A Reanalysis of *Bernissartia fagesii*, with Comments on its Phylogenetic Position and its Bearing on the Origin and Diagnosis of the Eusuchia

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Abstract

The precise affinities of the small Early Cretaceous crocodylomorph *Bernissartia fagesii* DOLLO, 1883 have been unclear. We review the anatomy of *B. fagesii* and present evidence that it is closely related to the Eusuchia, as was originally suggested by DOLLO but contrary to the hypothesis of BUFFETAUT (1975, 1982). *Bernissartia fagesii* displays features that have been considered diagnostic of the Eusuchia, including a biconvex first caudal vertebra and at least one procoelous caudal vertebra. Revised diagnoses of *B. fagesii* and of the Eusuchia are presented, and the implications of *Bernissartia fagesii* as an outgroup to the Eusuchia are discussed with regard to phylogenetic relationships among living crocodylians.

Key-words: *Bernissartia*, Crocodylia, Eusuchia, systematics, Lower Cretaceous.

Résumé

Les affinités précises du petit crocodylomorphe éocrétacé *Bernissartia fagesii* DOLLO, 1883 n'étaient pas établies. *B. fagesii*, d'après la revision anatomique, est proche des Eusuchia. Ceci avait été suggéré par DOLLO, mais avait été contredit par BUFFETAUT (1975, 1982). *B. fagesii* présente des caractères diagnostiques des Eusuchia, entre autres une première vertèbre caudale biconvexe et au moins une vertèbre procèle. Des diagnoses modifiées de *B. fagesii* et des Eusuchia sont présentées; les implications de *B. fagesii* comme "outgroup" des Eusuchia sont discutées en considérant les relations phylogénétiques parmi les crocodiliens vivants.

Mots-clefs: *Bernissartia*, Crocodylia, Eusuchia, taxionomie, Crétacé inférieur.

Introduction

The origin and phylogeny of the eusuchian crocodylomorphs has recently become a center of controversy (DENSMORE, 1983; BUFFETAUT, 1985; TARSITANO, 1985). A missing element in these studies has been a careful reconsideration of early, primitive eusuchians and their close relatives rof mesosuchian grade. Taxa that have been considered as eusuchians or close eusuchian relatives include *Hylaeochampsa vectiana* OWEN, 1874, *Stomatosuchus inermis* STROMER, 1925, *Leidyosuchus*

LAMBE, 1908, an unnamed small form from the Lower Cretaceous Glen Rose Formation of Texas (LANGSTON, 1973, 1974), *Bernissartia fagesii* DOLLO, 1883, several species of the genus *Shamosuchus* MOOK, 1924 (= *Paralligator* KONZUKOVA, 1954- EFIMOV, 1982), *Dolichochampsa minima* GASPARINI & BUFFETAUT, 1980, and, atoposaurs such as *Theriosuchus pusillus* OWEN, 1878 (BUFFETAUT, 1982). These taxa are crucial to the interpretation of eusuchian phylogeny because, as the immediate outgroups and most primitive members of the Eusuchia, they provide the most accurate assessment of morphological characters primitive for the group.

Our purpose in this paper is to describe selected morphological features of *Bernissartia fagesii* in order to determine its phylogenetic relationships, as evidenced by shared derived characters. Our approach concentrates on those features found in the type specimen that may be tied into a broader cladistic framework (CLARK, 1986; NORELL, 1988), rather than a detailed redescription of the specimen. The goals of this analysis are: 1) to provide a revised diagnosis for *Bernissartia fagesii*, 2) to determine its relationship to the Eusuchia and to other advanced neosuchians (BENTON & CLARK, 1988), 3) to provide a revised diagnosis of the Eusuchia, and 4) to use *Bernissartia fagesii* as an outgroup in polarizing characters bearing on relationships within the Eusuchia.

Bernissartia fagesii has from the time of its discovery been considered to have an important bearing on the origin of the Eusuchia. In his initial description of the species DOLLO (1883) recognized a close affinity between *Bernissartia* and eusuchians. In a phylogenetic diagram in this paper he indicated that *Bernissartia* may even be more closely related to brevirostrine eusuchians than to longirostrine eusuchians such as *Gavialis* and thoracosaurs. In support of this, he noted that its dorsal osteoderms are arranged in more than two longitudinal rows, as in eusuchians but not mesosuchians, and he suggested (p. 334) that the *choana* is in a position intermediate between that of eusuchians (in which it lies within the pterygoids) and that of mesosuchians (in which it lies anterior to the pterygoids). DOLLO did not comment explictly on whether the vertebrae had the procoelous condition found in eusuchians, but in his taxonomic

conclusions he grouped *B. fagesii* with taxa having the primitive amphicoelous vertebral condition.

Throughout the last century *Bernissartia fagesii* has generally been considered a mesosuchian, often placed in the family Goniopholididae (e.g., ROMER, 1956) rather than the family that DOLLO erected for it (the Bernissartidae, which was later implicitly emended, by LYDEKKER, 1887, to Bernissartiidae). KÄLIN (1955), however, dissented with this view and considered *Bernissartia* to be a eusuchian. KÄLIN's brief comments on *Bernissartia* included the observation (p. 756) that the "narines internes très probablement bordées seulement par les ptérygoïdes", and he described the vertebrae, without elaborating, as being procoelous.

The most recent, and most thorough, reconsideration of *Bernissartia fagesii* was published by BUFFETAUT in 1975. BUFFETAUT found that the vertebrae are gently amphicoelous, not procoelous, and he noted that the *choana* is not demonstrably bordered by the pterygoids anteriorly. BUFFETAUT considered the multiple rows of dorsal osteoderms to have evolved convergently in *Bernissartia fagesii* and eusuchians, noting that this condition has been reported (DOLLO, 1914) in a dyrosaur, a group that BUFFETAUT (1975, 1982) considered to be only distantly related to eusuchians. For these reasons he considered *Bernissartia fagesii* to be more primitive than some other mesosuchians, in particular the atoposaur *Theriosuchus pusillus*.

MORPHOLOGY AND RELATIONSHIPS OF *Theriosuchus*

As with *Bernissartia fagesii*, a close relationship between *Theriosuchus pusillus* and eusuchians has been suggested since the time of its description (OWEN, 1879). For example, DOLLO (1883) placed *T. pusillus* in the same family with *B. fagesii*, although with a question mark. The arguments in favor of a close relationship between *T. pusillus* and eusuchians were given their strongest exposition by JOFFE (1967), and most of these arguments were later elaborated by BUFFETAUT (e.g., 1982). In support of this hypothesis, JOFFE cited three features that would indicate close affinities. First, she described the dorsal osteoderms of *T. pusillus* as lacking an anterior process, the absence of which is a derived feature of eusuchians. Second, she described the vertebrae as procoelous rather than amphicoelous. And third, she considered the depression in the pterygoids into which the *choana* exits as similar to the condition found in eusuchians.

A detailed redescription of *Theriosuchus pusillus* has been presented by CLARK (1986), and he noted several weaknesses in this hypothesis. First, an anterior process is present on the dorsal osteoderms. Second, some of the vertebrae (including trunk vertebrae) are indeed procoelous, but others are amphicoelous and one caudal vertebra may even be opisthocoelous. Third, the depression into which the *choana* exits is no more like that of eusuchians than is this area in most other "mesosuchians." In addition, CLARK noted several primitive features of *T. pusillus* and other atoposaurs, including the presence of a small antorbital fenestra, extensive expo-

sure of the ventral surface of the basisphenoid, and a coracoid that is much shorter than the *scapula*.

HIGHER LEVEL TAXA OF CROCODYLOMORPHA

The phylogenetic relationships and systematic categories of the fossil relatives of crocodylians have recently been revised by CLARK (1986) and BENTON & CLARK (1988), and we will utilize that framework rather than the traditional one. Two problems with the traditional system were addressed by CLARK. First, the content of crocodylian higher taxa has been based upon the criterion of whether fossil taxa have "enough" of the "key" crocodylian characters; because of the subjectivity in such decisions there has not, for example, been an agreement on the definition of the Crocodylia, even though the broad outlines of their relationships are agreed upon (see CRUSH, 1984 and BUSBY & GOW, 1984 for contrasting views). Second, many of the taxa are paraphyletic grade groups, and taxonomy should be based upon monophyletic clades (HENNIG, 1966; WILEY, 1981). CLARK resolved these problems by creating a new taxonomy based upon the concept (GHISELIN, 1984; GAUTHIER *et al.*, 1988) that higher taxa should be defined on the basis of relationships rather than on the characters that diagnose them. He therefore proposed that the Crocodylia should be restricted to the descendants of the most recent common ancestor of the living taxa (the crown group), thus excluding all "mesosuchians" and "protosuchians" as well as some eusuchians.

CLARK recognized monophyletic groups on the basis of a detailed cladistic analysis of the Crocodylomorpha, and new names were applied to groups that had not been previously recognized. The group including the "Mesosuchia" and the Eusuchia has been named the Mesoeucrocodylia by WHETSTONE & WHYBROW (1983). The Neosuchia was erected by BENTON & CLARK (1988) for eusuchians and those mesoeucrocodylians that are most closely related to eusuchians, including the atoposaurs, the goniopholidids, the dyrosaurs, the pholidosaurs, *Shamosuchus*, and *B. fagesii*.

The definition of the Eusuchia in a taxonomy based upon evolutionary relationships rather than the characters with which they are recognized is problematic. Historically, the Eusuchia has been more or less equivalent in content to the crocodylian crown group, but it was not based explicitly upon this concept. Although HUXLEY (1875) listed many characters in his original diagnosis of the group he did not precisely define its content, listing only the thoracosaurs and *Gavialis* (with a question mark) as its members. Over the last century the Eusuchia has come to include all of those taxa with procoelous vertebrae and the *choana* included completely within the pterygoids, regardless of whether they were supposed to be descended from the closest common ancestor of living crocodylians (e.g., STEEL, 1973). As will become clear below, these features did not appear simultaneously in the evolution of the Crocodylia, procoelous vertebrae having a more general distribution than a *choana* enclosed completely within the pterygoids. This latter

feature might be chosen as the basis for recognizing the Eusuchia, but a single character cannot be relied upon to have evolved only once, and it may become modified in some of the descendants (GHISELIN, 1984).

We consider this problem to have two possible solutions. Either the taxon Eusuchia can be abandoned in lieu of its virtual equivalence to the Crocodylia, or it can be redefined on the basis of a specific set of relationships. Because several taxa that have historically been placed in the Eusuchia lie outside of the crocodylian crown group, CLARK (1986) chose to consider the Eusuchia to include the crocodylian crown group plus these taxa: *Stomatosuchus inermis*, *Hylaeochampsa vectiana* and *Leidyosuchus*. Thus, CLARK defined the Eusuchia as the descendants of the closest common ancestor of these taxa. The question of whether *Bernissartia fagesii* is a eusuchian or not now becomes a question of whether it is as closely related to crocodylians as are any of these three taxa.

Bernissartia Material

Bernissartia fagesii is known from only a few specimens. All of these specimens are from the Early Cretaceous of
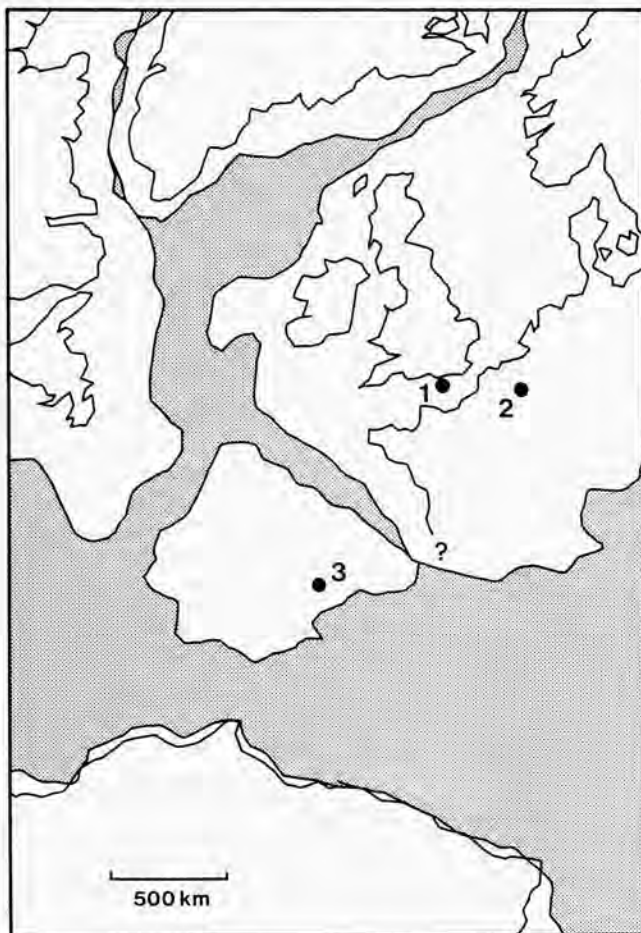

Fig. 1. – Localities of *Bernissartia* specimens. Continental configurations in the Early Cretaceous (Berriasian-Barremian) (adapted from TERRA MOBILIS™ 1.3). 1) Isle of Wight, United Kingdom. 2) Bernissart, Belgium. 3) Galve, Spain.

western Europe (Fig. 1), although BUFFETAUT & FORD (1979) mention some possible occurrences outside of this area. The most complete specimen of *B. fagesii* is the lectotype (IRScNB n° R 46) described by DOLLO (1883) and BUFFETAUT (1975). It was collected from the Bernissart Clay (Berriasian ? – Lower Aptian) in a coal mine at Bernissart, not far from Mons (Belgium), along with numerous specimens of *Iguanodon bernissartensis* (NORMAN, 1987). A second, fragmentary skeleton referred by DOLLO to *B. fagesii* and lacking a skull was found at the same site. Fragmentary remains from the Wealden of S. England have been referred to *Bernissartia* by BUFFETAUT & FORD (1979) but consist mainly of isolated teeth. An exceptionally well preserved cranium and associated skeleton of *Bernissartia*, though probably not *B. fagesii*, from Lower Cretaceous deposits near Galve in east central Spain has been given a preliminary description by BUSCALIONI, *et al.* (1984) and BUSCALIONI (1986). We have examined all of these specimens, but our comments are based primarily upon the Belgian specimens.

DESCRIPTION

The overall shape of the skull (Fig. 2) is similar to that of some alligatorids, such as *Caiman*, with a *rostrum* that is broader than in, for example, most extant crocodylids (sensu NORELL, 1989). The skull has been dorsoventrally flattened by diagenetic processes, and we believe that this accounts for the peculiar narrowing at the anterior end of the orbits noted by BUFFETAUT (1975). The anterior part of each orbit is interpreted here to have been artificially narrowed by the crushing of the lacrimal. In life the orbits were probably more rounded, like those of typical (nongavialid) extant crocodylians. The outer surface of the skull is sculptured, but the details are not well preserved on the lectotype skull. The *premaxillae* are similar to those of living crocodylians in being horizontally oriented and in having an expanded area anterior to the *nares*. This expansion is not, however, as great as in living crocodylians, resulting in an anterodorsal, rather than dorsal, orientation of the *nares* similar to that of *Leidyosuchus*. An internarial bar is absent from the specimen so that the *nares* are confluent. Ventrally, the *premaxillae* meet along the midline posterior and anterior to the small incisive *foramen*. They contact the *maxillae* posteriorly on the palate along a transversely oriented suture. A gentle notch is formed at the contact between the *premaxilla* and *maxilla*, but it is not as well developed as in *Goniopholis* and *Crocodylus*. The enlarged fourth dentary tooth occludes inside the lateral edge of the *rostrum* in a small depression, rather than lying lateral to the *rostrum* as in extant crocodylids. This depression has only a narrow lateral wall, however, so that a ventral notch is present in lateral view. This area differs from the condition in *Shamosuchus* (KONZUKOVA, 1954) and extant alligatorids, which lack any notch in lateral view. Five subconical, evenly spaced premaxillary teeth are present.

The nasals widen at their anterior ends where they form the posterior border of the *nares*. Posteriorly, the nasals
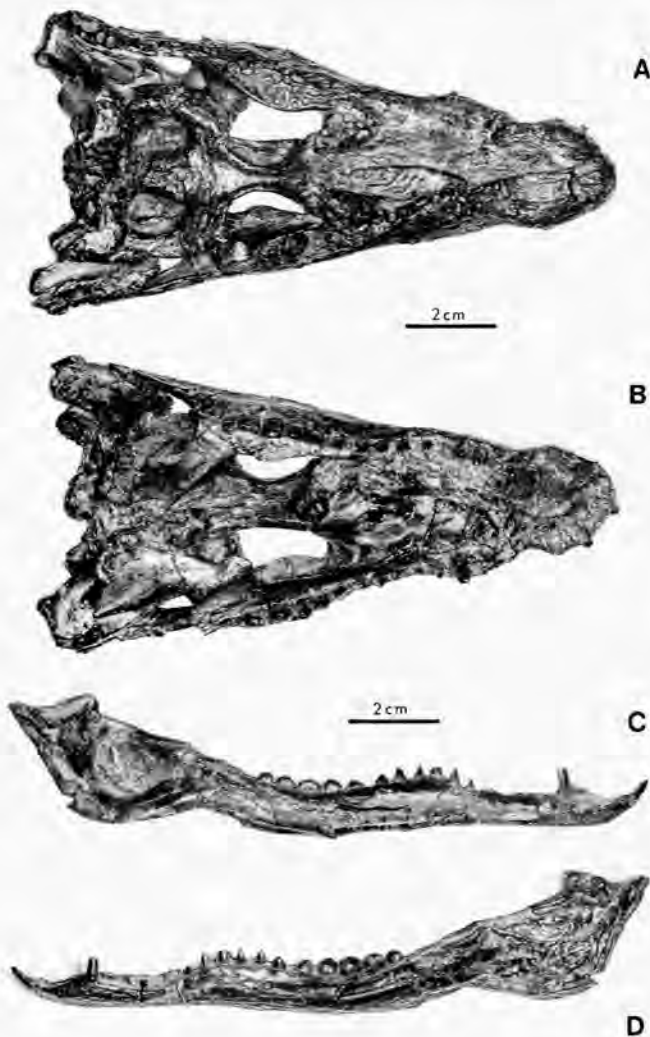
Fig. 2. – Lectotype cranium and mandibles of *Bernissartia fagesii* DOLLO 1883. A) dorsal view, B) ventral view, C) lingual mandible view, D) labial mandible view.

meet the lacrimals laterally. The lateral edge of each nasal is generally straight, but a gentle convexity is present. The *maxillae* form most of the *rostrum*. They are nearly flat dorsally, and their lateral borders are festooned in two waves. The *maxillae* lack the pronounced convexity over the fifth tooth found in many extant crocodylians. Each *maxilla* contains 16 teeth. Most teeth are conical; teeth 5 and 6 are enlarged and teeth 13 though 16 are bulbous and carinate. Small pits lie on the palatine portion of the *maxillae* medial to the 7th and 8th teeth for reception of the corresponding lower dentition. *Canthi rostrali* (longitudinal ornamentations anterior to the orbit) are not present on the dorsal surface of the *maxillae*, although it is difficult to be certain because they may be obscured by crushing. Antorbital *fenestrae* are absent.

The prefrontals are narrow and do not extend medially to meet on the midline. A robust prefrontal pillar is present, but details of its construction are poorly preserved and exposed. The lacrimals are broad and flat, about as broad as long.

The frontals are fused and have a narrower interorbital breadth than in most adult crocodylids, approaching the condition seen in *Alligator*. The interorbital area of the frontal has a concave dorsal surface, with its lateral edges forming a supraorbital rim. The ventral surface of the frontal is anteroposteriorly concave in lateral view, elevating the orbits above the contour of the skull. This condition is like that found in many extant adult Crocodylia as well as most juveniles. The fronto-parietal suture lies between the supratemporal *fenestrae* near their anterior ends, so that the frontal enters into the anterior borders of the *fenestrae*.

The parietals are fused and form a wide, flat, sculptured region between the supratemporal *fenestrae*. In dorsal view the parietal extends posteriorly along the midline beyond the edge of the occiput, to form a point that gives a "double arch" effect to the occiput.

The postorbitals are relatively large, approaching the size of the squamosals. The dorsal, sculptured portion of each postorbital distinctly overhangs the postorbital bar, so that the latter is inset from the edge as in eusuchians. The area on the postorbital between the supratemporal *fenestrae* and the orbits is broad and sculptured, unlike that of *Theriosuchus pusillus* (OWEN, 1879; CLARK, 1986) and other atoposaurs (WELLNHOFER, 1971). A groove for the ligaments of the external ear muscles (SHUTE & BELLAIRS, 1955) lies along the lateral edge of each postorbital, continuous with that on the squamosal. The postorbital bar is massive, similar in size to that of comparably-sized *Gavialis* skulls. A small bump is present on its anterior edge, immediately dorsal to its contact with the jugal, as in adult *Gavialis*. The anterolateral angle of the postorbital is gently rounded. A small postorbital process appears to be present extending posteroventrally along the anterior edge of the quadrate, but as in some *Alligator* it does not meet the quadratojugal (NORELL, 1988).

The squamosals are narrower lateral to the supratemporal *fenestrae* than in most eusuchians, indicative of the moderately large supratemporal *fenestrae* (similar in size to those of *Leidyosuchus formidabilis*). Thus, although the orbits are larger than the supratemporal *fenestrae*, this is in part due to the larger relative size of the orbits in small animals (see DODSON, 1975). The posterolateral corners of the squamosal form sharp points. The cranioquadrate passage is enclosed by the squamosal, otoccipital, and quadrate, and the contact of the bones is broad and robust.

The palatines are long, very slender, and parallel-sided, lacking any lateral indentations. The palatines extend anteriorly between the *maxillae* to the level of the 10th maxillary tooth, where they expand slightly. Although this region is difficult to interpret, the anterior extension of the palatines may be squared off, with a broad, straight anterior edge, as in alligatorids. Prefrontal pillars contact the palatines at about 1/3 the distance from the anterior margin of the latter. Due in part to the

narrowness of the palatines, the suborbital *fenestrae* are large, as in many living crocodylids but in contrast to *Shamosuchus* and extant alligatorids.

The contradictory descriptions of the position of the *choana* on the type skull are undoubtedly due to the poor preservation in this region. In the Spanish skull of *Bernissartia* (BUSCALIONI, 1986; pers. obs.), the *choana* is well preserved and does not lie within the pterygoids, strongly supporting BUFFETAUT's assessment of its position in the *B. fagesii* lectotype specimen (BUFFETAUT, 1975). In the Spanish skull, the pterygoids are inflected medially anterior to the *choana* but do not meet.

The pterygoid flange is extremely thick anterolaterally and thins posteriorly. Apparently no palatine *bullae* were present; the presence of pterygoid air-spaces is difficult to determine due to extensive breakage in this region. As in other neosuchians the pterygoids were probably fused posterior to the *choana* (contrary to fig. 1 of BUFFETAUT, 1975), but this region is poorly preserved on the type. An anterior process of the ectopterygoid borders the posterior part of the maxillary tooth row as in crocodylids. A large rugose medial process enters the suborbital *fenestra* laterally (Fig. 2), as in *Osteolaemus*. The ectopterygoid flange extends to the posterior tip of the pterygoid flange. The lateral part of the ectopterygoid extends dorsally to contact the postorbital on the medial surface of the postorbital bar, and, as in *Gavialis* and to a lesser extent alligatorids, a posterior ectopterygoid process extends along the medial surface of the jugal (NORELL, 1989). Anteromedially, the ectopterygoid abuts the posterior maxillary teeth, as in extant crocodylids and *Gavialis*.

The jugal is about twice as deep below the orbit as it is posteriorly, ventral to the infratemporal space. Below the orbit, the dorsal border of the jugal is convex and slightly everted, forming the ventral margin of the orbit. The postorbital bar is inset from the body of the jugal, and is unsculptured and columnar.

The occiput has been slightly crushed but several features are preserved. The otoccipital (exoccipital and opisthotic) protrudes well onto the occipital condyle. The dorsal surface of the basioccipital is smooth, not keeled, within the *foramen magnum*. The ventral part of the basioccipital is fragmented and difficult to interpret. Most of the otoccipital is poorly preserved, but the paroccipital process is well preserved, and it forms a shelf over the quadrate. The supraoccipital has a vertical ridge on its posterior surface along the midline. The post-temporal *fenestrae* are obscured by crushing and matrix but are not as large as in *Alligator*. The basisphenoid is not well preserved, but it is not broadly exposed on the ventral surface of the skull as in *Theriosuchus pusillus* (CLARK, 1986). The Spanish skull has a well preserved narrow basisphenoid.

The quadratojugal is heavily sculptured ventrolaterally and forms a small part of the condyle for the mandibular articulation. The quadratojugal forms the posteroventral border of the infratemporal space and is exposed on the dorsomedial surface of the jugal. A process of the qua-

dratojugal extends anteriorly along the medial surface of the jugal, as in gavialids and alligatorids. The region of the quadratojugal spine is broken but the Spanish specimen has a well-developed spine projecting anterodorsally into the infratemporal fenestra (BUSCALIONI, *et al.*, 1984; pers. obs.). The quadratojugal does not appear to exclude the quadrate along a straight suture, so that the quadratojugal is parallel-sided and without constrictions.

The quadrate extends only a short distance posterior to the occiput. It is not sculptured on its ventrolateral edge, but dorsally a longitudinal ridge extends from the mandibular articulating surface to the opening of the cranioquadrate passage. The mandibular articulating surface extends dorsally onto this ridge. No siphonial opening is present on the dorsolateral surface anterior to the internal auditory opening. The siphonial *foramen* near the articular condyle is very distinct. A shallow depression lies on the dorsal surface of the quadrate immediately anterior to the articular surface.

The mandible (Fig. 2 C & D) is long and gracile and is festooned in a pattern complementing that of the maxilla. A lateral mandibular *fenestra* is absent from its typical position between the angular, surangular, and dentary, similar to the condition in atoposaurids and many goniopholidids. The retroarticular process is shorter than in extant adult crocodylians, and the siphonial *foramen* lies towards the medial edge of the articular's dorsal surface, as in living crocodylids. The retroarticular *fossa* posterior to the articular *fossa* on the mandible's dorsal surface is smooth, similar to *Caiman crocodilus*, and is not divided by a longitudinal ridge into two lateral *fossae* as in *Crocodylus*. The medial border of the retroarticular process is concave. The posterior border of the internal mandibular *fossa* is formed by the anterior process of the articular, which is anteriorly concave. The surangular has a relatively flat dorsal surface, and it does not form part of the articular *fossa*. The angular is strongly arched ventrally. It is broadly exposed on the ventral surface of the retroarticular process and extends the posterior border of this process. The splenial takes part in the short mandibular symphysis. An anterior splenial *foramen* is not obvious, but this region is badly crushed on both *rami*. However, this *foramen* is present on the Spanish specimen (pers. obs.).

Positions for approximately nineteen teeth are present in each dentary. The anterior teeth are conical and are constricted at their bases. They lack serrations, but the enamel is crenulated (BUFFETAUT & FORD, 1979). The third and fourth teeth are the largest and occupy a common *alveolus* as in most species of *Leidyosuchus* and *Goniopholis* and in *Diplocynodon* POMEL, 1847. The other dentary teeth are set in individual sockets or are separated by interalveolar septa. The posterior five teeth are bulbous and ovoid in dorsal view, with an antero-posterior longitudinal axis.

The confusion over the vertebral morphology of *Bernissartia fagesii* is due to the preservation of the vertebrae on the type specimen in blocks that include many verte-

brae in articulation. Although the articulating surfaces of the *centra* on most vertebrae cannot be seen, nearly all of the exposed vertebrae, including examples of cervical and trunk vertebrae, are amphicoelous. However, the first caudal vertebra is biconvex, as in living crocodylians (HOFFSTETTER & GASC, 1969), and the second caudal vertebra is distinctly procoelous. The condyles on the first caudal vertebra are less developed (more gently convex) than in living Crocodylia and extend to the edges of the *centrum* rather than forming a distinct hemisphere surrounded by a flat surface.

The *axis* has a low neural spine and a small but distinct hypapophysis on its ventral surface. Cervical vertebrae three through six also possess moderately developed hypapophyses in the form of small knobs. A small process is present on the anterior part of the lateral surface of the *axis* neural arch, as in *Gavialis* (BAUR, 1886). This process has been identified as a diapophysis in *Gavialis*, but its homology with this feature is tentative because it has not been demonstrated that the axial rib articulates to it. The *centra* of the cervical vertebrae are laterally constricted, more so than those of the trunk vertebrae.

At least 14 trunk vertebrae are present, but most are missing neural arches. The *centrum* of the anterior of the two sacral vertebrae appears to have a concave anterior surface. At least the first five caudal vertebrae have long, broad transverse processes, and the neural spines are high on at least the first seventeen vertebrae. Haemal arches are present throughout the caudal vertebrae. These arches are very long and bend posteriorly. The ribs in the mid trunk series are thin, with wide anterior flanges. Both dorsal and ventral armor shields are preserved. The outer surface of both dorsal and ventral osteoderms is heavily sculptured. Two transverse rows of nuchal osteoderms are present in the cervical region, and 25 transverse rows of dorsal body osteoderms are present

in the trunk region. Caudal osteoderms appear to be absent. The nuchal osteoderms occur two to a row, rows 3 through 21 of the trunk osteoderms are arranged four to a row, and more anterior and posterior rows of trunk osteoderms are arranged 2 per row.

All of the dorsal osteoderms are imbricate with a smooth area on the anterior dorsal surface where the overlying osteoderm articulates. They lack the anterior process typically present on the dorsal osteoderms of all "proto-suchians" and "mesosuchians". The dorsal osteoderms are heavily sculptured and have longitudinal keels. The osteoderms in the lateral rows each have a single keel, and those in the medial rows display an unusual feature of having two keels per osteoderm, similar to the supposed atoposaur *"Alligatorium" paintenense* (WELLN-HOFER, 1971; CLARK, 1986). All of the dorsal osteoderms are similar in anteroposterior length, but the osteoderms in the medial row are about twice as broad as they are long, while the osteoderms of the lateral row are nearly square.

The ventral osteoderms are incompletely preserved, but at least four longitudinal rows and 15 transverse rows were originally present. Each osteoderm is nearly square, and they are imbricated so that the anterior edge of one lies dorsal to the posterior edge of the next. The osteoderm is smooth on the anterior part of its ventral surface where it is imbricated.

ONTOGENETIC STAGE OF *Bernissartia* SPECIMENS
The known specimens of *Bernissartia* display several features that are commonly present in juvenile members of extant species and in "dwarf" species (e.g., *Alligator sinensis* FAUVEL, 1879 and *Osteolaemus tetraspis* COPE, 1860). These features include the short posterior extent of the quadrates beyond the occiput, the relatively short and wide muzzle, large orbits, elliptical and obliquely

Table 1.
Distribution of characters

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Atoposauridae	0	0	0	0	0	1	0	1	?	0	0	0	0	0	0	0
Goniopholididae	0	1	0	1	1	B	B	0	0	0	0	0	0	1	0	0
Dyrosauridae	1	2	0	1	1	0	1	0	0	0	2	?	1	1	0	0
Bernissartia	0	2	1	1	1	1	0	0	1	0	1	1	1	?	0	0
Leidyosuchus	2	2	1	1	1	0	0	1	2	1	2	1	1	1	1	0
Crocodylia	2	2	1	1	B	0	1	1	2	1	2	1	1	1	1	1
CI's[1]	1	1	1	1	.5	.33	.33	.5	1	1	.66	1	1	.5	1	1

B = Both states present
SOURCES: Atoposauridae (including *Theriosuchus pusillus*) – OWEN (1879), WELLNHOFER (1971), CLARK (1986); Goniopholididae – OWEN (1878a, 1879), HULKE (1878), DOLLO (1883), HOOLEY (1907), MOOK (1967), BUFFETAUT (1982), CLARK (1986), NORELL (1988); Dyrosauridae – TROXELL (1925), PIVETEAU (1935), SWINTON (1950), BUFFETAUT (1982), STORRS (1986); *Bernissartia fagesii* – this study, BUSCALIONI (1986); *Leidyosuchus* – ERICKSON (1976); Crocodylia – WERMUTH (1953), NORELL (1988).
1 – Consistency indices for the character distributions displayed in the cladogram in Figure 3.

oriented supratemporal *fenestrae*, and the narrow, dorsally concave shape of the frontal above the orbits (KĀLIN, 1933). Although the Spanish specimen may well be a juvenile (BUSCALIONI, *et al.*, 1984), we interpret *Bernissartia fagesii* to be a dwarf species and the lectotype specimen to be an adult. The high degree of fusion along cranial sutures, the presence of interalveolar septa between teeth, the heavy sculpture on both the cranium and body osteoderms, and the heavily worn teeth strongly suggest this, although it is impossible to be certain.

Relationships of advanced neosuchians

In the following section we examine the distribution of 16 discrete characters in order to recognize shared derived character states diagnosing monophyletic groups among advanced neosuchians. We emphasize that this is not, however, a comprehensive analysis because we do not consider the characters shared between longirostrine forms, including *Gavialis* and dyrosaurs, except when they also occur in some brevirostrine forms. For a discussion of this problem, see BENTON & CLARK (1988). Included in this analysis are the crown group of living crocodylians (gavialids, alligatorids, and crocodylids), the primitive eusuchian *Leidyosuchus formidabilis* ERICKSON, 1976, the primitive neosuchian families Atoposauridae, Goniopholididae (which may not be monophyletic, CLARK, 1986), and Dyrosauridae, and *Bernissartia fagesii* (Table 1). *Shamosuchus* is not included because as far as can be determined from the literature (MOOK, 1924; KONZUKOVA, 1954; SUN, 1958; EFIMOV, 1983) it is identical with *Bernissartia fagesii* in the 9 features for which it can be scored (we are unable to score it for characters 5, 9, and 13), although one of these is apparently variable (see discussion below). The unnamed primitive eusuchian from Texas (LANGSTON, 1974) is not included because it has not yet been described, and the primitive eusuchians *Hylaeochampsa vectiana*, *Stomatosuchus inermis* and *Dolichochampsa minima* and the primitive neosuchian Pholidosauridae are not included because the conditions of the majority of characters are not known. The primitive conditions for neosuchians are discussed by CLARK (1986) and BENTON & CLARK (1988), and they are coded as (0) in the following discussion.

CHARACTER DESCRIPTIONS
1) Primitively in neosuchians the *choana* lies posterior to the palatine bones but does not lie within the pterygoids (0). In dyrosaurs and *Bernissartia*, the pterygoids form a small part of the anterior edge of the *choana* (BUFFETAUT, 1982), but the *choana* is in a position similar to that of other "mesosuchians" (1). In eusuchians the *choana* lies fully within the pterygoids, and it is situated much further posteriorly than in the primitive condition (2). We treat this character as ordered: 0 – 1 – 2.
2) Primitively in neosuchians an antorbital fenestra is present between the *maxilla* and lacrimal (0). The *fenestra* is absent but a *fossa* is present in this posi-

tion in many goniopholidids (1), and an antorbital *fossa* and *fenestra* are absent in eusuchians, dyrosaurs, *Bernissartia fagesii* and *Shamosuchus* (2). We treat this character as unordered, although it might be alternatively interpreted as two characters, the presence or absence of a *fenestra* and the presence or absence of a *fossa*.
3) Primitively in neosuchians the postorbital bar is not inset from the edge of the dorsal part of the postorbital (0). In eusuchians, *Bernissartia fagesii* and apparently in *Shamosuchus* the postorbital bar is inset from the edge of the postorbital (1).
4) Primitively in neosuchians the basisphenoid is exposed on the ventral surface of the braincase, and the length of this exposure is about equal to the length of the basioccipital bone (0). In all neosuchians except atoposaurs the basisphenoid is virtually unexposed on the ventral surface of the braincase (1).
5) Primitively in neosuchians an internarial bar is present (0). It is absent in most neosuchians except atoposaurs, some species of *Shamosuchus*, *Alligator*, and in *Osteolaemus tetraspis* (1). This character may be correlated with brevirostry, because it is found only in brevirostrine taxa, but it is not present in all brevirostrine taxa.
6) Primitively in neosuchians a lateral mandibular *fenestra* is present between the dentary, angular, and surangular (0). Atoposaurids, some goniopholidids (e.g., *Goniopholis*), *Bernissartia fagesii* and *Shamosuchus* lack a mandibular *fenestra* (1), whereas a *fenestra* is present in eusuchians and in dyrosaurs. This feature may be correlated with longirostry, because all longirostrine crocodylomorphs have a lateral mandibular fenestra, but it is also present in many brevirostrine taxa.
7) Primitively in neosuchians the retroarticular process of the mandible is short and projects posteroventrally (0). In eusuchians, dyrosaurs, and the supposed goniopholidid *Vectisuchus leptognathus* (BUFFETAUT & HUTT, 1980) the retroarticular process is long and extends posteriorly, often curving posterodorsally (1). This feature may be correlated with longirostry, because all longirostrine crocodylomorphs have an elongate retroarticular process, but it is elongate in all living brevirostrines as well.
8, 9 & 10) Primitively in mesoeucrocodylians all of the vertebrae are amphicoelous, including the first caudal vertebra, but the condition in the immediate outgroups of the Neosuchia is not known. In at least some goniopholidids all of the vertebrae are amphicoelous, including the first caudal vertebra (*Eutretauranosuchus delfsi* MOOK, 1967, U.S. National Museum of Natural History specimen 177121). In *Theriosuchus pusillus* the cervical vertebrae are procoelous and the trunk vertebrae are amphicoelous; at least one anterior caudal vertebra (of British Museum "Natural History" specimen 48216) appears to be opisthocoelous (CLARK 1986), but this latter vertebra could be a biconvex first caudal vertebra that

has been damaged (W. LANGSTON, pers. comm.). In *Bernissartia fagesii* at least some of the cervical and trunk vertebrae are amphicoelous, the first caudal vertebra is biconvex, and at least the second caudal vertebra is procoelous. The only reported vertebrae from *Shamosuchus* are amphicoelous, but the condition in anterior caudal vertebrae has not to our knowledge been investigated. In eusuchians the first caudal vertebra is more strongly biconvex than in *Bernissartia fagesii*, and all other vertebrae are procoelous. We treat this character complex as three separate characters:

8) Amphicoelous cervical vertebrae (0); procoelous cervical vertebrae (1).

9) Amphicoelous caudal vertebra (0); gently biconvex first caudal vertebra, remainder of caudal vertebrae procoelous (1); strongly biconvex first caudal vertebra, remainder of caudal vertebrae procoelous (2). The condition in *Theriosuchus pusillus* is considered unknown because of the various contradictory interpretations of the caudal vertebrae in this form. We treat this character as ordered: 0 – 1 – 2.

10) Amphicoelous trunk vertebrae (0); procoelous trunk vertebrae (1).

11) Primitively in neosuchians hypapophyses (ventrally projecting processes) are absent from all vertebrae (0). A hypapophysis is present on each cervical vertebra of *Bernissartia fagesii* but they are poorly developed (1). In extant crocodylians and dyrosaurs hypapophyses are well developed (2), especially in posterior cervicals and anterior thoracic vertebrae (HOFFSTETTER & GASC, 1969). In *Gavialis gangeticus*, however, hypapophyses are much less developed on the anterior cervical vertebrae than in other extant Crocodylia. We treat this character as ordered: 0 – 1 – 2.

12) Primitively in neosuchians the dorsal osteoderms are arrayed in two longitudinal rows (0). In *Bernissartia fagesii* they are arrayed in four longitudinal rows (1). *Shamosuchus* is reported to have five rows of dorsal osteoderms (KONZUKOVA, 1954), but this is very unusual because in all other crocodylomorphs, fossil and living, there is an even number of dorsal osteoderms. The dyrosaur *Congosaurus bequaerti* was reported by DOLLO (1914, p. 214) to have "quatre rangées longitudinales de plaques dorsales." However, in his detailed description of this material SWINTON (1950) did not repeat this observation, and he commented upon how poorly preserved the osteoderms were in this specimen. Until this feature is demonstrated to be present in *Congosaurus bequaerti* or some other dyrosaur, we will consider it to be unknown for the group.

13) Primitively in neosuchians the dorsal osteoderms have a short process extending anteriorly from the anterior edge, positioned near the lateral edge of the osteoderm (0). The dorsal osteoderms of *Bernissartia fagesii*, dyrosaurs, and eusuchians lack such a process (1).

14) Primitively in mesoeucrocodylians the coracoid is only slightly more than half the length of the *scapula* (0), although the condition in the immediate outgroups of the Neosuchia is unknown. In most neosuchians the coracoid is about as long as the *scapula* (1). This character may be correlated with longirostry, because all longirostrine taxa, where known, have the derived condition, but it is also present in brevirostrine living crocodylians.

15) Primitively in neosuchians the dorsal osteoderms have a flat, unsculpted area on the anteriormost part of the dorsal surface where the overlying osteoderm immediately anterior to it articulates (0). Most eusuchian dorsal osteoderms lack this flat, unsculpted area (1), although in primitive eusuchians and *Osteolaemus tetraspis* at least some of the dorsal osteoderms are imbricated and there is a depression along the anterior edge of the dorsal surface.

16) Primitively in neosuchians the dorsal osteoderms in most of the trunk region are approximately twice as broad as they are long (0). This is true of the medial row of dorsal osteoderms in *Bernissartia fagesii*, and at least some of the dorsal osteoderms of *Leidyosuchus formidablis*. In extant crocodylians all of the dorsal osteoderms are approximately as long as they are broad (1).

CHARACTERS NOT CONSIDERED

In addition to those features that are not considered because they are found only in longirostrine forms, we do not include the following characters in the analysis because 1) they are poorly known among the taxa included in the analysis, 2) there is excessive intraspecific variation, or 3) they vary continuously and are not amenable to an analysis of discrete characters: A) the breadth of the palatines (2,3); B) the shape of the anterior end of the palatines (3); C) the size of the supratemporal *fenestra* and the correlated feature of whether the frontal enters the border of the supratemporal *fenestra* (3); D) the length and shape of the *rostrum*, including the shape of the lateral edge at the contact between the *premaxilla* and *maxilla* (2,3); E) the pattern of muscle scars on the ventral surface of the quadrate (1); F) the pattern of articulation between the prefrontal pillars (1); G) the size and shape of the suborbital fenestra (1,3); H) the relative lengths of the postorbital and squamosal on the skull table (3); I) the breadth of frontals between orbit (3); J) the size of the quadratojugal spine (1); K) the presence or absence of a spine on the postorbital bar (1); L) breadth of postorbital bar (1); M) shape of mandibular articulation surface of the quadrate (1); N) the size and number of palpebrals (1); O) the presence or absence of a "diapophysis" on the axis neural arch (1); and P) the length of the atlas intercentrum (1). The presence or absence of ventral osteoderms is not considered because it is difficult to be certain whether its absence in fossil specimens is real or an artifact and because the condition varies among the outgroups of the Neosuchia.
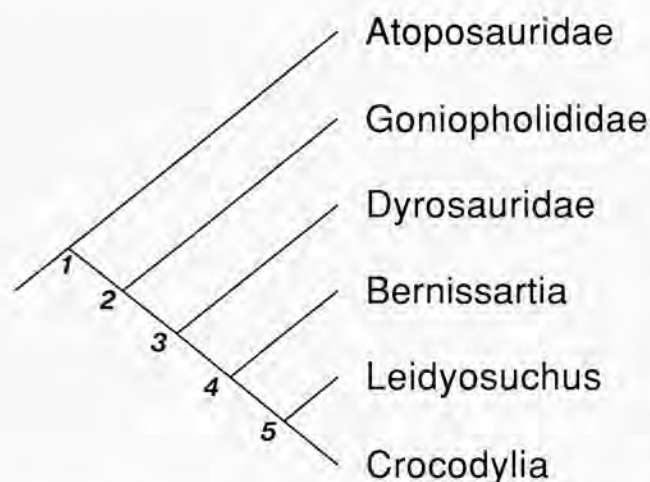
Atoposauridae

Goniopholididae

Dyrosauridae

Bernissartia

Leidyosuchus

Crocodylia

Fig. 3. – Most parsimonious cladogram explaining the character distributions in Table 1. Numbers at nodes correspond with the distribution of synapomorphies in Appendix 1.

RELATIONSHIPS

In a maximum parsimony outgroup analysis (MADDI-SON, *et al.*, 1984) of the character distributions outlined in Table 1, a single cladogram was found to be most parsimonious (Fig. 3). This cladogram indicates that *Bernissartia fagesii* is the sister-taxon to the Eusuchia. This cladogram was constructed using a hypothetical ancestor (all zeros) as a root based on the character discussions above, and treating multistate characters within a single basic taxon as polymorphism rather than uncertainty. This is justified because many of our basic taxa are associations of several species into putative monophyletic groups. Changes within single basic taxa were counted to account for polymorphisms. This clado-gram has a length of 28 steps if only the informative characters (those characters not changing uniquely on terminal branches) are counted. The consistency index for the distribution of these characters is .704. At a length of 29 an additional tree preferring dyrosaurs as the first eusuchian sistergroup was found. However, all of the 9 trees with a length of 31 or less preserved the monophyly of the eusuchian taxa included in this analysis (*Leidyosuchus* and the Crocodylia).

The characters considered in this analysis indicate that atoposaurs are not as closely related to eusuchians as are goniopholidids, dyrosaurids, and *Bernissartia fagesii*. Even if the isolated caudal vertebra that appears to be ophisthocoelous in *Theriosuchus* is considered to be bi-convex, the evidence does not favor atoposaurs being more closely related to eusuchians than are goniopholi-dids. Thus, procoelous cervical vertebrae apparently evolved convergently in *Theriosuchus* and in eusuchians. The close relationships between eusuchians and dyro-saurs indicated by this analysis is surprising and to our knowledge has not been previously suggested. It is outsi-de the scope of this work to examine the question of dyrosaur relationships in detail. The relationships among dyrosaur taxa have not been studied in depth, therefore

the question of primitive dyrosaur character conditions is unknown until such studies are undertaken.

The interrelationships of *Bernissartia fagesii* and *Shamo-suchus* are unclear at present. With only one exception they share the same states of all of the characters included in the analysis where the condition is known for *Shamo-suchus*. The one character that is not shared is variably present in *Shamosuchus*; unlike in *Bernissartia*, an inter-narial bar is present in several species of *Shamosuchus*, but *S. major* EFIMOV, 1983 is figured as lacking a bar (EFIMOV, 1983, fig. 2). The general shape of the skull is very similar in the two genera, and one species, *S. ances-tralis* KONZUKOVA, 1954, has bulbous teeth similar to those of *Bernissartia fagesii* (KONZUKOVA, 1954). The narrower frontals of *Bernissartia fagesii* may be helpful in interpreting the relationships of the two forms, but the extensive variability in frontal width among eusuchians makes it a difficult character to evaluate. Of perhaps more importance is the broad palatine and small suborbi-tal fenestra of *Shamosuchus*, which is very similar to the conditon found in extant alligatorids but unlike the nar-row palatines and large suborbital fenestrae found in other neosuchians. Until *Bernissartia fagesii* is directly compared with the extensive material of *Shamosuchus* in the USSR we prefer to leave the interrelationships of these two genera unresolved.

The clade composed of *Leidyosuchus* and the living Crocodylia is supported by five or six characters. The differences in the number of character changes at this node are due to differences in the optimization of homo-plasious characters to the tree. Using accelerated trans-formation, in which parallel losses of characters are maximized, the clade composed of *Leidyosuchus* and the Crocodylia is supported by changes in characters 1, 8, 9, 10, and 15. Using delayed transformation, in which parallel gains are maximized, an additional character (character 11) supports this clade. To aid in the interpre-tation of character stability and change we have included character consistency indices in Table 1.

The characters occurring on the branch leading to *Lei-dyosuchus* and the Crocodylia do not constitute a dia-gnosis of the Eusuchia, however. The Eusuchia additio-nally includes *Hylaeochampsa vectiana* and *Stomatosu-chus inermis* (CLARK, 1986), and this necessitates a modi-fication to the diagnosis of the group. Elongate cervical hypapophyses (state 2 of character 11) are found in *Leidyosuchus* and all extant crocodylians, but they are absent in *Stomatosuchus inermis*. In his description of *Stomatosuchus inermis*, STROMER (1925, p. 7) stated "Auffällig ist das völlige Fehlen einer ventralen Median-leiste und einer deutlichen Hypapophyse im Gegensatz zu allen recenten *Crocodilia*. "However, the illustration of a cervical vertebra accompanying his description (pla-te 1, figure 4) shows a distinct protuberance on the ven-tral surface of the *centrum*, similar to the small but distinct hypapophyses of *Bernissartia fagesii*. Similarly, the cervical vertebrae of the primitive eusuchian *Dolicho-champsa minima* (GASPARINI & BUFFETAUT, 1980) and isolated procoelous cervical vertebrae from the

Cretaceous of Australia (MOLNAR, 1980) lack elongate hypapophyses, so that these forms all lie outside the clade comprising *Leidyosuchus* and living crocodylians.

The diagnosis of the Eusuchia is problematic because several of the apparent derived characters of the group cannot be determined for *Hylaeochampsa vectiana* and *Stomatosuchus inermis*. Indeed, the single derived eusuchian character that can be determined for *Hylaeochampsa vectiana*, the choana lying within the pterygoids, cannot be verified in *Stomatosuchus inermis* (STROMER, 1925, p. 5), and the procoelous cervical and trunk vertebrae of the latter cannot be verified in *Hylaeochampsa vectiana*. (If the procoelous vertebrae from the Wealden of England that were described as *Heterosuchus valdensis* by SEELEY (1887) are referable to *Hylaeochampsa vectiana* then procoelous trunk vertebrae are present in this taxon; however, individual specimens containing elements diagnostic of both taxa are not known, so the synonymy has yet to be established.) The phylogenetic position of *Stomatosuchus inermis* is less clear than that of other eusuchians because the only feature placing it within the Eusuchia (procoelous trunk vertebrae) may occur independently in another noneusuchian taxon, *Theriosuchus pusillus*. Unfortunately, all of the material of this taxon was destroyed during World War II, and STROMER's description and figure are the only remaining evidence of this taxon until new material comes to light.

This problem in diagnosing a group in which the most primitive members are poorly known is a general one in paleontology. If the poorly known taxa are taken into consideration, then the diagnosis must be restricted to those characters that can be verified in these taxa. In extreme instances such as this, it is impossible to diagnose the group at all without making untestable assumptions about the condition of these characters in the poorly known taxa. Yet, they cannot be ignored unless we are willing to make subjective and arbitrary determinations of how completely known a taxon must be before it affects our diagnosis of the group.

In diagnosing the Eusuchia we choose to maximize the number of potential synapomorphies by assuming that the derived condition is present in the poorly known primitive forms. As more information becomes known about the distribution of these characters among primitive members of the group, the diagnosis will almost certainly be revised to include fewer of these characters. Furthermore, when the form from the Glen Rose Formation of Texas is described (LANGSTON, 1974) the diagnosis of the Eusuchia will need further modification.

The following features are considered here to diagnose the Eusuchia: 1) the *choana* lies completely within the pterygoids and is positioned near their posterior ends (unknown for *Stomatosuchus*), 2) the cervical and trunk vertebrae are procoelous (convergently evolved in *Theriosuchus*, unknown for *Hylaeochampsa*), 3) the condyles on the biconvex first caudal vertebra are strongly convex (unknown for *Hylaeochampsa vectiana* and *Stomatosuchus inermis*), and 4) the dorsal osteoderms lack

a smooth, raised area anteriorly on the dorsal surface where the osteoderms are imbricated (unknown for *Hylaeochampsa vectiana* and *Stomatosuchus inermis*). These characters were common to alternative optimizations of characters to the tree in Fig. 3. A lateral mandibular *fenestra* may also be diagnostic of this clade, but it can be interpreted either to have evolved separately in dyrosaurs and eusuchians or to have evolved in the common ancestor of dyrosaurs, *Bernissartia fagesii* and eusuchians and to have been lost in *Bernissartia fagesii*. The only feature that BENTON & CLARK (1988) recognized as diagnosing the crocodylian crown group was a narrow, parallel-sided scapular blade, in contrast to the expanded dorsal edge of the scapula that is found primitively in neosuchians. However, an expanded scapular blade is found in some specimens of extant species. The features of the osteoderms cited above appear to diagnose the extant Crocodylia, but the relationships of the several species of *Leidyosuchus* and the diagnosis of the living Crocodylia are in need of further study.

The similarity between the dorsal osteoderms of *Bernissartia fagesii* and those of *"Alligatorium" paintenense* are striking and possibly indicate a close relationship. In both forms the dorsal osteoderms have two keels in a similar position rather than the single keel found on the dorsal osteoderms in many crocodylomorphs. Apparently in *"A." paintenense*, however, only two rows of dorsal osteoderms are present. Unfortunately, the unique type specimen of this taxon was destroyed during World War II, and all that remains is a cast. It is therefore not possible to dermine if perhaps the lateral rows of dorsal osteoderms were folded beneath the specimen, which is exposed in dorsal view. The dorsal osteoderms of the supposed goniopholidid *Vectisuchus leptognathus* (BUFFETAUT & HUTT, 1980) also have two keels, but unlike in the other two taxa one of these keels is very close to the lateral edge and the other is curved.

IMPLICATIONS OF *Bernissartia fagesii* FOR RELATIONSHIPS AMONG EXTANT CROCODYLIANS

The relationships among extant crocodylians have recently become a point of contention due to the conflicting results of biochemical and morphological analyses. Traditionally (e.g., WERMUTH, 1953), three groups of living crocodylians have been recognized, often at the familial taxonomic level – gharials (Gavialidae), alligators and caimans (Alligatoridae), and crocodiles (Crocodylidae). The false gharial, *Tomistoma schlegeli* MÜLLER, 1838 has been considered on morphological grounds to be a crocodile. Biochemical analyses of immunological distance and protein allozymes (DENSMORE, 1983), however, indicate that the false gharial forms a clade with the gharial and not with the crocodiles.

Following the publication of the biochemical analyses, BUFFETAUT (1985) re-evaluated the morphological evidence and concluded that *Tomistoma schlegeli* is indeed closely related to gharials. BUFFETAUT did not, however, utilize outgroups in his analysis, and it is unclear how he arrived at the character polarities that he proposed. Due

to its close relationship to eusuchians, *Bernissartia fagesii* is a crucial taxon in determining character polarities within the group. Because it is equally parsimonious to consider dyrosaurids as the eusuchian sistergroup (Fig. 3), dyrosaurids also bear importantly upon this question. Relationships among dyrosaurids are unclear, however, and dyrosaurid morphology has not been studied in detail sufficient for our purposes, therefore primitive character conditions and character variation within the group is difficult to assess.

When *Bernissartia fagesii* is used to polarize the characters discussed by BUFFETAUT his conclusion is not supported (as discussed in more detail by NORELL, 1988 and NORELL, 1989). The morphology of *Bernissartia fagesii* is instead consistent with the hypothesis (NORELL, 1988) that gharials are the sister-group to all other crocodylians.

One of the features cited by BUFFETAUT (1985) as a derived feature of gharials and *Tomistoma schlegeli* was a large spine on the quadratojugal extending anterodorsally into the infratemporal fenestra. The presence of just such a spine on the quadratojugal of the Spanish specimen of *Bernissartia*, and in the supposed goniopholidid *Eutretauranosuchus delfsi* (MOOK, 1967), strongly argues that this feature is primitive for eusuchians.

A second feature cited by BUFFETAUT was the presence of a small spine on the anterior surface of the postorbital bar in adult *Gavialis gangeticus* and juvenile *Tomistoma schlegeli*. Its presence in *Bernissartia fagesii* indicates that this, too, is a primitive eusuchian feature that has been retained in *Gavialis* and modified in other crocodylians.

A strikingly primitive feature of *Gavialis gangeticus* is that, as in *Bernissartia fagesii*, the dorsal osteoderms occur in only four longitudinal rows rather than the six or more rows found in other extant crocodylians (ROSS & MAYER, 1983). An additional lateral row of enlarged keratinous scutes is present in young individuals of *Gavialis gangeticus* but osteoderms apparently never ossify and these lateral rows are absent in adults (ROSS & MAYER, 1983). Such unossified rows could have been present in *Bernissartia fagesii* but of course only those osteoderms that ossified are preserved in the fossil record. The lack of the lateral rows of osteoderms therefore indicates that alligatorids and crocodylids, including *Tomistoma schlegeli* share the derived feature of having six or more rows of dorsal osteoderms.

The pattern of bones surrounding the infratemporal space in *Bernissartia fagesii* indicates that several features found in gavialids and alligatorids are primitive for eusuchians, and that crocodylids and *Tomistoma schlegeli* share the derived features (NORELL, 1988). The first of these is a posterior process of the ectopterygoid that lies at the base of the postorbital bar on the internal surface of the jugal. This process is present in *Bernissartia fagesii*, alligatorids, and gavialids, but it is absent in crocodylids and *Tomistoma schlegeli*. The morphology of the posteroventral corner of the infratemporal *fenestra*, as seen in ventromedial view, is also similar in alligatorids, gavialids, and *Bernissartia fagesii*. This corner is formed by the quadratojugal, which extends anteriorly along the medial surface of the jugal ventral to the infratemporal *fenestra*. In crocodylids there is no such extension of the quadratojugal and the jugal forms the posteroventral angle of the infratemporal *fenestra*. Alligatorids and gavialids also have a distinctive process descending posteroventrally from the postorbital along the anterior edge of the quadrate; this process may be present in *Bernissartia fagesii*, however its presence is difficult to ascertain because sutures in this region are unclear.

The great breadth of the postorbital bar in *Bernissartia fagesii* suggests that the similar condition in *Gavialis gangeticus* is a primitive eusuchian feature rather than a specialization of gavialids. The narrower bar of crocodylids and alligatorids would therefore be a shared derived feature. The bar of at least some species of *Shamosuchus* does not appear to be broad (KONZUKOVA, 1954), but that of *Leidyosuchus formidabilis* is unusually broad (ERICKSON, 1976).

One feature of the ectopterygoid may indicate that crocodylids and gavialids have retained a primitive condition that is modified in alligatorids. The anterior process of the lateral part of the ectopterygoid in *Bernissartia fagesii* and most crocodylids borders the maxillary tooth row, whereas in alligatorids the *maxilla* forms a shelf posteromedial to the tooth row that excludes the ectopterygoid from bordering on the tooth row (NORELL, 1988). At least one species of *Shamosuchus, S. ulgicus* EFIMOV, 1983 is figured as having a maxillary border to the *alveoli* (EFIMOV, 1983).

The dorsal osteoderms of *Bernissartia fagesii* are unusual among "mesosuchians" in having well-developed keels. Keels are present on the dorsal osteoderms of all extant crocodylians (although they are sometimes absent on the osteoderms of the medial row), but only one keel is present, in contrast with the paired keels of *Bernissartia fagesii*. Keels are absent from the osteoderms of primitive eusuchians, however, including *Leidyosuchus formidabilis* (ERICKSON, 1976), thoracosaurs (TROEDSSON, 1924), "*Crocodylus*" *clavis* COPE, 1872 (U.S. National Museum specimen 12719), and the primitive alligatorid *Brachychampsa montana* (NORELL, CLARK & HHUTCHISON, in prep.).

Revised diagnosis

Bernissartia fagesii DOLLO, 1883

TYPE-MATERIAL: DOLLO did not designate a type specimen, so BUFFETAUT (1975) designated IRScNB R 46, a skeleton with cranium and mandibles, as the lectotype. A second specimen included by DOLLO in the original description, a partial skeleton lacking a skull, is the paralectotype IRScNB R 118.

FORMATION AND AGE: Bernissart Clay, Berriasian (?) – Lower Aptian, Lower Cretaceous.

TYPE-LOCALITY: "Fosse Sainte-Barbe" coal mine, Bernissart, Hainaut, Belgium.

REFERRED SPECIMENS: 1) Isolated teeth from the Wealden of the Isle of Wight have been referred to the genus (BUFFETAUT & FORD, 1979), but their identification rests largely upon their occurrence in the same formation as the type specimen. BUFFETAUT & FORD also reviewed several other possible occurrences of *Bernissartia* outside of the Wealden based upon isolated teeth. 2) A fragmentary postcranial skeleton from the Wealden of Hastings, England (British Museum «Natural History» specimen 37712) is probably referable to *Bernissartia* (BUFFETAUT & FORD, 1979). 3) A skull and skeleton of this genus from near Galve, Spain (BUSCALIONI, *et al.*, 1984; BUSCALIONI, 1986), in the private collection of J.M. HERRERO, may belong to a different species. It is from Lower Cretaceous beds of early Barremian age.

REVISED DIAGNOSIS: *B. fagesii* is distinguished from all other crocodylomorphs by the presence of a small depression on the dorsal surface of the quadrate and the combination of a biconvex first caudal vertebra, procoelous caudal vertebrae, and amphicoelous cervical and trunk vertebrae. It is unusual in having enlarged, bulbous posterior maxillary and dentary teeth similar to those of somme alligatorids, a broad postorbital bar similar to that of *Gavialis gangeticus*, a mandible lacking a lateral *fenestra*, mandibular teeth 3 and 4 lying in a common *alveolus*, dorsal osteoderms each with two longitudinal keels, and ventral osteoderms. It differs from all other crocodylomorphs except *Shamosuchus* in having the combination of a *choana* bordered anteriorly by the palatines, amphicoelous trunk vertebrae, and dorsal osteoderms in more than two longitudinal rows. Based upon the published descriptions of the several *Shamosuchus* species, *Bernissartia fagesii* differs in having a slight notch on the ventral edge of the *premaxilla/maxilla* contact, a notch in the lateral edge at this contact that is slightly deeper than in *Shamosuchus*, a narrower interorbital breadth to the frontal, larger suborbital fenestrae and narrower palatines, a maxillary shelf excluding the ectopterygoid from the medial borders of the posterior *alveoli*, and in lacking a spectacle or other such ridges immediately anterior to the orbits.

Acknowledgments

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Appendix

Synapomorphies for taxa in the cladogram in Figure 3. Changes in characters refer to numbers of character descriptions in the text. ACCTRANS optimizes for convergent reversals and DELTRANS for convergent gains. Synapomorphies that are common to both optimizations are indicated in bold face. For specifics regarding these protocols consult the documentation for PAUP version 3.0 © David Swofford, Illinois Natural History Survey.

ACCTRANS
    Node 1 to 2   2, **4, 5, 14**
    Node 2 to 3   **1, 2**, 4, 5, **11**, 12, **13**
    Node 3 to 4   **3, 9**
    Node 4 to 5   **1, 8, 9, 10, 15**

DELTRANS
    Node 1 to 2   **4, 5, 14**
    Node 2 to 3   **1, 2, 11, 13**
    Node 3 to 4   **3, 9**, 12
    Node 4 to 5   **1, 8, 9, 10**, 11, **15**