (Fig. 1), dated as Middle Eocene -level of reference in the correlation tables of the European Paleogene : Mp 14- (Russell *et al.* 1982 ; Franzen & Haubold 1986 ; Schmidt-Kittler 1987). Also considered as cf. *Iberosuchus* are : STUS 349 (Fig. 4), a dentary lacking the symphyseal area, probably belonging to a juvenile individual ; STUS 13701 (Fig. 5), a dentary, anteriorly and posteriorly incomplete, with part of the splenial attached anteriorly; and STUS 1259 (Fig. 6), a left articular fragment lacking the retroarticular process. These specimens come from the Caenes site (Duero basin, Salamanca province, Spain) (Fig. 1), dated as Middle Eocene-level of reference, regarding the correlation tables of the European Paleogene : Mp 16 - (Cuesta 1991 ; Schmidt-Kittler 1987).

Institutional abbreviations - MHNT : Muséum d'Histoire Naturelle de Toulouse, Toulouse, France. STUS : Sala de las Tortugas, Universidad de Salamanca, Salamanca, Spain.

Description - The specimen from Issel is the most complete one, but it will require further preparation for finer details. It is comparatively described with the mandibular fragments from the Caenes outcrop, emphasizing their dissimilarities. The mandibles are laterally compressed and high. The symphysis reaches posteriorly the level of the 8th alveoli in the Issel specimen. The symphysis is spoon-like, with its maximum width at the level of the 4th tooth. Seen from above the anterior outline is gently rounded back to the 4th tooth, behind which the mandible is slightly constricted transversely. In lateral view, the dorsal outline of the dentary is slightly concave, forming a wave from the 4th tooth towards the posterior end. The splenial comprises one-half of the length of the symphysis. The Spanish specimens lack much of the symphysis : STUS 13701 begins at the 4th tooth, and STUS 349 at about the 7th tooth.

The dentaries are all slightly sculptured, with a vermiciform and striated ornamentation. The STUS 349 (Fig. 4.2) specimen shows in detail some features of the dentary that are not exposed on the other specimens. Below the upper portion of the dentary in lateral view, a series of vascular foramina opens backwards. A groove runs backwards from the last foramen, subparallel to the dorsal edge of dentary, as is commonly the case in Crocodylomorpha (Walker 1990). The dentary displays a longitudinal depression on its lower lateral half, which is most evident anteriorly (also visible in STUS 13701, pl. 4). A wrinkled surface for attachment to the surangular occurs laterodorsally. A probable sutural area for the angular is exposed ventrolaterally. The posterior end of the dentary, which would have been concealed by the surangular, is broken off. Posteriorly, the lower edge of the dentary exhibits the dorsal border of the external mandibular fenestra (Fig. 7).

In medial view, the anterior upper wall below the alveoli is vertical, forming a subtriangular area. A

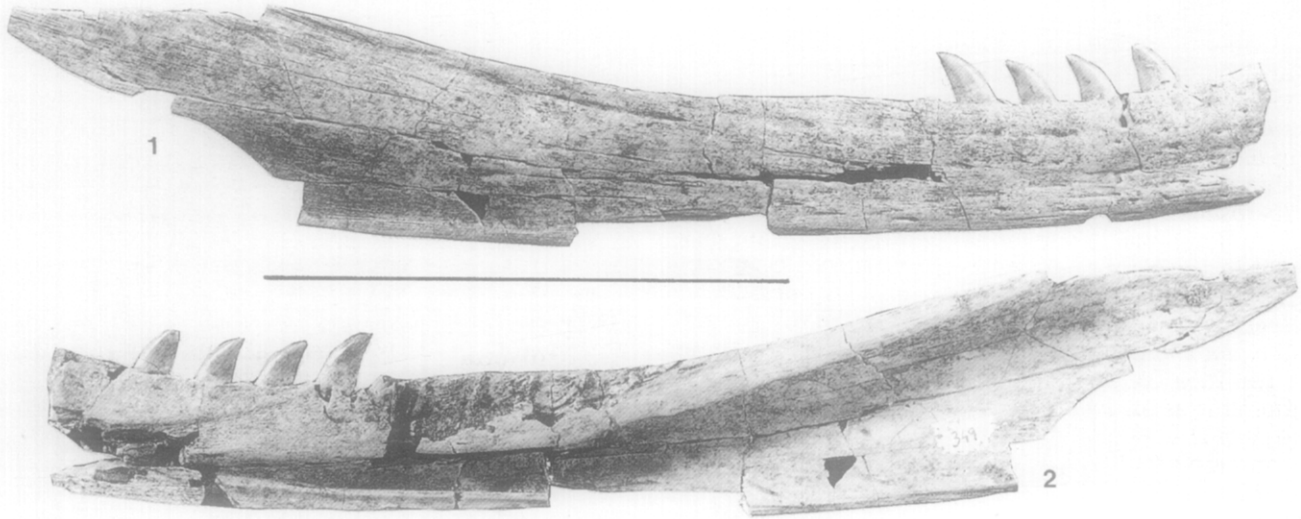


FIGURE 4 - Cf. *Iberosuchus* (STUS 349). A relatively small right dentary attributed here to a juvenile specimen (Eocene) : "Caenes"-Cabrerizos site, Salamanca province, Spain). (1) lateral and (2) medial views. Scale bar = 10 cm. *Un dentaire droit relativement petit, attribué ici à un exemplaire juvénile (Éocène moyen). (1) Vue latérale ; (2) Vue médiale.*

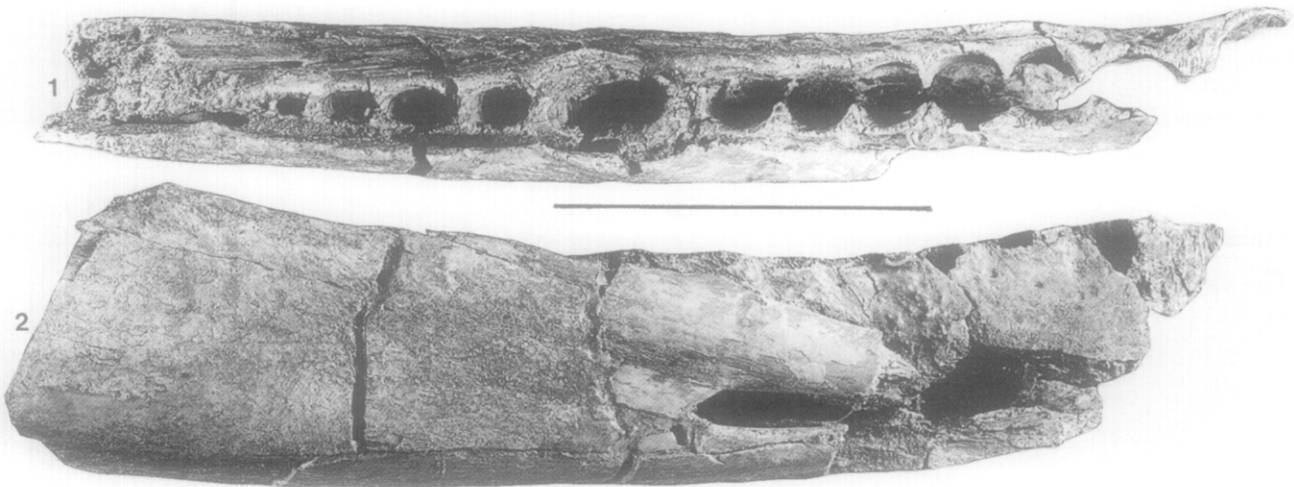


FIGURE 5 - Cf. *Iberosuchus* (STUS 13701). Fragment of left dentary and splenial (Eocene : "Caenes"-Cabrerizos site, Salamanca province, Spain). (1) dorsal and (2) medial view. Scale bar = 10 cm. *Fragment de dentaire et splénial gauches (Éocène moyen. (1) Vue dorsale ; (2) Vue médiale.*

series of vascular foramina is present below the tooth row. The splenial reaches the upper border of the dentary at the level of the 11th alveolous. The anterior dorsal sutural area for the splenial in the dentary is a concave surface, unlike that of extant crocodiles. The ventral part of the medial walls of the posterior alveoli are formed by the dentary, although the upper medial border of the mandible is formed by the splenial. Behind the tooth row, the surangular would have sheathed the upper edge of the dentary. A ridge marks the position of the ante-

rior end of the surangular on the inner side of the dentary. In the STUS 349 specimen (Fig. 7), the Meckelian canal gives off a dorsolateral sinus that passes forward from the 12th-13th teeth. The ventral suture between dentary and splenial faces medially, and it slopes dorsomedially behind, differing from extant crocodiles, where this suture is always medial.

In all of the mandibles, the dentary bends almost at a right angle to meet the splenial ventrally, forming

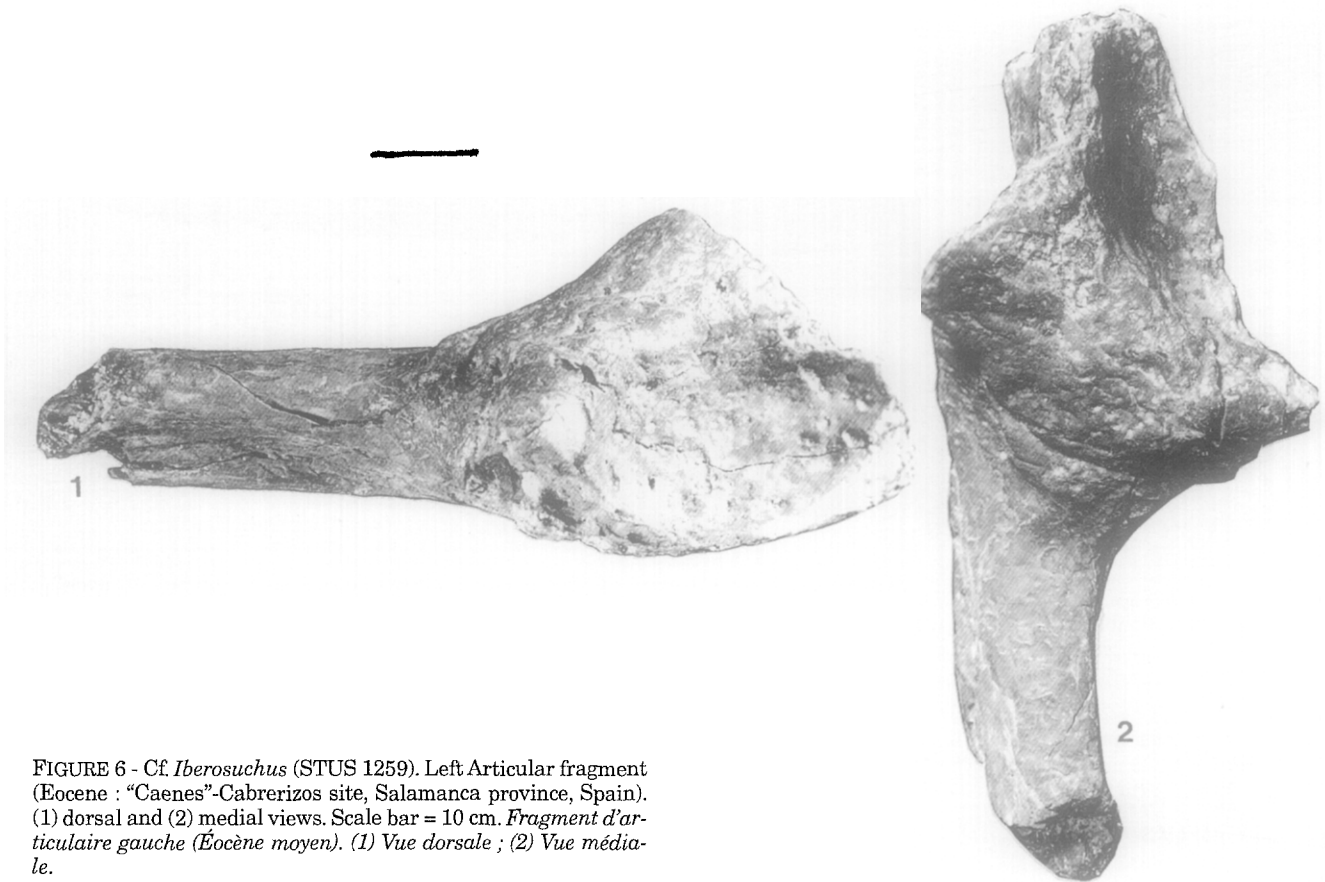


FIGURE 6 - Cf. *Iberosuchus* (STUS 1259). Left Articular fragment (Eocene : "Caenes"-Cabrerizos site, Salamanca province, Spain). (1) dorsal and (2) medial views. Scale bar = 10 cm. *Fragment d'articulaire gauche (Éocène moyen). (1) Vue dorsale ; (2) Vue médiale.*

half of the ventral surface of the mandible, whereas the other half is formed by the splenial.

The splenials of the Issel specimen and of STUS 13701 are robust behind the symphysis. In this area a large slot-like foramen opens medially, dividing the splenial into two branches. We think that this foramen is homologous to the *foramen intramandibularis oralis* described in some extant crocodiles (Norell 1989). It occurs at the level of the 10th tooth and runs forward into the symphysis. Dorsal and ventral to the foramen, the branches of the splenial are thick transversely (Fig. 8), but posteriorly the splenial becomes a thin lamina.

The Issel mandible and STUS 13701 are of the same size (see Figs 2, 3, 5). The only difference that can be noted is the presence of an abnormal enlarged diameter of 11th tooth in the Spanish specimen. However, no tooth with such an enlargement is evident on the small sized specimen from Caenes.

The articular (STUS 1259 : pl. 5) is particularly pneumatized, being its lateral wall composed of cancellous bone. The glenoid fossa for the articulation with the quadrate is broken laterally, and has lost part of the outer articular surface. The internal part of the glenoid fossa extends anteroposteriorly.

A shallow ridge separates the two cotyles of the glenoid fossa. On its medial side, the articular develops a shelf that bends downwards. The anterior portion of this shelf reaches the descending articular process, and its posterior end projects medially. Probably this shelf continued posteriorly along the retroarticular process. A foramen is present in the medial face of the articular below the shelf. The bone surface of both the glenoid fossa and the medial shelf is porous. The anterior descending process of the articular is a narrow rod. The lateral part of the rod is smooth, and there is a foramen in this face, as in Recent crocodiles. The surangular participated in the cranio-mandibular articulation.

The mandible from Issel and STUS 349 retain several teeth *in situ*. The 4th mandibular tooth is the largest, and its crown is twice as high as the other ones. The post-caniniform teeth are homodont in size and shape. They are laterally compressed, with the apex of the crown curved distally. The mesial margin of the crown is convex, and the distal one is slightly concave or straight. A series of isolated denticles -zipodont dentition (modified from Langston 1975), see definition of the term below- is displayed along the mesial and distal margins.

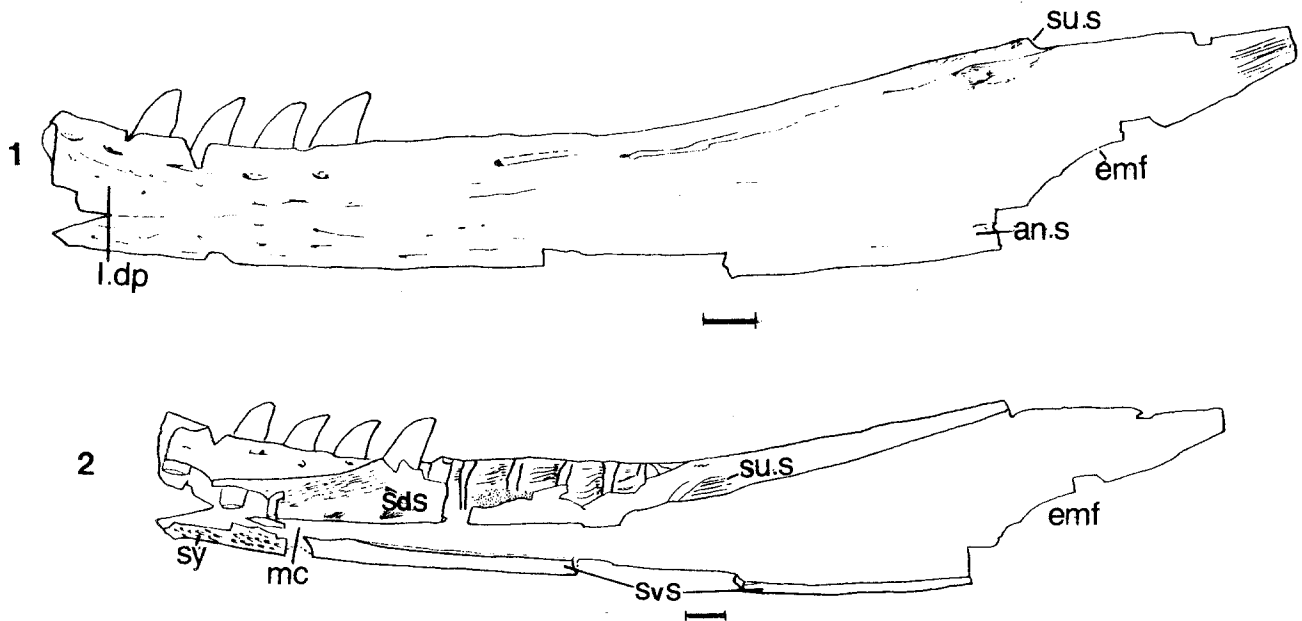


FIGURE 7 - Lateral (1) and medial (2) views of the STUS 349 right dentary (Middle Eocene : "Caenes"-Cabrerizos site, Salamanca province, Spain). The mandible is interpreted as belonging to a juvenile individual. Abbreviations : an.s, angular suture ; emf, external mandibular fenestra ; l.dp, lateral depression of the dentary ; mc, Meckelian canal ; sd.s, dorsal suture of the splenial ; sv.s, ventral suture of the splenial ; su.s, surangular suture ; sy, symphyseal area. Scale bar = 1 cm. Vue latérale (1) et médiale (2) du dentaire droit STUS 349 (Éocène moyen : "Caenes"-Cabrerizos, Salamanca, Espagne). La mandibule est interprétée comme appartenant à un juvénile. Abréviations : an.s, suture avec l'angulaire ; emf, fenêtre mandibulaire ; l.dp, dépression latérale du dentaire ; mc, canal de Meckel ; sd.s, suture dorsale du splénial ; sv.s, suture ventrale du splénial ; su.s, suture avec le surangulaire ; sy, aire symphysaire.

THE TAXONOMIC STATUS OF *A. CRASSIPRORATUS*

At present, no apomorphic features have been proposed to define the phylogenetic position of *Iberosuchus macrodon*. On the other hand, no direct comparison between the material here described and the holotype of *Iberosuchus* (an anterior portion of a snout) is possible. However, the combination of characters shown by the material described is similar to and consistent with those traditionally proposed for the characterization of *Iberosuchus* (Antunes 1975). These features are : the presence of laterally compressed tooth crowns, with the apex curved distally ; the presence of mesial and distal *carinae*, on which a number of isolated denticles

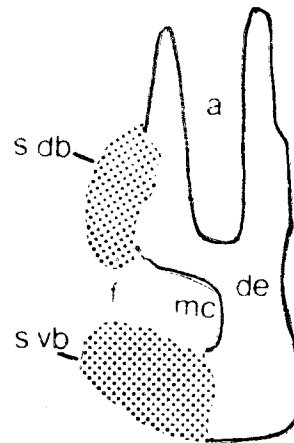


FIGURE 8 - Schema of a transverse section of the anterior part of the left mandible STUS 13701 (middle Eocene : "Caenes"-Cabrerizos site, Salamanca province, Spain), showing the anterior view of the two splenial branches (s.db, dorsal branch of splenial ; and s.vb, ventral branch of splenial) and the slot-like foramen (f) for the Nervus Trigemini (intramandibularis pars oralis). Abbreviations : a, alveolus ; de, dentary (showing the vertical inner and outer walls) ; mc, Meckelian canal.

Schéma de la coupe transversale de la partie antérieure de la mandibule gauche STUS 13701 (Éocène moyen : "Caenes"-Cabrerizos, Salamanca, Espagne), montrant en vue antérieure les deux branches du splénial (s.db, branche dorsale du splénial ; s.vb, branche ventrale du splénial) et le grand foramen (f) du nerf trijumeau (intramandibularis pars oralis). Abréviations : a, alvéoles ; de, dentaire (montrant les murs extérieur et intérieur verticaux) ; mc, canal de Meckel.

(serrated margins) can be delimited - that is the definition of ziphodonty *sensu* Legasa *et al.* 1994 - ; the vermiculated skull sculpture ; a spoon-like premaxillae palatal shelf (*Iberosuchus* holotype) *vs.* a spoon-like mandibular symphysis (specimens described above) ; a premaxillo-maxillary notch *vs.* a hypertrophied 4th mandibular tooth ; and a deep rostrum *vs.* a deep mandible. All of these similarities are symplesiomorphies for Metasuchia, but their combination is unique among the typical crocodilian Eocene European fauna (except *Bergisuchus*, see below). Thus, we assume these similarities of the material here described and *Iberosuchus* as an indication that they probably belong to the same taxon. Therefore, conjoining this criterium with the paleogeographic and chronostratigraphic proximity, the studied specimens are herein assigned to *cf. Iberosuchus*. With the present available material the problem of the taxonomical nomenclature of the holotype of *Atacisaurus crassiproratus* cannot be properly solved. In the event that this species turned out to be a synonym of *Iberosuchus macrodon*, the priority of the Issel specimen denomination would introduce a modification in the specific name of *Iberosuchus* with the new combination *I. crassiproratus*.

COMPARISON WITH THE OTHER EUROPEAN NON-EUSUCHIAN ZIPHODONT CROCODILES

The only other European Tertiary crocodile that presents a similar combination of character states than the mandibles described above is *Bergisuchus dietrichbergi* (Berg 1966 ; Buffetaut 1988). Comparing the material described with the mandible of *Bergisuchus*, several differences are noted. The mandible of *Bergisuchus* is half the size of the smallest of the mandibles described here (i.e. STUS 349), which we believe is an immature specimen (see description). The profuse sculpturing of the Messel crocodile suggests that it is not a juvenile specimen, but a small sized adult, as it has been confirmed by other recently found material (Rauhe *et al.* in prep.). Furthermore, *Bergisuchus* displays a lower number of teeth, arranged in a short space, behind the 4th tooth (11 alveoli versus 14 alveoli in the analysed specimens). The dorsal margin of the dentary has a pronounced concave arch behind the 4th tooth in *Bergisuchus*. The 4th tooth occurs on an elevation of the dentary, and this bone bends strongly forwards reducing considerably the height of the anterior end of the mandible. None of these features are displayed in the described specimens. The caniniform 4th tooth in *Bergisuchus* has an alveolar diameter that is about four times the diameter of the remaining teeth, whereas in the Issel specimen the

diameter of the 4th tooth is no more than twice that of the other teeth.

RESULTS OF THE PHYLOGENETIC ANALYSIS

We present a first attempt at determining the phylogenetic position of *cf. Iberosuchus* based on mandibular characters. For the phylogenetic analysis we have considered *Notosuchus* WOODWARD, 1896 as the outgroup. We have selected the ingroup intending to falsify the hypothesis that relates the non-eusuchian ziphodont crocodiles from the European Tertiary record with the Sebecosuchia and the Trematochampsidae.

The data matrix (Fig. 9) was analysed using the implicit enumeration (i.e.) option of the 1.5 version of the "Hennig 86" program (Farris 1988), resulting a single most parsimonious cladogram (Fig. 10). The character coding (Appendix 1) is a result of the analysis of character transformation along the major clades of Crocodylomorpha : Crocodyliformes, Mesoeucrocodylia, Metasuchia, and Neosuchia, assuming the monophyly of these clades (Benton & Clark 1988 ; Parrish 1991 ; Sereno & Wild 1992).

The node A (Fig. 10) is defined by the dorsal prolongation of the dentary ascending behind the tooth row [#4], and by the antero-posterior elongation of the glenoid fossa of the articular [#14]. Both characters are primitive (i. e. *Sphenosuchus* HAUGHTON, 1924) in Crocodylomorpha. Like the outgroup, the ingroup taxa show the derived condition, with the exception of the node C : (Peirosauridae + *Trematochampsia* + Neosuchia). The reversion of the traits #4 and #14 could define Neosuchia, but they are missing values for Peirosauridae and *Trematochampsia oblita* (see Fig. 9).

The anteroposterior enlargement of the glenoid fossa shown by *Baurusuchus* and *cf. Iberosuchus* is less developed than that of *Notosuchus*. The condition shown in *Notosuchus* has been related with the capability of mandibular propalinity (Clark *et al.* 1989 ; Bonaparte 1991).

Node B is not defined because of the missing values of the data matrix. However, there is a basal dichotomy supported by the most parsimonious distribution of characters that define the node C and the node E (Fig. 10).

Node C is well supported by the presence of two sinusoidal waves in the dorsal margin of dentary [#1], a lateromedially expanded dentary [#2], and the presence of heterodonty along the dentary series [#3]. Character #1 is a basal synapomorphy defining Neosuchia (*sensu* Benton & Clark 1988). However, neither *Trematochampsia* nor the

	1	2	3	4	5	6	7	8	9	0	1	1	1	1	1	1
<i>Notosuchus</i>	0	0	0	1	0	-	0	0	0	0	1	0	0	1	0	0
<i>Sebecus</i>	0	0	0	-	1	0	-	0	-	0	0	0	0	0	-	0
<i>Baurusuchus</i>	0	0	0	1	1	-	1	1	0	0	0	0	0	0	1	1
cf. <i>Iberosuchus</i>	0	0	0	1	1	0	1	1	0	0	0	0	0	0	1	0
<i>Eremosuchus</i>	0	0	0	-	-	0	-	-	-	-	0	0	1	-	1	
Peirosauridae	1	1	1	-	-	-	1	0	0	0	0	0	0	0	0	B
<i>Trematochampsia</i>	1	1	1	-	0	-	0	0	1	-	1	1	0	-	B	
Neosuchia	1	1	1	0	0	1	0	0	1	1	1	1	1	-	0	0

FIGURE 9 - Data matrix of the polarity of 15 mandibular characters. [0] = primitive condition ; [1] = derived condition ; [B] = both ; [?] = missing data. The outgroup taxon is *Notosuchus terrestris*. The chosen ingroup comprises the traditional members of Sebecosuchia - *Sebecus* (*S. icaeorinus* and *S. huilensis*) and *Baurusuchus* (*B. pachecoi*)-, *Eremosuchus* (*E. elkoholicus*), the Peirosauridae (*Peirosaurus torminni* and *Lomasuchus palpebrosus* GASPARINI *et al.*, 1991), *Trematochampsia* (*T. oblita* and *T. taqueti*), and Neosuchia as a single terminal taxa. All of the above mentioned species have been directly revised by the authors. *Matrice des données avec la polarité des 15 caractères mandibulaires*. [0], plésiomorphe ; [1], dérivé ; [B], polymorphisme ; [?], donnée inconnue. Le groupe externe est *Notosuchus terrestris*. Le groupe interne comporte les membres traditionnels de Sebecosuchia - *Sebecus* (*S. icaeorinus* et *S. huilensis*) et *Baurusuchus* (*B. pachecoi*) -, *Eremosuchus* (*E. elkoholicus*), les Peirosauridae (*Peirosaurus torminni* PRICE, 1955 et *Lomasuchus palpebrosus* GASPARINI *et al.*, 1991), *Trematochampsia* (*T. oblita* et *T. taqueti*), et Neosuchia comme un seul taxon terminal. Toutes les espèces mentionnées ci-dessus ont été vues et étudiées par les auteurs.

Peirosauridae have ever been related to any major clade of Crocodylomorpha, and hence, more information would be needed to include them within Neosuchia. The node is supported by other ambiguous characters, such as a Meckelian canal narrow and shallow in the post-symphysial region [#6], and the reversion of the trait #4. Both traits are unknown in *T. oblita* and the Peirosauridae. The *Trematochampsia* + Neosuchia clade is defined by an ambiguous trait, the presence of a short and robust anterior process of the surangular [#10] (unknown in the former taxon), and three synapomorphies. They share the disposition of the splenial attached to the medial face of dentary, remaining almost unexposed in ventral view [#9], the absence of marginal serrations composed by true isolated denticles on the teeth [#11], and conical teeth [#12]. In *Trematochampsia taqueti* the teeth display crenulated crown margins. Crenulated teeth differ from ziphodont teeth in having no distally curved crown apex, and they possess distal and medial rough margins which are constructed by anastomosed ridges. It is considered here as the derived condition, differing from the primitive one -teeth with serrated margins. The presence of conical

teeth [#12] might be treated as a synapomorphy of Neosuchia (with the exception of Atoposauridae) and Eusuchia. However, the primitive expression of the trait #11 is convergent in some genera of Eusuchia -e.g. *Pristichampsus* GERVAIS, 1853, the Chinese pristichampsid *Planocrania* LI, 1976 or the Australian genus *Quinkana* MOLNAR, 1981.

The node E includes the traditional members of Sebecosuchia (*sensu* Gasparini *et al.* 1991), *Eremosuchus* and cf. *Iberosuchus*. This node is defined in the present cladogram by a longitudinal depression of the dentary [#5] that forms a deep fossa around the mandibular external fenestra. In *Sebecus* and *Baurusuchus* the fossa is extended on the surangular and the angular, but this extension cannot be observed in cf. *Iberosuchus* and *Eremosuchus* due to the preservation of the remains.

Cf. *Iberosuchus* is the sister group of (*Baurusuchus* + *Eremosuchus*), sharing a slot-like foramen opening anteriorly in the medial side of the splenial (#8), and splenials broad and robust (#7). The trait #8 is unknown in *Eremosuchus* and in the holotype of *Sebecus icaeorhinus*, but Langston (1965, p. 15,

fig. 3) figured a small foramen (primitive condition) in *S. huilensis* LANGSTON, 1965. The trait #7 is unknown in *Sebecus*. Non-eusuchian crocodiles possessing broad to robust splenials have also stout and/or enlarged mandibles, as in the pholidosaur *Teleorhynchus* OSBORN, 1904, the thalattosuchians (e.g. *Metriorhynchus* MEYER, 1830), the neosuchian *Goniopholis* OWEN, 1841, and also in the Peirosauridae. So, trait #7 seems to be distributed convergently, although the derived condition never appears in members of Eusuchia.

The relationship between *Eremosuchus* and *Baurusuchus* is founded on the presence of a very pronounced sigmoidal tooth row that contrasts with the semi straight ventral edge of the dentary [#15] (convergent within the Peirosauridae in *Peirosaurus*, and also in the species *Trematochampsia oblita*). In the present cladogram *Eremosuchus* is defined by one autapomorphy [#13] -constricted base of the tooth crown. However, this condition is widespread distributed among Crocodylomorpha, and other taxa, out of the focus of this analysis, exhibit it.

CONCLUSIONS

The character analysis and the resulting cladogram (Fig. 10) confirm the primitive condition of the mandible of the specimens here denominated cf. *Iberosuchus*. Thus, *Atacisaurus crassiproratus* is not an eusuchian crocodile, and the successive synonymies, that assigned this material to the Eusuchia *Asiatosuchus germanicus* or to *A. depressifrons* (Berg 1966 ; Berg & Crusafont 1970 ; Vasse 1992) are not valid. The phylogenetic interrelationships of node E (? Sebecosuchia) are still tentative. The available mandibles of *Sebecus* and *Eremosuchus* are very fragmentary, and a complete revision of the Sebecosuchia and related taxa would be necessary to accomplish an unambiguous definition of this node. However, this analysis furnishes a preliminary assumption for further studies on other metasuchian evidence from the Tertiary of Europe and North Africa. The African species *Eremosuchus elkoalicus*, only known from the anterior portion of a dentary, is another ziphodont crocodile geographically and chronologically close to the described specimens.

In this phylogeny, *Trematochampsia* shares six synapomorphies (traits #1, #2, #3, #9, #11, and #12) with the Neosuchia, whereas the remaining members of the trematochampsids (*Eremosuchus*, *Peirosaurus*, and *Iberosuchus*) are placed in different phylogenetic contexts. *T. oblita* possesses a more derived mandible than *Eremosuchus* or cf. *Iberosuchus*, and the affinity between this species and the remainder "trematochampsids" is only based on the presence of a sigmoidal tooth row (#15). According

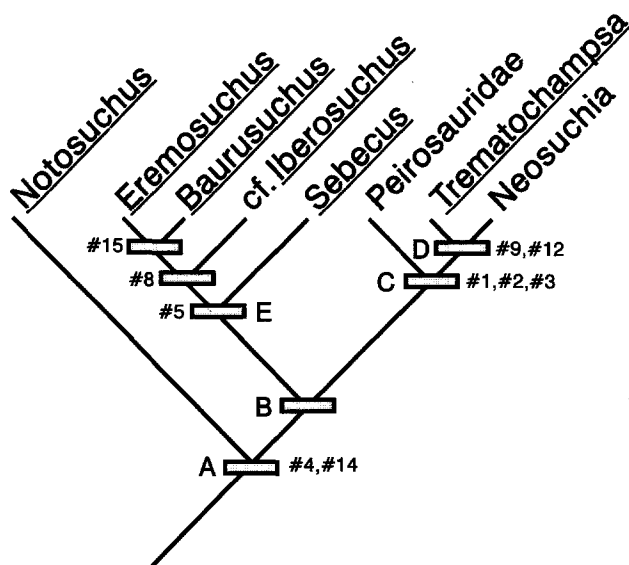


FIGURE 10 - Cladogram showing the phylogenetic position of cf. *Iberosuchus*. The node E comprises the traditional Sebecosuchia in which *Eremosuchus* and cf. *Iberosuchus* are placed. The analysis of the data matrix produced this unique tree with a length of 17 evolutionary steps and $ci=0,88$. On the cladogram only the unambiguous synapomorphies have been distributed. Complete definition of the nodes (*: ambiguous ; * : reversed) : A [#4, #11, #14] ; B [#7*, #11*] ; E [#5] ; (cf. *Iberosuchus* + (*Baurusuchus* + *Eremosuchus*)) [#8] ; (*Baurusuchus* + *Eremosuchus*) [#15] ; C [#1, #2, #3, #4*, #14*] ; D [#7*, #9, #10*, #11, #12]. Cladogramme montrant la position phylogénétique de cf. *Iberosuchus*. Le noeud E comprend les formes habituellement regroupées dans les Sebecosuchia, parmi lesquelles *Eremosuchus* and cf. *Iberosuchus* ont été placés. L'analyse de la matrice de données génère un arbre unique avec une longueur de 17 pas évolutifs et un indice de cohérence (Ci) de 0,88. Sur le cladogramme ont été distribuées seulement les synapomorphies non ambiguës. La définition complète des noeuds est (*: ambiguës ; * : reversion) : A [#4, #11, #14] ; B [#7*, #11*] ; E [#5] ; (cf. *Iberosuchus* + (*Baurusuchus* + *Eremosuchus*)) [#8] ; (*Baurusuchus* + *Eremosuchus*) [#15] ; C [#1, #2, #3, #4*, #14*] ; D [#7*, #9, #10*, #11, #12].

to the present analysis, the "trematochampsids" are considered as a polyphyletic taxon. The mandibular data are also congruent with the results of previous analysis based on skull characters (Gasparini *et al.* 1991).

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Appendix 1 : character coding

- 1 - Dorsal edge of dentary : straight or just showing a single concave arch behind the caniniform tooth (0) ; edge sinusoidal, that is, with two concave waves (1).
- 2 - Mandibular compression : compressed dentary, formed by vertical medial and lateral laminae (0) ; transversely expanded dentary, almost as wide as high, and with a convex lateroventral surface (1).
- 3 - Trends in the variation in the size of the post-caniniform dentary teeth : homodonty, same size along the dentary tooth row (0) ; heterodonty, waves of variation of teeth size along the dentary (1).
- 4 - Posterior development of the dentary : the dentary extends posteriorly at the same height than the tooth row (0) ; a dorsal prolongation of the dentary ascends behind the tooth row (1).
- 5 - Lateral surface of the dentary : without a longitudinal depression (0) ; presence of a longitudinal depression (1). This character does not concern the sculpture of the bone.
- 6 - Meckelian canal : deep and expanded dorsoventrally, extending anteriorly, without constriction, almost to the central area of the symphysis (0) ; narrow and shallow in the post-symphysial region (1).
- 7 - Splenial posteriorly to the symphyseal area : thin (0) ; presence of a medial thickening of the dorsal half of splenial, which becomes broad and robust posterior to the symphysis (1).
- 8 - Foramen intramandibularis oralis : small or absent (0) ; big slot-like foramen (1).
- 9 - Ventral exposition of splenials : the splenial bends ventrally to meet the dentary, forming part of the ventral border of the mandibular ramus (0) ; the splenial is attached to the medial face of dentary, and remains almost unexposed in ventral view (1).
- 10 - Anterior process of the surangular : long, slender, and narrow (0) ; short and robust (1).
- 11 - Edge of the tooth crown : serrated, with meso-distal series of isolated denticles (Legasa *et al.* 1994) (0) ; smooth (1).
- 12 - Shape of the tooth crown : compressed (0) ; conical (1)
- 13 - Base of the tooth crowns : continuous with the root (0) ; constricted (1).
- 14 - Orientation of the glenoid fossa of the articular : transverse (0) ; antero-posteriorly enlarged (1).
- 15 - Tooth row in dorsal view : straight (0) ; sigmoidal (1).

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F. ORTEGA & A.D. BUSCALIONI
 Unidad de Paleontología
 Dept. de Biología
 Universidad Autónoma de Madrid
 28049 Cantoblanco
 Madrid, Spain

Z. GASPARINI
 Departamento de Paleontología de Vertebrados
 Museo de La Plata
 1900 La Plata, Argentina