

# The small crocodile *Bernissartia fagesii* from the Lower Cretaceous of Galve (Teruel, Spain)

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## Abstract

A complete skeleton of *Bernissartia fagesii* from the Lower Barremian of Galve (Spain) is described. This individual is probably younger than the type of *B. fagesii* from Belgium, its ontogenetic age, 4 to 6 years, has been estimated by a direct method based on skeletochronology. *Bernissartia* displays a unique combination of character-states: frontal very narrow between the orbits, no lacrimonasal suture, palatal cavity with a warped lateral contour, orbits with an anterolateral notch, and bulky teeth in the rear of the maxilla and mandible.

*Bernissartia fagesii* has hitherto been a controversial species, its phylogenetic position inferred primarily from the uncertain position of the *choana* and of confused interpretation of the vertebral morphology. The Spanish specimen demonstrates that the *choana* is almost surrounded by the pterygoid and the vertebral centra are best described as procoelous. An analysis of character polarities of cranial and postcranial features yielded two cladograms, where *Bernissartia* is the sister group of *Leidyosuchus* (Eusuchia). Both taxa share some traits that are not present in the other taxa within the clade Neosuchia (here represented by the genera *Theriosuchus*, *Hyposaurus* and *Goniopholis*): four rows of dorsal osteoderms, scutes without a lateroanterior peg, first biconvex caudal centrum and procoelous vertebrae. But with respect to Eusuchia *Bernissartia* retains some primitive character-states in the dorsal armor and skull. It is therefore regarded as one of the closest related taxa to the Eusuchia, within the Neosuchia clade.

**Key words:** Crocodylomorpha, Neosuchia, Phylogeny, Skeletochronology, Lower Cretaceous, Spain.

## Resumen

Se describe el esqueleto completo de un ejemplar procedente del Barremiense inferior de Galve (Teruel), atribuido a *Bernissartia fagesii*. El ejemplar es probablemente un individuo más joven que el tipo de *B. fagesii* de Bélgica. Su edad ontogénica (4 a 6 años) ha sido estimada mediante el método directo de esqueleto-cronología. *Bernissartia* presenta una única combinación de estadios de carácter: frontal estrecho entre las órbitas, sutura lacrimo-nasal ausente, cavidad palatina con un contorno alabeado, órbitas con una escotadura anterolateral, dientes voluminosos en la zona posterior del maxilar y mandíbula. *Bernissartia fagesii* ha sido, por otra parte, una especie controvertida, su posición filogenética fue determinada por la incierta posición de la coana y la equivocada interpretación de su morfología vertebral. El ejemplar español demuestra que la coana está casi delimitada por el pterigoides y que los centros vertebrales se ajustan mejor a la definición de procelia. A partir de un análisis de polaridad de caracteres en rasgos craneales y posteraneales, se proponen dos cladogramas donde *Bernissartia* es el grupo hermano de *Leidyosuchus* (Eusuchia). Ambos taxa comparten algunos rasgos que no están presentes en los restantes taxa del clado

Neosuchia (representado por los géneros *Theriosuchus*, *Hyposaurus* y *Goniopholis*): cuatro filas de osteodermos dorsales, osteodermos sin cejilla anterolateral, primera vértebra caudal biconvexa. Pero *Bernissartia* retiene algunos estadios de carácter primitivos respecto a Eusuchia, en la armadura dorsal y cráneo. Por consiguiente, es considerado como un taxon estrechamente emparentado con Eusuchia, dentro del clado Neosuchia.

**Palabras clave:** Crocodylomorpha, Neosuchia, Filogenia, Esqueleto-cronología, Cretácico Inferior, España.

## Introduction

In a preliminary note on the crocodiles from Bernissart, DOLLO (1883) gave the first description of *Bernissartia fagesii*, and proposed a monotypic family Bernissartidae for the taxon. DOLLO originally had two specimens, from the Bernissart Clay (Lower Cretaceous) at Bernissart at his disposal. He described and figured only the better preserved of the two (registered as IRScNB R46). In 1975 BUFFETAUT published a paper on *B. fagesii*, and discussed the more controversial and noticeable characters of the species. Among the two specimens available from Bernissart BUFFETAUT selected IRScNB R46 as the lectotype of *B. fagesii*. No other complete specimens were known, but isolated teeth from the Wealden of England and Spain had been reported (BUFFETAUT & FORD, 1979; ESTES & SANCHIZ, 1982; BUSCALIONI & SANZ, 1984; SANZ *et al.*, 1984). Some years ago, a new complete specimen of *Bernissartia* was discovered in the Lower Barremian of Spain (Galve, province of Teruel). The skull was partially described in a preliminary study, and referred to as an immature individual of *Bernissartia* sp. (BUSCALIONI *et al.*, 1984).

*Bernissartia fagesii* has been a controversial species of uncertain phylogenetic position. It has been regarded either as a "mesosuchian" level crocodylian, within a new family Bernissartidae (DOLLO, 1883; BUFFETAUT, 1975) or as a new goniopholidid (LYDEKKER, 1888). KALIN (1955) regarded it as a more advanced crocodile that should be included in the Eusuchia. Much of this controversy derives from differing interpretations of the relationships of the *choana* and the pterygoid bones, and

the nature of the articulation between the vertebral centra, the classical bases for separating the "mesosuchian" and eusuchian grades.

Of the two taxonomic proposals (a "mesosuchian" or eusuchian), the first was considered as more reasonable because *Theriosuchus* OWEN, 1879 was proposed as the probable ancestor of the Eusuchia (JOFFE, 1967), owing to the backward position of the *choana* and the presence of semiprocoelous vertebral centra. However, recent studies on character distribution among a large number of Mesozoic crocodylomorphs (CLARK, 1986) and of a few "metamesosuchians" (BUSCALIONI, 1986) suggest that *Theriosuchus* and the Atoposauridae were more distantly related to the eusuchians than other families; in this sense, *Bernissartia* was closer to the Eusuchia.

We think the new specimen from Galve would help to complete the knowledge of the genus *Bernissartia*. We have compared the Spanish and Bernissart specimens by means of an analysis of character polarities, and we have included in this analysis some other taxa (see discussion). Our aim is not to propose a precise phylogenetic relationship of *Bernissartia*, but to define and discuss those apomorphic traits shared by this genus and its probable sister group. New data provided by the Spanish specimen are evaluated to see if they may modify the proposed relationships of *Bernissartia* as the closest sister group of the Eusuchia clade.

### Systematic paleontology

CROCODYLOMORPHA (WALKER, 1970)

NEOSUCHIA (BENTON & CLARK, 1988)

Family BERNISSARTIDAE DOLLO, 1883

Genus *Bernissartia* DOLLO, 1883

*Bernissartia fagesii* DOLLO, 1883

Horizon – *Berriasian* (?)–Lower Aptian

Specimens – Lectotype: I.R.Sc.N.B. R46 (Institut Royal des Sciences Naturelles, Brussels) from the Bernissart Clay at Bernissart (Belgium), and CR82 from the clay pit ("Cerrada Roya") of Galve (province of Teruel, Spain).

*Emended Diagnosis* – Small sized crocodile, with mesorostral skull. Frontal very narrow and slightly concave along the interorbital space. No lacrimo-nasal suture. Splenial is scarcely or not involved in the mandibular symphysis. Palatal cavity with a warped contour at its lateral side. Orbits with an anterolateral notch and cur-

ved lateral edge. Posterior teeth of the *maxilla* and dentary bulky, with blunt crowns, the last four teeth with a notable mesiodistal length. The third and fourth mandibular teeth of "caniniform" type. Dorsal armor containing 17-19 transverse row of 4 osteoderms (not including nuchals and caudals, both with two osteoderms). Paraxial scutes with one or two keels and without a lateroanterior peg. First caudal vertebra biconvex. Centra with low and flat posterior condyles but deep cotyles. *Choana* almost surrounded by the pterygoid, not divided by a sagittal *septum*.

### MATERIAL

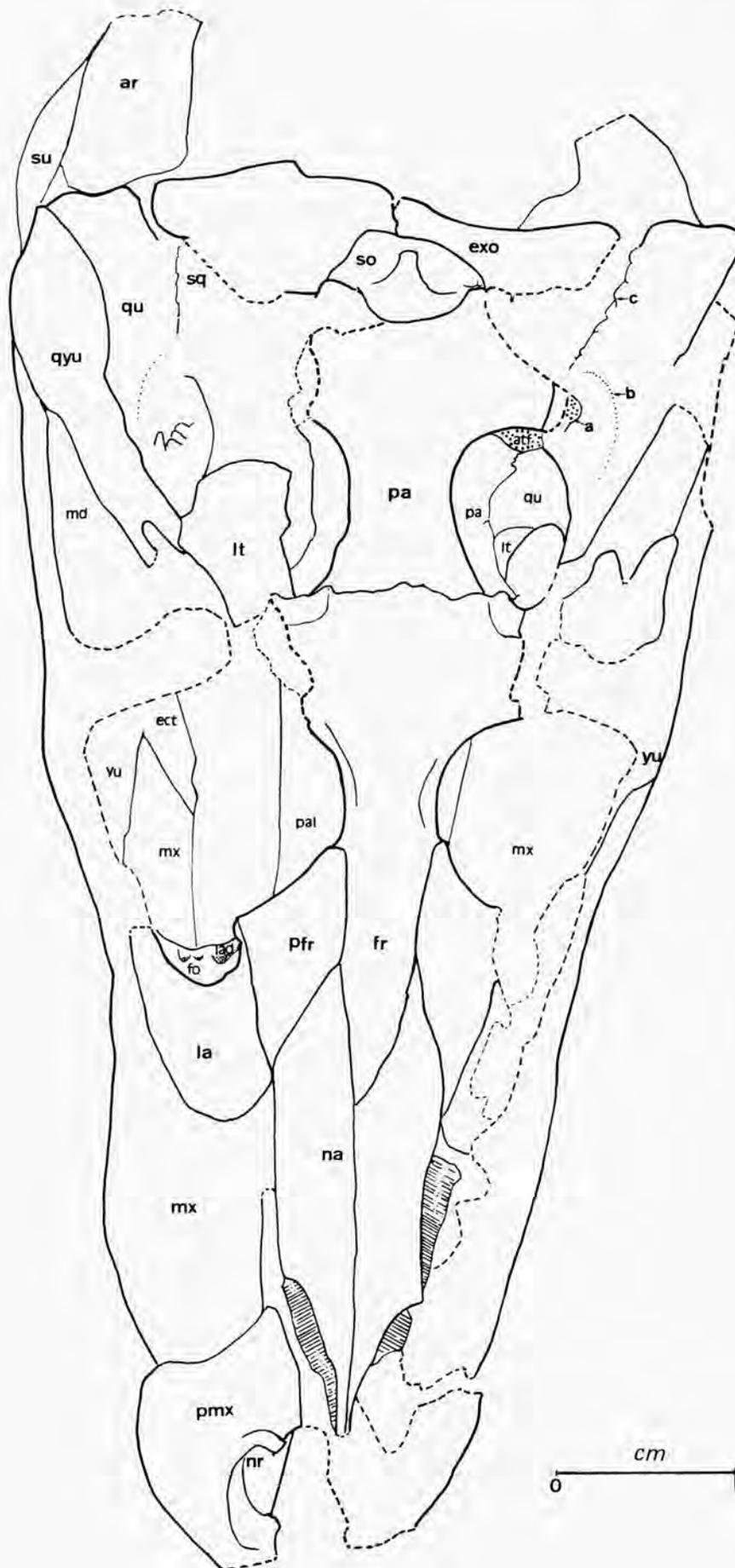
The Galve crocodile was found in a clay pit, Lower Barremian in age (DIAZ *et al.*, 1984). The skeleton was exposed in dorsal view showing a slight dorsoventral compression mainly in the postcranial region. Thus, the dermoskeleton hides the axial skeleton. The specimen belongs to a private collector, but the skull, that was removed from the matrix, is provisionally housed at the Universidad Autonoma in Madrid. The detached skull was completely prepared, and the remainder of the skeleton is kept as disarticulated elements: dermoskeleton with axial parts, and appendicular elements. The initials CR refer to the topographic location in Galve, Cerrada Roya. CR82-000 to CR82-003 include four successive disarticulated parts of the dermoskeleton (cervical, anterior dorsal, posterior dorsal, sacral and caudal). CR82-01 left *femur*, CR82-02 *ulna*, CR82-03 *radius*, CR82-04 right *humerus*, CR82-05 distal fragment of the *tibia*, and CR82-06 proximal and distal tarsals. These elements have been freed from the clay matrix.

### DESCRIPTION

Skull (Plate 1). The dorsal part of the skull is skewed slightly to the left. A fracture at the level of the fronto-nasal suture has slightly displaced the snout laterally to the axial plane. The snout also displays some fractures in the premaxillo-maxillary area, and the anterior tips of the *premaxillae* are broken away. The bones are thin, ornamented with shallow pits in the frontal and parietal. The skull is low with a *rostrum* of medium length (preorbital/cranial length ratio about 0.50-0.60). The squamosals and postorbitals are damaged dorsally, thus exposing the anterior processes of the quadrates and quadratojugals (Figure 1).

The supratemporal *fenestra* is smaller than the orbit (supratemporal *fenestra* / orbital length ratio 0.59).

Fig. 1 – Schema of skull (CR82) of *B. fagesii* from the Lower Cretaceous of Galve (Spain) in dorsal view. ar, articular; atf, anterior temporal *fenestra*; ect, ectopterygoid; exo, exoccipital; fr, frontal; fo, foramina; la, lacrimal; lad, lacrimal duct; lt, laterosphenoid; md, mandible; mx, *maxilla*; na, nasal; nr, external *nares*; pa, parietal; pfr, prefrontal; pmx, *premaxilla*; qu, quadrate; qyu, quadratojugal; so, supraoccipital; sq, squamosal; su, surangular; yu, jugal. Arrows indicate: a-otic recessus; b-otic notch; c-suture between squamosal and quadrate. Striped area represents the sutural surfaces of the nasals. Broken lines delimit the damaged areas of the specimen.



Their long axis is parasagittal. In the temporal *fossa*, the lateral expansions of the parietal occupy almost all the medial edge of the superior temporal *fossa* and the frontal enters in the very anterior margin of the supratemporal *fenestra*. The laterosphenoid lies anteromedially within the *fossa*. The quadrate forms the lateral border of the temporal *fossa*, showing posteromedially a long suture with the parietal. A small anterotemporal *foramen* is present. In the right supratemporal *fenestra* some of the elements that comprise the *fossa* are disarticulated, and the lateromedial surface of the laterosphenoid is exposed (Figure 1).

The parietal is sagittally long, and its width is about the same all along the bone. In the Belgian specimen the parietal bar is crushed along the midline, which makes it appear shorter than in the Spanish specimen. The fronto-parietal suture is forward. The postero-medial edge of the parietal is slightly concave; a smoothly developed parasagittal knob occurs laterally at either side of this concavity, probably at the parieto-squamosal suture. There is no dermoccipital spine.

The posterior contours of the squamosals can be interpreted in the Galve specimen, in relation to the exoccipitals, and posterolaterally in relation to the quadrates. They are posterolaterally expanded, as occurs in the Belgian *B. fagesii*. Only the anterior portion of the parieto-squamosal suture is shown in the specimen.

The frontal is very narrow between the orbits (about 4.5 mm in width), is slightly concave, but this is more evident in the Belgian specimen. A long acute anterior process projects between the nasals anteriorly. The frontal is almost unornamented in its anterior part.

The postorbital is damaged, and the postorbital bar is crushed. It probably was sub-dermal. Part of the fronto-postorbital suture can be seen better on the left side of the specimen. In the Belgian specimen, the postorbital is large with squared lateral edges. The suture with the frontal is medially placed.

The infratemporal *fenestra* is triangular, the lateral side is relatively long. It is bordered by the quadratojugal posteriorly and laterally by the jugal, although the quadratojugal probably forms a small part of the posterolateral side of the infratemporal *fenestra*.

The quadratojugal is narrow in its anterior part, and does not reach the base of the postorbital bar (Figure 1). A relatively long *spina quadratojugal* is present. Posteriorly the quadratojugal broadens and reaches the lateral condyle of the quadrate, but it does not participate in the cranio-mandibular articulation. It is dorsally ornamented except for the most posterior tip (the Belgian specimen is unornamented laterally). This tip is accentuated by a pronounced notch lateroventrally. The quadratojugal seems to be deep, in lateral view, although it is partly obscured by the dorsoventral crushing.

The jugal seems to be wide in its anterior part. It is poorly preserved mainly in its orbital edge (Figure 1). Posteriorly the lateral ornamented face of the jugal is vertical. The jugal is elevated below the infratemporal *fenestra* and its ventral outline is straight. Its ventral edge is relatively

short anteroposteriorly because the *maxilla* extends far backwards and the jugal has a short suture with the quadratojugal.

The dorsal surface of the quadrates may be followed anteroposteriorly. Both otic notches and the otic recessus can be recognized. The quadrates do not extend posteriorly beyond the level of the occipital condyle. The trochlear section is trapezoidal and high. The exterior condyle expands laterally and the medial condyle expands ventrally. The intercondylar area is shallow concave. In the dorsal face of the quadrate a crest runs from the *trochlea* to the base of the paroccipital process. This crest delimits a medial subvertical face of the quadrate, from the dorsal one.

The occipital region is not fully exposed, some cervical vertebrae remain in articulation with the skull, and the matrix hides the ventral part of the occipital region.

The supraoccipital is slightly bent in the specimen. It is divided sagittally from its top to bottom by a thick axial crest. The median joint of the opposite exoccipitals clearly separates the supraoccipital from the *foramen magnum*. At either side of the nuchal crest, the postoccipital processes are placed just below the parietal knobs.

The exoccipitals have a rough external surface with tiny pits. In the lectotype of *B. fagesii* and in the specimen from Galve the exoccipitals parallel an anterodorsal-posteroventral plane, but the preservation is poorer in the Spanish specimen. The anterodorsal plane close to the squamosal is not as deep as in the Belgian *Bernissartia* specimen. This may be due to an ontogenetic cause. Each exoccipital contacts the dorsomedial face of the quadrate laterally, where the crest of the quadrate ends. Similarly, in the Belgian specimen the lateral edge of the exoccipital is curved and overhangs the dorsomedial process of the quadrate, thus, in ventral view, the exoccipital overlaps the quadrate.

The orbits have a distinctive outline, showing an anterolateral notch that contrasts sharply with their curved anteromedial contours. The orbits are 10-11 mm wide and 15-16 mm long. The interorbital distance (4.6 mm) is less than the width between the supratemporal *fenestra*. The orbits are bordered by unornamented rims. In the lectotype of *B. fagesii*, the orbits are connected laterally by a convex expansion of the jugal (this area is broken away in the Galve specimen).

The nasals are relatively wide, especially posteriorly end where the width is about 1/3 that of the snout. A slender anterior process of the opposing nasals projects toward the nares, but it is not clear that it reached the posterior edge of the opening. The naso-premaxillary suture is long. It is disarticulated in the Galve specimen (Figure 1). The prefrontal is subtriangular in shape, with an acute anterior end. The prefrontal is in contact with the nasal all along its posterior edge. It is unornamented except for an area in front of the orbits. In *B. fagesii*, the orbital margin of the prefrontal is very prominent. The descending pillar of the prefrontal reach the palatines. It is thick, being wide above and having a probably broad medial process. The prefronto-lacrimal suture is distinct

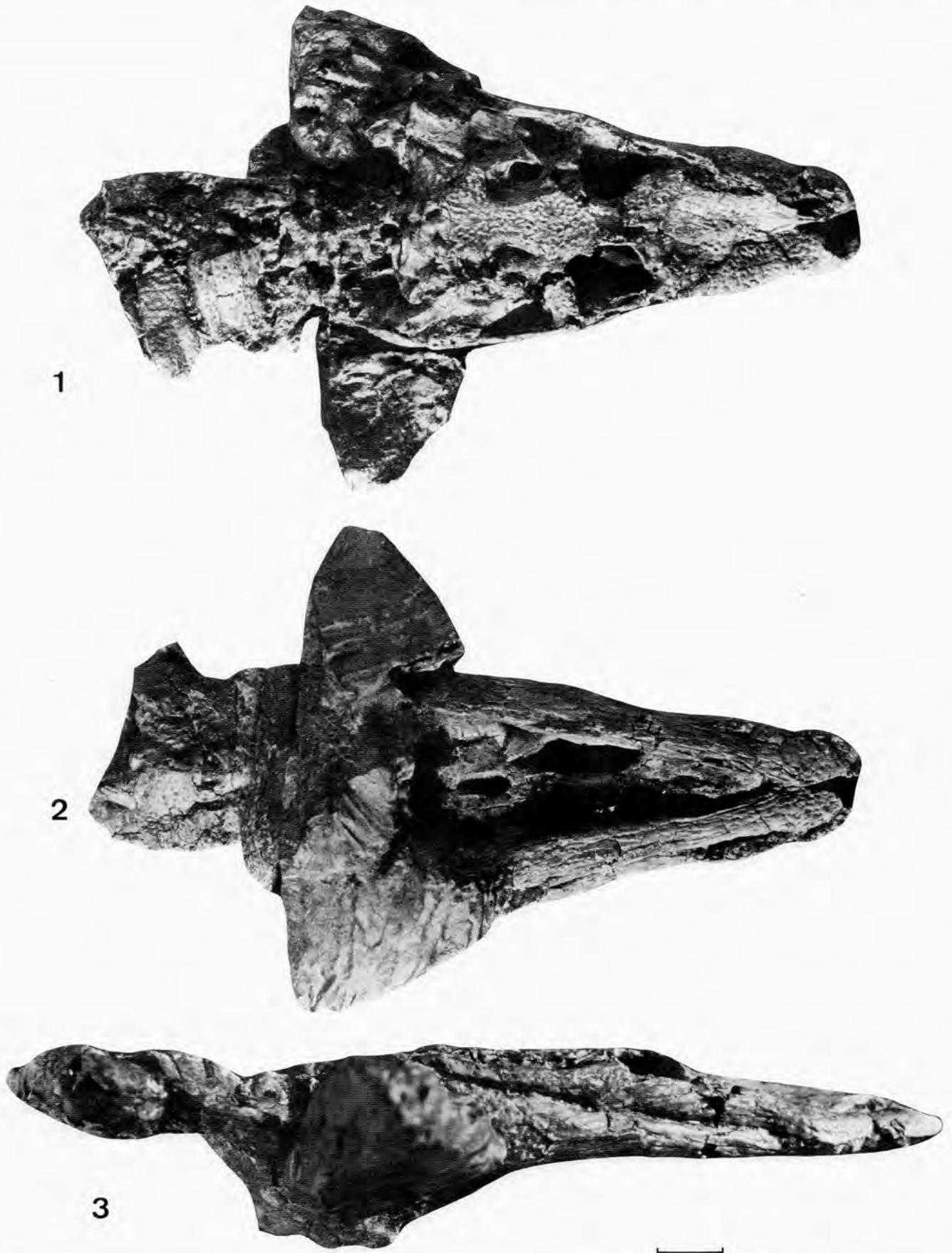


Plate 1 – Skull of *Bernissartia fagesii* from the Lower Cretaceous of Spain. The specimen has the cervical vertebrae exposed. 1. Dorsal view; 2. Ventral view; 3. Lateral view (right side). Scale bar 1 cm.

in the orbital edge, lies medial to the lacrimal duct, as in *Osteolaemus*.

The left lacrimal is damaged, and the right one contains some fissures. The right lacrimal has a short posterior process on the lateral margin of the orbit, its tip is broken. Besides the lacrimal duct there are two other *foramina* in the anterior notch of the orbit. The lacrimals are wide, and end anteriorly at the tip of the prefrontals; thus they do not contact the nasals. A preorbital *foramen* is absent.

The left *premaxilla* is badly crushed but the right one is almost complete. The premaxillary is longer than wide. In the Belgian *B. fagesii* the *premaxillae* end in an acute anterior tip. The lateral wall of the *premaxilla* is lower than the maxillar festooning. There is a short notch in the labial edge of the skull that contains the premaxillary-maxillary suture. The external *nares* are undivided by a narial septum. They are anteriorly placed in the *premaxillae*. The posterior edge of the *nares* is thick, and is visible in lateral view. The ventral side of the *premaxillae* is hidden by the mandible. The *alveoli* are not clearly visible. There were five premaxillary teeth, each *premaxilla* lacks the first tooth, but the next four teeth seem to be present in each side. Of these, the first and second are widely spaced from the third and fourth, which are also smaller than the first and second.

The *maxilla* is long and low, mainly in the anterior part where festooning is marked. The *maxilla* is strengthened posteriorly in correlation with the enlargement of the bulky posterior teeth. On the ventral side, the maxillo-palatine suture is U-shaped, and the *maxilla* does not have a posteromedial process directed toward the palatines. The maxillopalatine suture reaches the level of the space between the 9th and 10th teeth.

The palatal cavities are long and narrow. They end anteriorly opposite the anterior end of the orbits in the present specimen, but in the type of *B. fagesii* they extend beyond this point. Laterally, the palatine vacuities are constricted as in the Belgian specimen of *B. fagesii*, and also in *Osteolaemus*, owing to the presence of a prominent shelf of the *maxilla* medial to the *alveoli* and the anterior contour of the ectopterygoid process (Figure 2).

The palatine bar has its lateral edges parallel except anteriorly. A palatine ascending pillar (that supports the prefrontal pillar) is apparently lacking. Posteriorly, the palatines contact the pterygoid with two opposite posteromedially directed sutures. The palatines surround the anterior hollow of the *choana* medially, but they do not overlap the pterygoid as in *Theriosuchus*.

The ectopterygoid is robust. The anterior process of the ectopterygoid in the Galve specimen is partly hidden by the appressed mandible. In the lectotype of *B. fagesii* it contacts the *maxilla* with a rounded anterior end, the

posterior shelf of the *maxilla* separates the ectopterygoid from the alveolar border. The descending process of the ectopterygoid rests anteroposteriorly on the ventral surface of the pterygoid.

The pterygoid is expanded transversely. A deep and narrow *choana* is present in its ventroaxial face, and almost reaches the rear of the pterygoid. Opposite pterygoids are coalesced posteriorly; furthermore no suture is seen within the *choana*. There is no *septum* in the *choana*. The pterygoid flanges are only slightly extended ventrally. Ventrally, a thick median crest is present behind the parasagittal processes of the pterygoid. This crest belongs to the basioccipital, and the central Eustachian canal is recognized in this area. The basisphenoid is hidden above the pterygoid, as in Recent crocodylians.

#### Mandible

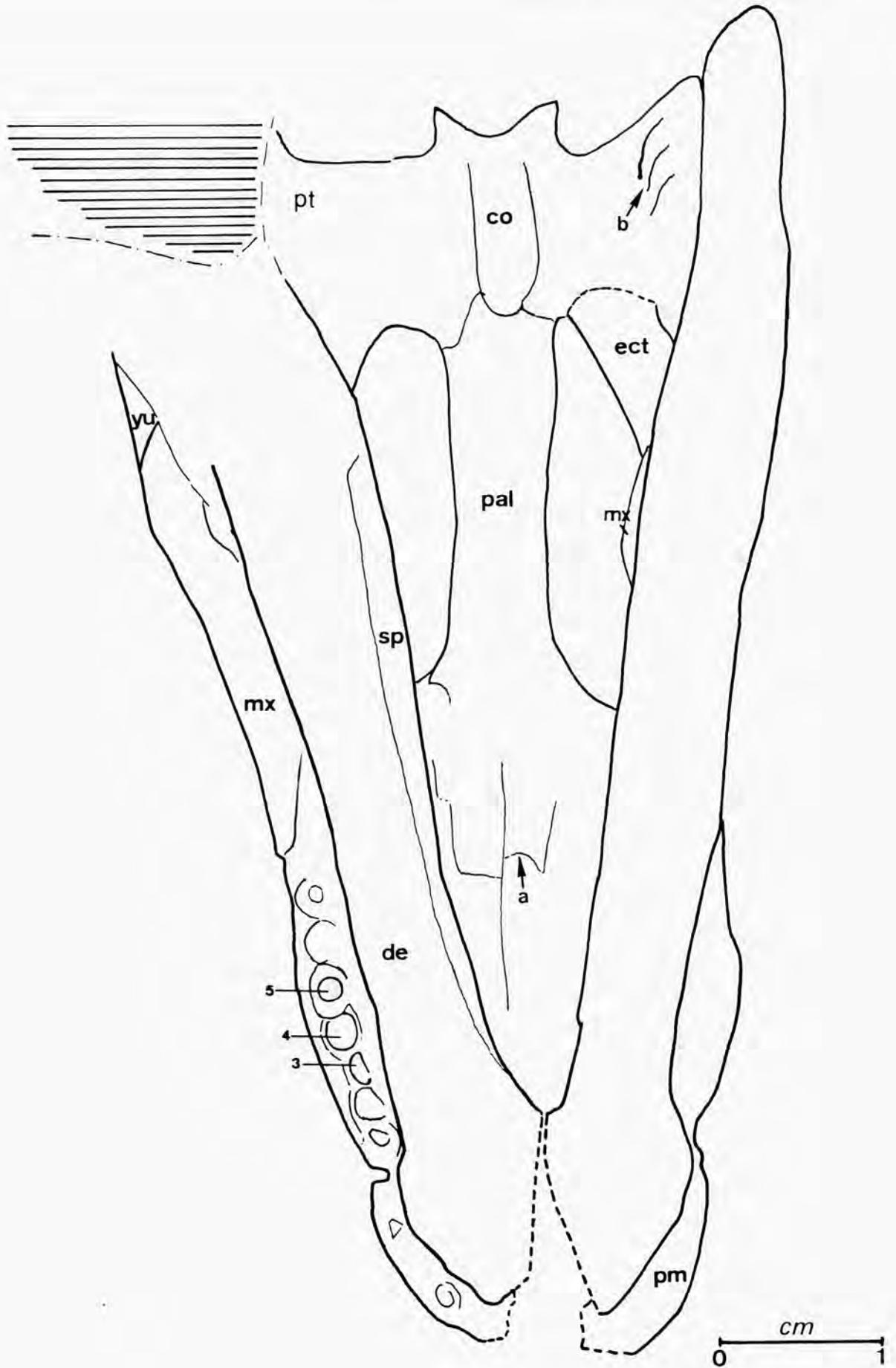
The mandibular *rami* diverge posteriorly at an angle of 20°-25°. The symphysis is short, about 13% of the length of the mandible. It may end at a level between the 4th and 5th teeth. There is no external mandibular *fenestra*. The dentary is superficially ornamented with small pits anteriorly and grooves posteriorly. The angular has a dense ornamentation compared to the dentary. Its ventral edge is strongly arched posteriorly, but anteriorly it becomes slightly concave. The angular forms a posterolateral lappet of the retroarticular process (Figure 3). The splenial is thin and flat, at most it barely enters the symphysis, and it may not reach it at all.

The articular is exposed in dorsal view. The retroarticular process is better preserved in the right mandibular *ramus*. The bone is long (the tip was broken away during the restoration). The median flange of the process is wide, bending posteromedially. On the dorsal side the process is distally upwardly incurved. In the Bernissart specimen the retroarticular process is broken posteriorly.

#### Dentition

The dentition is heterodont. The tooth morphology of *Bernissartia* is already known (BUFFETAUT & FORD, 1979; BUSCALIONI & SANZ, 1984). The anterior maxillary and dentary teeth are conical, whereas the posterior teeth are blunt and bulky. There are 16 maxillary teeth. Of six *alveoli* in the festooned area of the *maxilla*, the third, fourth and fifth, are respectively the largest in diameter. From the 6th to the 10th the teeth still keep their conical shape, but beginning with the 11th they display a different morphology, the crowns becoming globular and expanded mesiodistally (= anteroposteriorly). The three or four posterior teeth are even larger. In unworn teeth (BUSCALIONI, 1986), an occlusal crest extends from the mesial to the distal border of the crown. The crest is ornamented, as is the crown, with abundant ridges that

Fig. 2 – Schema of skull (CR82) of *B. fagesii* in ventral view. co, *choana*; de, dentary; ect, ectopterygoid; mx, *maxilla*; pal, palatines; pmx, *premaxilla*; pt, pterygoid; sp, splenial; yu, jugal. 3, 4 and 5 largest *alveoli* in the festooned part of the *maxilla*. The arrow a) shows the maxillo-palatine suture; the arrow b) shows the ectopterygoid-ptyerygoid suture. Broken lines are damaged areas of the specimen. Point and line delimit an striped area which represents the matrix. ▷



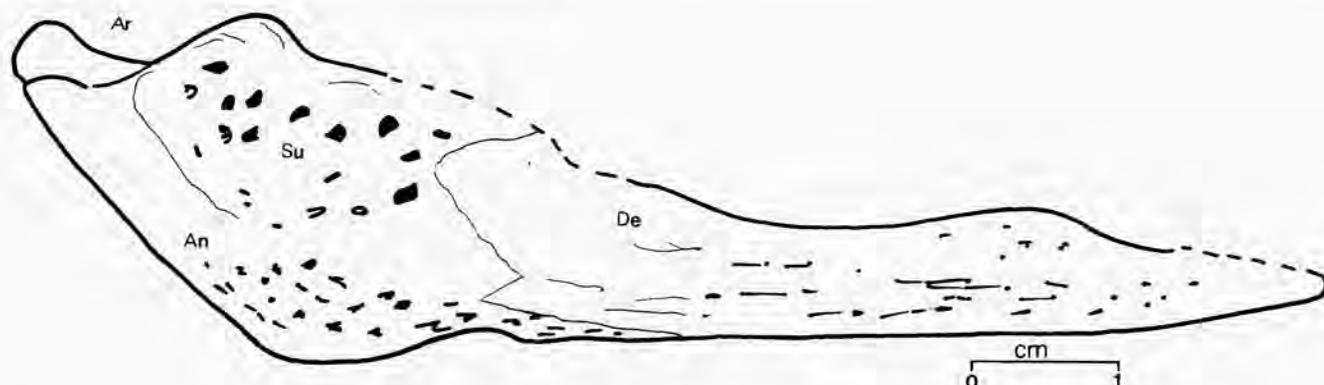


Fig. 3 – Schema of the mandible of *B. fagesii* (CR82) in lateral view. ar, articular; an, angular; de, dentary; su, surangular.

do not reach the base of the crown. The tooth is constricted at its base. The dentition is best exposed in the Belgian specimen (R 46), the posterior maxillary teeth are intercalated between the mandibular ones, the maxillary teeth being of greater diameter in relation to those of the mandible. The dentary is dorsally depressed to lodge the bulky maxillary teeth.

Except for the 3rd and 4th teeth the mandibular series are not exposed in the Galve specimen. These have long crowns which occupy the premaxillomaxillary notch. These teeth never have acute apices; the base of the crown is constricted. The crown ornamentation is made of longitudinal smooth, widely spaced ridges, which do not reach the base of the crown.

#### Postcranial skeleton

**Axial skeleton.** – The first three vertebrae are articulated with the skull. The *centra* are contained in the matrix and their neural arches are broken. The paired neural arches of the *atlas* are exposed. Ventrally, the body of the *atlas* (*intercentrum*) may be displaced laterally. The *axis* has a large *centrum*. On the Belgian specimen the neural spine of the second vertebra is better preserved in IRScNB R46. The second neural spine is long anteroposteriorly and its posterior edge is perpendicular to the horizontal plane, its dorsal margin straight. The neural spine is tall, and highest posteriorly.

The next cervical vertebrae are included in the small fragment CR-82001. Their dorsal and ventral faces are exposed. They have low and thick anterior hypapophyses. The last *centrum* is incipiently procoelous, and its posterior surface has a low condyle, which ends in a flat surface, and thus forms a truncated cone. The anterior articular surface is deeply concave. The number of preserved cervicals in the specimen is estimated at eight. First and second cervical ribs, as in Recent crocodiles, are long and sword-like. The articulation between the second rib and vertebra can not be seen.

#### Appendicular skeleton

**Pectoral girdle.** – Little is known about the *scapula* and coracoid of the Spanish specimen. In the Bernissart specimen the *scapula* has an expanded top, its anterior

edge is concave and the posterior is slightly convex. There is no tubercle in the basal part of the caudal side of the *scapula*, as occurs in some fossil eusuchian crocodiles (*Pristichampsus* GERVAIS, 1853 and *Diplocynodon* POMMEL, 1847). The acromial region is broad.

The shaft of the coracoid is medially narrow in *B. fagesii*. Pelvic girdle. – A fragment of *ilium* is the only element preserved in the Spanish specimen, and its anterior tip is lost. It is not elongated caudally. As in the lectotype of *B. fagesii*, the *ilium* is internally curved producing a lateral bend of the iliac blade. The anterior and posterior height of the *ilium* are the same.

#### Anterior extremity

**Humerus.** – (CR82-04) The proximal articulation seems large in relation to the shaft diameter. The head of the *humerus* bends medially. The head and the internal tuberosity together form a unique descending medial plane, in anterior view; dorsally both structures are notably enlarged (Figure 4B). The distal end of the *humerus* in the Belgian specimen presents an entepicondylar tubercle. The distal part of the *humerus* of the Galve specimen is contained in the matrix.

**Radius and ulna** have about the same length and shaft diameter (2 mm ulna, 1.5 mm radius). The proximal ulnar face has two concave articular sockets separated by a central crest.

#### Posterior extremity

**Femur** (CR82-01). – The proximal articulation is twisted approximately 125° respect to the shaft, unlike *Goniopholis* OWEN, 1841 where the torsion ranges from 150° to 160°; but is similar to that of the eusuchians. Posteriorly, the distal articulation has a narrow intercondylar space. The external condyle is divided by a short lateral notch (Figure 4A).

**Tibia and fibula** are of about the same size. The *tibia* presents distally the two *maleoli* (CR82-05). It is articulated with the *tarsus* (CR82-06). The proximal articulation of the *tibia* has one concave articular surface.

#### Dermatoskeleton

Both dorsal and ventral armors are present in *Bernissart-*

*tia*. The dorsal armor comprises three pairs of nuchal osteoderms which are followed by 17-18 transverse dorsal rows of 4 osteoderms, and it is completed distally by a few paired caudal scutes. The nuchals have curved convex lateral edges and the first one is as wide as long.

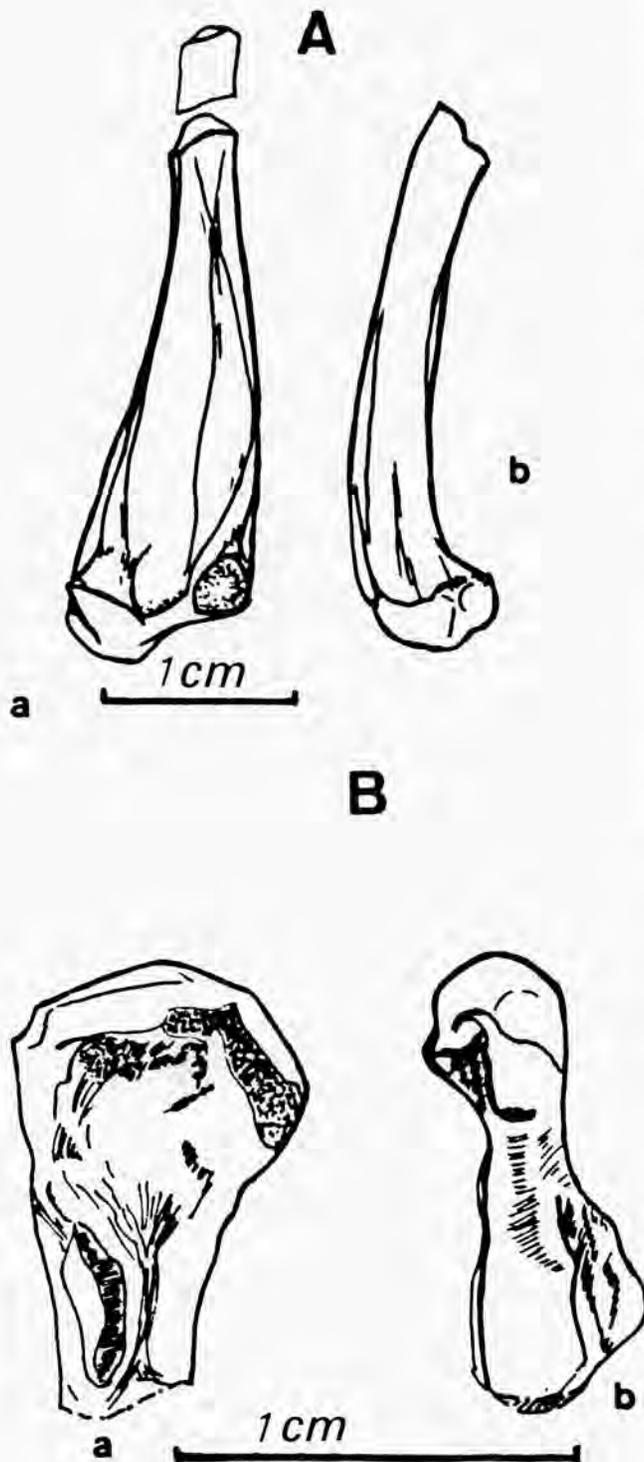


Fig. 4 - A. Distal fragment of the left femur of *B. fagesii* (CR82-01) a, posterior view; b, lateral view. B. Proximal fragment of the right humerus, a, anterior view; b, lateral view.

They may cover part of the neck. The dorsal osteoderms comprise two longitudinal rows on either side of the midline, arranged parasagittally and laterally. They are ornamented with small shallow pits. The medial scutes are twice as wide as they are long, but the lateral plates are more subquadrangular. In both longitudinal rows each scute overlaps the scute situated directly behind it: the ventral posterior border of one row lies in the dorsal edge of the next one. The parasagittal osteoderms have a straight medial margin and an oblique lateral one that fits (without suture) with the adjacent scute. One longitudinal keel is present on the parasagittal dorsal osteoderms at about the mid-length of the trunk. The lateral scutes bear a prominent mid-crest, that lengthens caudally as these scutes become more ovate toward the sacral region. The longitudinal rows of the caudal armor consist of two osteoderms, and most likely they did not reach the tip of the tail. In the lectotype of *B. fagesii*, the number of dorsal osteoderms is 19 (not including the nuchals). The caudal osteoderms extend as far as the 4th caudal vertebra. The ventral armor has four longitudinal rows. Medial and lateral scutes are of quadrangular shape. A smooth anterior area overlapped by the preceding scute may be recognized in some of them. The ventral scute is ornamented with densely placed small pits.

#### DISCUSSION

We have worked with a two data matrix, one based on 21 postcranial characters and the second on 30 cranial ones (Table 1). A basic assumption is the monophyly of the taxa involved in the analysis, based on the phylogenetic relationships of the Neosuchia (*sensu* BENTON & CLARK, 1988), omitting here the synapomorphies that would define this basal clade. The analyses of character polarities (see Appendix 1 and 2) are proposed on the basis of the outgroup criterion. Among the taxa involved, *Hyposaurus* OWEN, 1849 (a dyrosaurid) and/or *Theriosuchus* (an atoposaurid) were used as outgroups, and *Goniopholis*, *Bernissartia* and *Leidyosuchus* LAMBE, 1907 comprise the ingroup (Fig. 5A, 5B). We have introduced *Leidyosuchus* (an eusuchian) in this analysis to obtain an idea on the general condition of derivation shown in *Bernissartia*.

There are two resulting cladograms for the postcranial characters: *Goniopholis* as the sister group of (*Bernissartia* + *Leidyosuchus*) (Figure 5A) and the alternative (*Goniopholis* + *Bernissartia*) as the sister taxa of *Leidyosuchus* (Figure 11). The latter has been rejected because of the high number of reversions that would have to be explained (see Figure 11). This cladogram reflects a number of uncertainties about character-states owing to missing data, mostly in *Hyposaurus*.

In the cladogram (Fig 5A) of postcranial characters, the clade: *Goniopholis* + (*Bernissartia* + *Leidyosuchus*) is defined by five possible synapomorphies: traits (5),(13),(14),(20) and (8).

The primitive state of character (5) (anteriorly placed hypapophyses) can not be fully tested; it may be primitive

TABLE I

<i>Hyposaurus</i>	0	?	?	1	0	0	?	0	0	0	?	0	N	0	?	?	?	?	?	0	?
<i>Goniopholis</i>	0	?	0	0	1	1	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0
<i>Bernissartia</i>	1	0	1	0	1	1	1	?	0	0	?	0	1	1	1	?	0	1	1	?	0
<i>Leidyosuchus</i>	1	1	1	1	1	1	1	1	B	1	1	1	1	1	1	1	1	1	1	1	1
Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21

<i>Theriosuchus</i>	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	1	0	0	0	0	0	0	?	0	?	0	?	0		
<i>Goniopholis</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	?	1	1	0	0	1	0	1	0	0	1	0		
<i>Bernissartia</i>	0	0	0	0	1	0	1	1	0	1	0	1	0	0	1	1	0	1	1	0	0	0	1	1	?	1	0	?	1	
<i>Leidyosuchus</i>	B	1	1	0	0	1	0	1	1	B	B	1	1	1	1	1	1	1	1	1	B	B	1	1	1	1	1	1	0	
Character	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51

Data matrix for the polarities of postcranial characters (1 to 21) and cranial characters (22 to 51). ? = missing data; B = both character-states; N = character definition not applicable. Source of data: *Hyposaurus*; *H. natator* YPM, Yale Peabody Museum (N.953, 764 and 763); *Goniopholis*, *G. simus*, BMNH, British Museum Natural History, London Rf.41098; IRScNB, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Rf.1537, *G. crassidens*, BMNH-R.5259 and R.5814; *Bernissartia*, *B. fagesii*, IRScNB-R.46; *Leidyosuchus*, *L. formidabilis* (Erickson, 1976), *L. gilmorei* AMNH, American Museum Natural History Ref.5352, *L. sternbergii* AMNH-No.6533, *Leidyosuchus sp.* LACM, Los Angeles County Museum Rf.3087/45808.

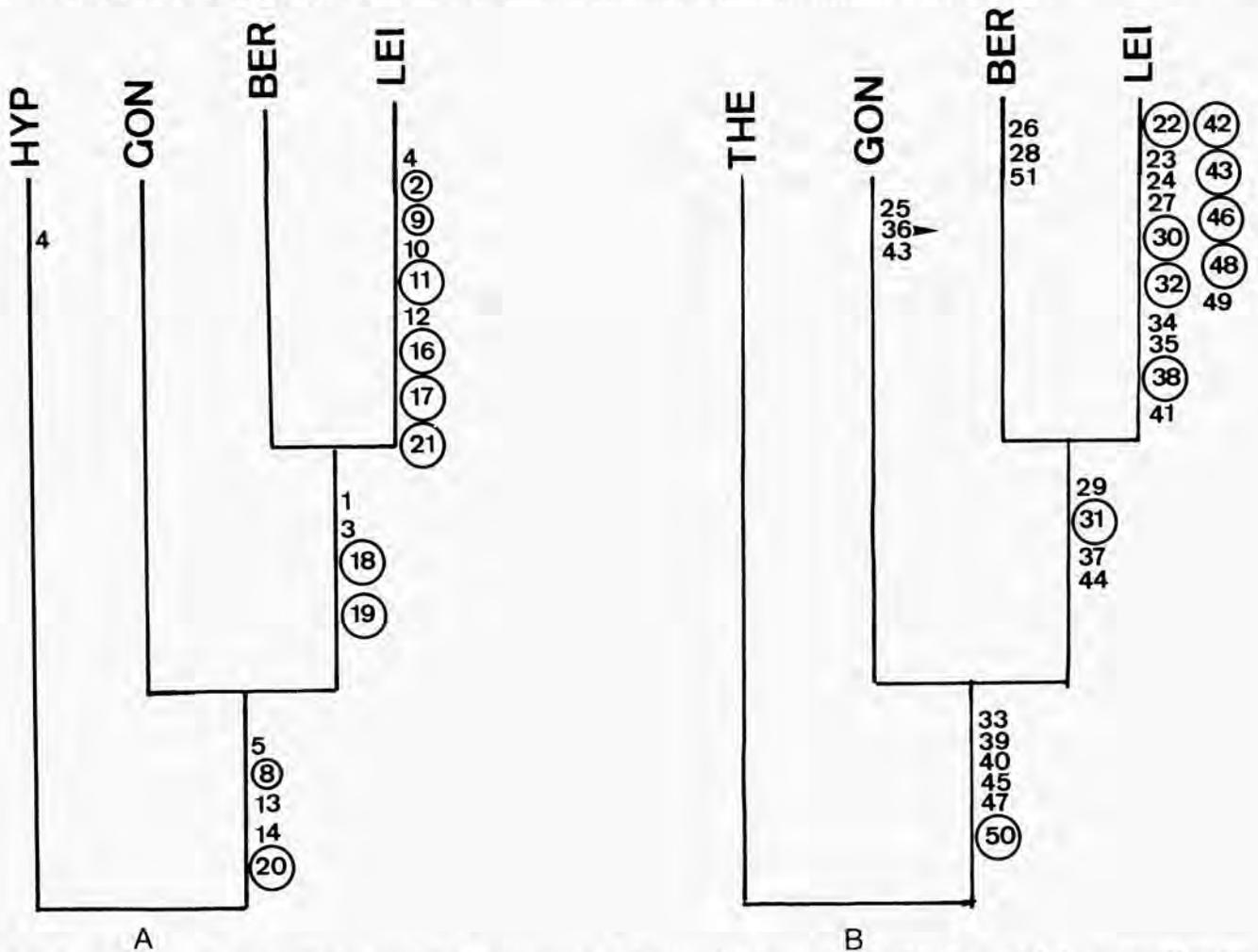


Fig. 5 – Cladograms depicting relationships of *Bernissartia* A. Postcranial characters (1 to 21); B. cranial characters (22 to 51). Characters in circle have doubtful distributions, due mainly to missing data (see table 1). Arrow indicates probable reversion. Taxa: BER, *Bernissartia*; GON, *Goniopholis*; LEI, *Leidyosuchus*; outgroups: HYP, *Hyposaurus*; THE, *Theriosuchus*.

in *Hyposaurus* and other dyrosaurs (BUFFETAUT, 1976; Langston in litt.), since also *Sebecus* SIMPSON, 1937 probably could present this trait (COLBERT, 1946). However, hypapophyses extending the full length of the ventral side of the centra (Figure 6), may be an autapomorphy of the Dyrosauridae in the Neosuchia clade.

The next three features occur in the pelvic girdle: *ischium* with the ventral blade expanded caudally (13); *ischium* with a single anterior proximal articulation (20); *pubis* spatulated ventrally (14) (Figure 7). The shaft of the *ischium* in *Hyposaurus* (*H. natator* TROXELL, 1925) differs basically from that of the other taxa, representing a

new autapomorphy in this genus or maybe of this species. It is narrow, and ends ventrally with a pointed and curved blade (Fig. 7). Thus, the plesiomorphic condition for trait (13) is presumed to be that seen in the Atoposauridae (*Alligatorellus* GERVAIS, 1871), in which the *ischium* is stout and presents a short ventrocaudal end (WELLNHOFER, 1971; fig. 5, p. 149).

The plesiomorphic state of character (20) is a double proximal articulation of the *ischium*, which has articular processes dorsally and anteriorly. This feature has only been tested in *Hyposaurus*, because the condition in the Atoposauridae is unknown. The proximal anterior process of the *ischium* in such taxa as *Steneosaurus*, (ANDREWS, 1913); *Orthosuchus*, NASH, 1975 is unique and faces dorsally. In the other genera involved, (*Goniopholis* and *Leidyosuchus*), the anterior process possesses a unique anterodorsal facet, and in Recent crocodylians (*Alligator mississippiensis* DAUDIN, 1802; WETTSTEIN, 1954) it faces directly anteriorly. In either case the derived condition would be that found in *Goniopholis* and *Leidyosuchus* (first derived character-state) and Recent crocodiles (second derived state), regardless as to whether the primitive condition is that seen in *Steneosaurus* or in *Hyposaurus*.

The clade *Goniopholis* + (*Bernissartia* + *Leidyosuchus*) share a wide distally spatulated *pubis* (trait 14), with a rather short neck. The primitive state is a *pubis* in which the shaft is long in relation to its distal width (long-necked *pubis*). The feature has been tested in *Hyposaurus* and may be present in *Alligatorellus*.

The next trait (8), involving the development of the odontoid process, has not been checked in *Bernissartia*. It has been tentatively placed at the base of the clade because the derived condition is shared by *Goniopholis* and *Leidyosuchus*.

*Bernissartia* and *Leidyosuchus* share four apomorphies: (1) and (3), related to the vertebral morphology, and (18) and (19) related to the dorsal armor.

The existence of procoelous centra (1) in *Bernissartia* has been controversial, KÄLIN (1955) describing the condition correctly whereas DOLLO (1883), LYDEKKER (1888), BUFFETAUT (1975) and CLARK (1986) believed the *centra* to be amphicoelous. We have interpreted the cervical *centra* of the Spanish *Bernissartia* as procoelous, avoiding deliberately the terms "semiprocoelous" (BUFFETAUT, 1982) or "incipient *procoelia*" (BUSCALIONI & SANZ, 1987a). We believe that as in *Theriosuchus* there are different degrees of development of the articular condyle, ranging from a convex condyle to a low (somewhat flattened) articular surface. This variability may be related to different topographic positions. Among the isolated centra we have available from Galve, the cervical vertebrae present a higher truncated cone, than do the dorsals (Figure 8). Most of the vertebrae do not display a convex condyle, but the anterior articular surface is concave (in many cases deeply concave). There is little evidence in the fossil record for evaluating the variability. Use of only one term, procoelous, make the discussion of the character polarity more restrictive and parsimonious.

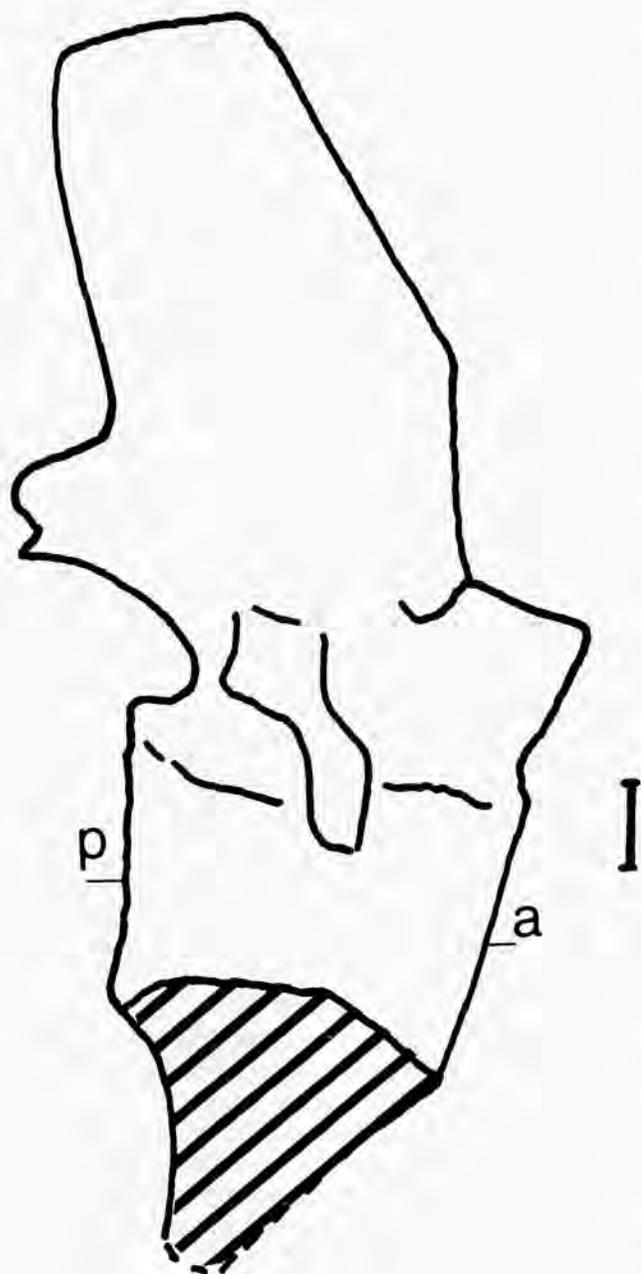


Fig. 6 – Schema of an anterior vertebra of *Hyposaurus* (YPM. 753, Yale Peabody Museum) showing the broad-based hypapophysis (striped area). a., anterior face; p., posterior face.

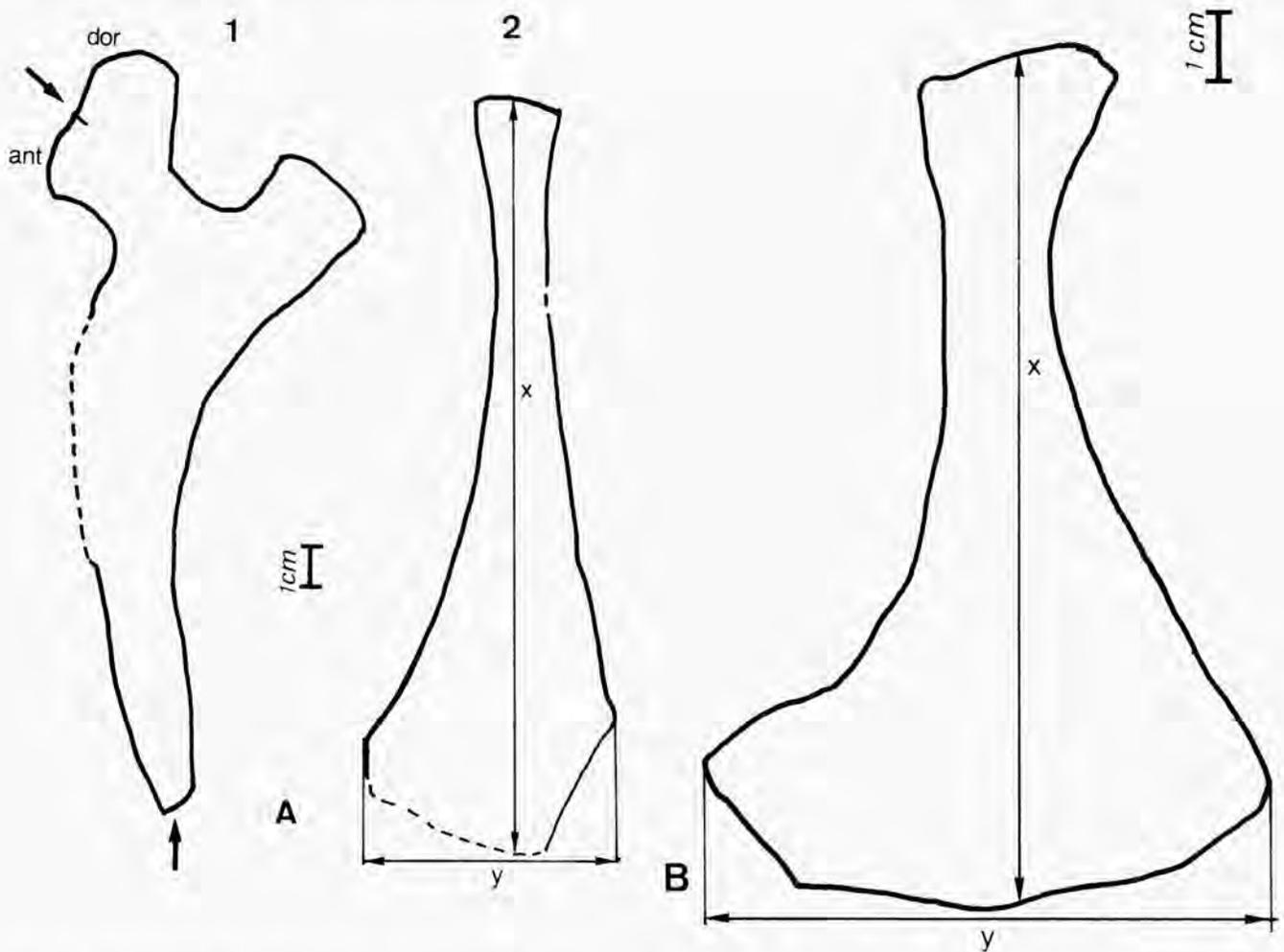


Fig. 7 – Schema of the *ischium* and *pubis* of (A) *Hyposaurus* (YMP. 753). 1. *Ischium*: (a) pointed and curved blade; (b) double proximal articulation of the *ischium*; dor, dorsal articular process. ant, anterior articular process. 2. *Pubis*, lines refers to the trait long-neck *pubis* (x) in relation to its width (y). ( $y/x$ ) = 0.34. *Pubis* of (B) *Leidyosuchus* (LACM-45808) (Los Angeles County Museum). ( $y/x$ ) = 0.66.

Fig. 8 – Isolated dorsal vertebra (CR-1) (from “Cerrada Roya”, Galve province of Teruel, Spain) attributed to *Bernissartia*. 1. Lateral view; 2. Posterior view; 3. Ventral view. ac, anterior cotyle; pc, posterior condyle; pre, prezygapophysis. ▷

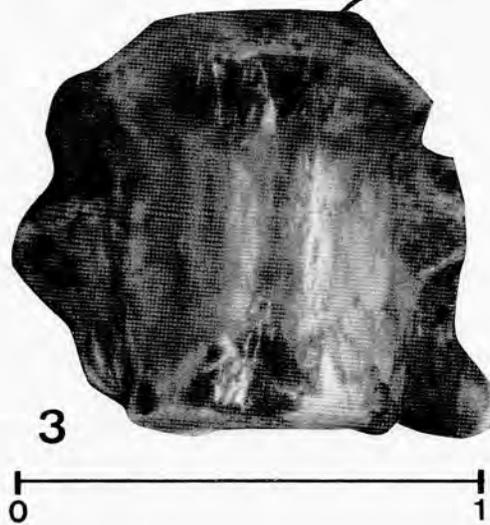
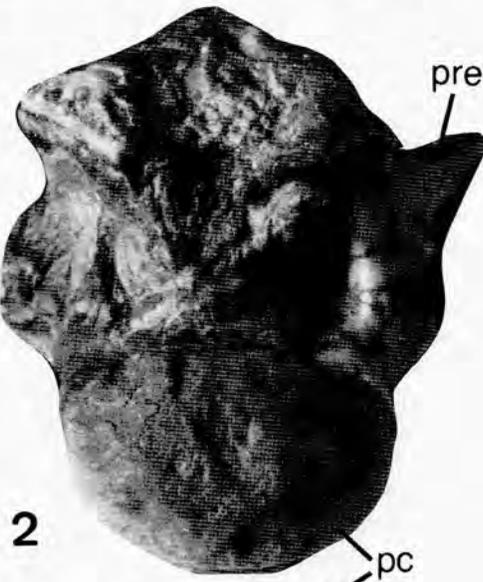
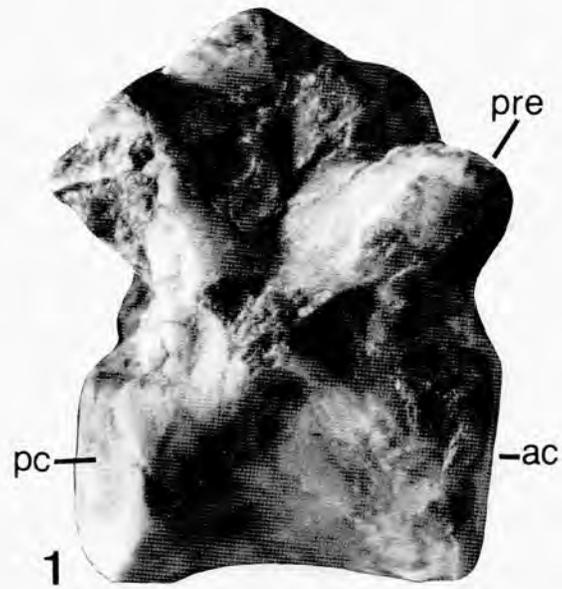
monious, since only one derived state is considered. We propose here a broad definition of procoelia (anterior articular surface concave, posterior condyle convex or truncated), so it is best to describe *Bernissartia* as having a procoelous condition. If this definition of the trait is not accepted, this feature of *Bernissartia* must be considered autapomorphic.

The first caudal vertebra has been described as biconvex by BENTON & CLARK (1988), and we concur with this conclusion. The distribution of this trait is poorly known in other non-eusuchian fossils, thus the primitive state is uncertain. CLARK (1986) defines it as the absence of the anterior condyle. That should imply that the first caudal may be amphicoelous or procoelous. Thus, the derived condition should be an opisthocoelous or biconvex *centrum*. Opisthocoely of the first caudal never has been regarded as the probable primitive condition, at least in

the Neosuchia, although it may occur in *Theriosuchus*. The vertebra described as opisthocoelous (CLARK, 1986) from the British *Theriosuchus pusillus* specimen, shows enough characters to be the first caudal, but further study is needed to confirm this.

To conclude, the axial skeleton of *Bernissartia* shows two derived characters: – procoelous centra and a biconvex first caudal. However, the genus retains some primitive traits: a relatively tall second neural spine (2), and low cervical hypapophyses (4). This latter feature (see Appendix 1 and Table 1) may be regarded as an apomorphy of *Hyposaurus* (and other dyrosaurids) convergent with *Leidyosuchus* (and other Eusuchia).

The traits related to the dorsal armor contain missing data on *Hyposaurus*. The dermal armor of the dyrosaurids is not yet well known, but has been reported in one species (*H. bequaerti* DOLLO, 1914), which shows the



derived character of more than two rows of osteoscutes in the dorsal armor (BUFFETAUT, 1982; LANGSTON *in litt.*).

*Bernissartia* and *Leidyosuchus* dorsal scutes lack the anterolateral peg present in numerous neosuchians (18). Both have four rows of osteoderms (19) (see ERICKSON, 1976 for *Leidyosuchus*). The presence of an anterolateral peg in the medial scutes, is here considered as plesiomorphic (see also, FREY (1988)). We think that among the Atoposauridae only *Theriosuchus* possesses this peg (BUSCALIONI & SANZ, 1988), whereas CLARK (1986) reports that it is lacking in this taxon, and regards its absence as the primitive condition.

In *Bernissartia* traits (18) and (19) are derived in relation to the neosuchian genera considered here. However, the other primitive features (*vis à vis* *Leidyosuchus*) in the dorsal armor such as nuchal and dorsal scutes in continuity (17), found in Atoposauridae and *Goniopholis* are retained. The nuchal osteoderms are imbricated (21), like the dorsals. The scutes overlap anteroposteriorly, as previously reported by DOLLO (1883) and BUFFETAUT (1975, plate V). CLARK (1986), however, attributed the derived non-imbricated (sutured or adjacent dorsal osteoderms) condition to *Bernissartia*. He has correlated the non-imbrication with the absence of an anterolateral peg (CLARK, 1986; BENTON & CLARK, 1988). But the Eusuchia do not possess a peg whereas dorsal and ventral osteoderms are imbricated in some eusuchians, and pegs may be absent in some "mesosuchians" with overlapping osteoderms e.g., *Alligatorellus* (WELLNHOFER, 1971, fig. 6, p. 152)). Thus, we think that these characters are independent of each other.

As shown in the cladogram (Figure 5), the best defined taxon is *Leidyosuchus*. Several traits are represented as autapomorphies for this taxon, but many contain missing data: (2), (7), (11), (16), (17) and (21). Feature (9), morphology of the scapular shaft, shows both character-states (referred in the data matrix as B), *Leidyosuchus formidabilis* (ERICKSON, 1976) showing the primitive condition. Only characters (4) (high hypapophyses (see above)), (10) (coracoid expanded ventrally (Figure 9)), and (12) (iliac blade higher posteriorly (Figure 10)), are fully tested.

For the coracoid, the primitive condition is present not only in the involved taxa (*Goniopholis*, *Hyposaurus* and *Bernissartia*) but also in *Theriosuchus*. The iliac blade (12) in *Leidyosuchus*, as is common in most Eusuchia (e.g. *Pristichampsus*, *Diplocynodon*, and Recent forms), has a posterior blade higher than the anterior one.

*Hyposaurus* is not represented in the data matrix of cranial characters. *Goniopholis* data apply exclusively to the European species *G. simus* OWEN, 1878. Some differences between the North American and European goniopholidids have been reported by BUFFETAUT (1982) and CLARK (1986). Some of these have been used in Appendix 2. In the cladogram (Figure 5B) *Goniopholis* is the closest relative of *Bernissartia* + *Leidyosuchus*. This clade is supported by four synapomorphies: acute anterior process of the frontal (29), frontal barely ente-

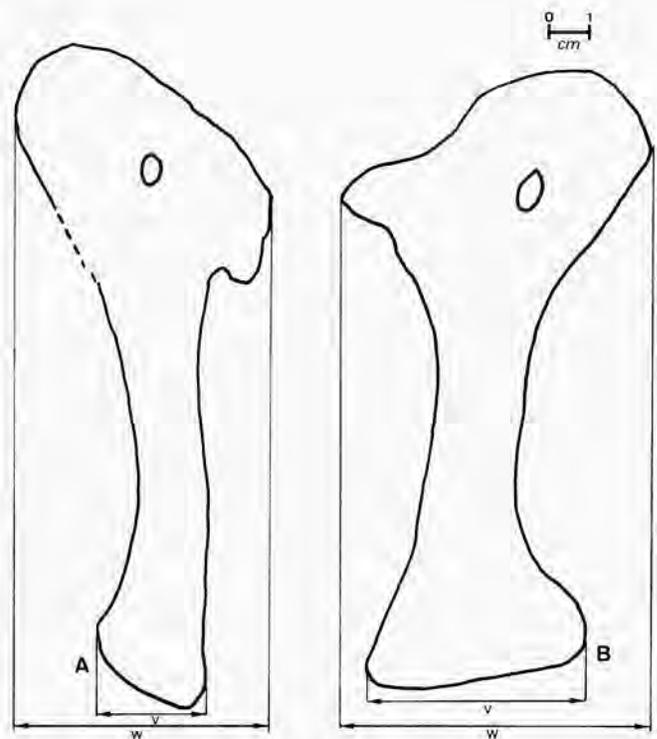


Fig. 9 – Schema of the coracoid of (A) *Hyposaurus*, representing the primitive condition, and (B) *Leidyosuchus* the derived condition. W, maximum dorsal width; V, maximum ventral width. V/w ratio in (A) = 0.44, in (B) = 0.72.

ring the temporal fossa (31), posterolateral projection of the squamosal not lobulate (37), and absence of a pre-orbital foramen (44).

*Bernissartia* is defined by three apomorphies. The splenial is scarcely or not involved in the mandibular symphysis (26); the frontal is narrow between the orbits (28), and somewhat longitudinally concave; and there is no lacrimo-nasal suture (51).

#### PHYLOGENETIC RECONSIDERATIONS AND CONCLUSIONS

The Spanish specimen has been identified as *Bernissartia fagesii* because it displays the same combination of character-states.

In both of our cladistic analyses *Bernissartia* is the sister group of *Leidyosuchus* (Figure 5A,B). The new data available in the Spanish specimen seem to confirm the phylogenetic position of *Bernissartia*, as one of the closest sister groups of the Eusuchia (here represented by *Leidyosuchus*) (BUSCALIONI, 1986; BENTON & CLARK, 1988; CLARK, 1986). However, if we consider the cladogram of the Neosuchia and Eusuchia by BENTON & CLARK (1988), then the "Glen Rose" crocodile is the closest sister group of the Eusuchia (Figure 12A). The node of this clade ("Glen Rose" + Eusuchia) was defined by: "choana nearly within pterygoid" and "procoelous vertebrae" (*op. cit.* p. 338). Both of these derived characters are already present in *Bernissartia*. Thus,

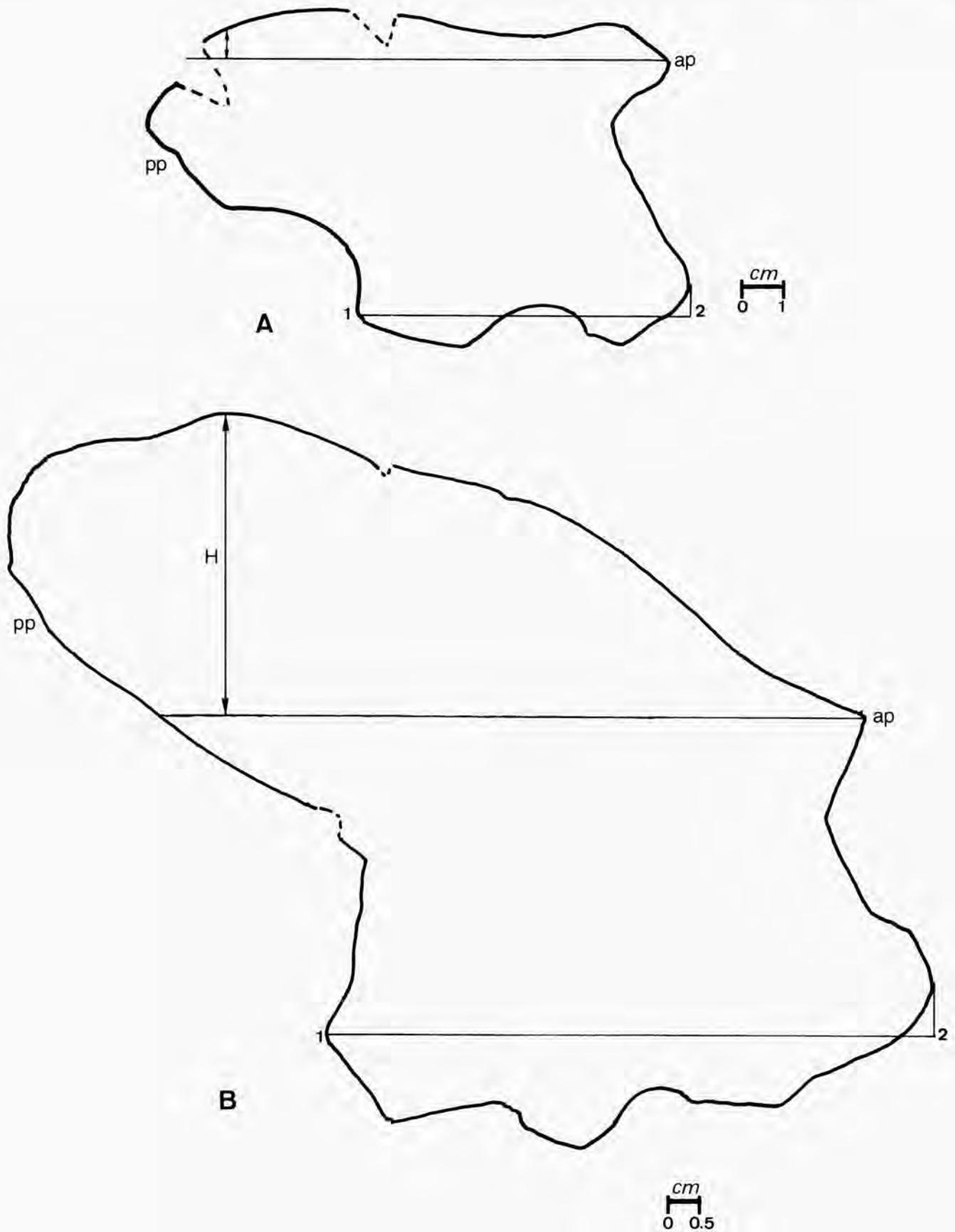
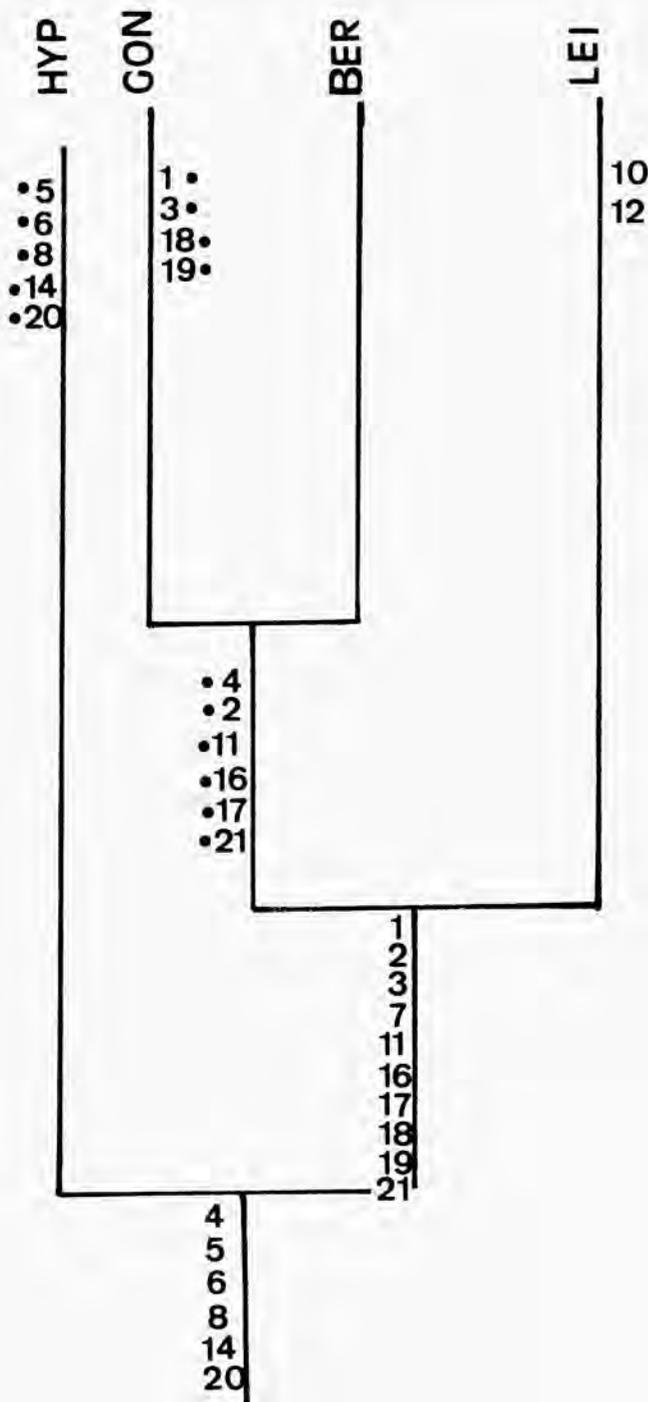


Fig. 10 – Schema of the *ilium* of (A) *Hyposaurus* for the primitive condition and (B) *Leidyosuchus* representing the derived character-state. ap., anterior process; pp, posterior process. 1-2 line reference for A and B, the parallel pass through ap. H, height of the posterior process.



it would be possible to enclose as a clade the nest *Bernissartia* + *Shamosuchus* MOOK, 1924 with the "Glen Rose" taxon as its sister group (Figure 12B). In fact, if we represent the distribution of the derived character-states (resulting from the present study) shared by *Bernissartia* and the Eusuchia in this cladogram (Figure 12B), *Shamosuchus* and the "Glen Rose" crocodile may be closer to *Bernissartia* than to the Eusuchia. However, our knowledge of these two taxa is too incomplete to draw positive conclusions; there is many missing data for *Shamosuchus* (= *Paralligator*) and the Glen Rose crocodile, and even in *Paralligator* the centra seems to be amphicoelous (KONJUKOVA, 1954). A detailed analysis will be necessary taking into account the new data on *Bernissartia* to determine their respective positions relative to the Eusuchia. Thus, we think that *Bernissartia* belongs in the

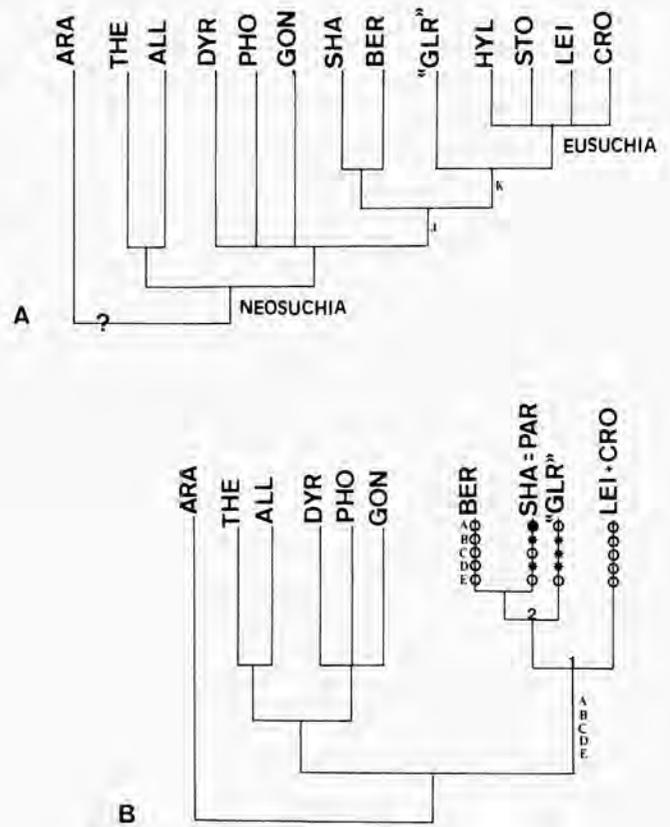


Fig. 11 – Rejected cladogram of postcranial characters of the relationships of *Bernissartia*. This cladogram has been rejected because of the high number of reversions (black dots). Many of the uncertainties about character-states are due to missing data, mostly in *Hyposaurus*.

Fig. 12 – Cladograms on the relationships of the Neosuchia and Eusuchia. ARA, *Araripesuchus*; THY, *Theriosuchus*; ALL, *Alligatorellus*; DYN, dyrosaurids; PHO, pholidosaurids; GON, *Goniopholis*; SHA, *Shamosuchus*; BER, *Bernissartia*; GLR, Glen Rose crocodile; HYL, *Hylaeochampsia*; STO, *Stomatosuchus*; LEI, *Leidyosuchus*; CRO, *Crocodylus*; PAR, *Paralligator*. A. From BENTON & CLARK, 1988. J node is defined by: a. osteoderms in more than two longitudinal rows; b. osteoderms do not overlap; another possible synapomorphy-biconvex first caudal vertebra. K node is defined by: a. *choana* nearly within the pterygoid; b. procoelous vertebrae (*op. cit.*, pp. 337-338). B. Hypothetical cladogram on the relationships between the most derived taxa of the Neosuchia and Eusuchia. Node 1, would contain the apomorphic traits of the above node K (cladogram A) which are already present in *Bernissartia*. Node 2 is not defined. A, B, C, D and E are the derived characters shared by *Bernissartia* and the Eusuchia (*Leidyosuchus* + *Crocodylus*). A, *Procoelia*; B, Biconvex first caudal; C, More than two rows of dorsal scutes; D, no preorbital fenestra; E, dorsal osteoderms without an anterolateral peg. Asterisks denote missing data; black circles, reversions; circles, derived character-states.

closest related group of the Eusuchia, as a member of the clade Neosuchia.

**THE ONTOGENETIC AGE OF THE SPANISH *BERNISSARTIA***  
The Spanish specimen of *B. fagesii* is somewhat shorter than the lectotype of the species from Bernissart (Table 2). In our preliminary note (BUSCALIONI *et al.*, 1984) we noticed some differences in the relative proportions of the skull, that probably indicate an immature individual. We have used two methods for estimating the ontogenetic age of the Galve specimen. One of them is a directly based on skeletochronology, that allows us to test the individual age by the number of LAC ("ligne d'arrête de croissance") (CASTANET, 1982; BUFFRENIL, 1980a). The second approach is an indirect method utilizing morphometric data.

For the skeletochronology method we used a proximal fragment of the *femur* for a thin section (150 micron). The LACS are opaque (Figure 13) and four to six can be counted in the cortex. The cortical tissue is mainly pseudolamellar or lamellar bone. Toward the medullary cavity the tissue becomes fibrous and intracortical resorption is evident around the medullary cavity, which may have obscured a few LACs.



Fig. 13 – Section of the metaphysis of the *femur* (150 micron of thickness). The arrows in the cortex show the number of LAC (1 to 4) of the individual. ? represents possible lost LAC (one or two) due to endosteal resorption. Magnification x 20.

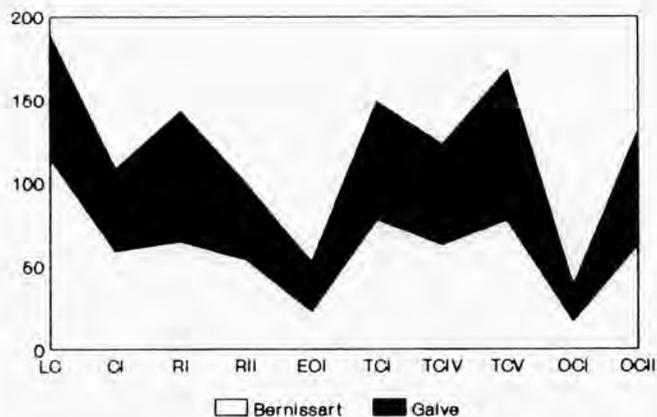


Fig. 14 – Graphic representation in area of the cranial indices of the two specimens of *Bernissartia fagesii*. Y axis represents the values from Table 2. Cranial indices are specified in the caption of Table 2.

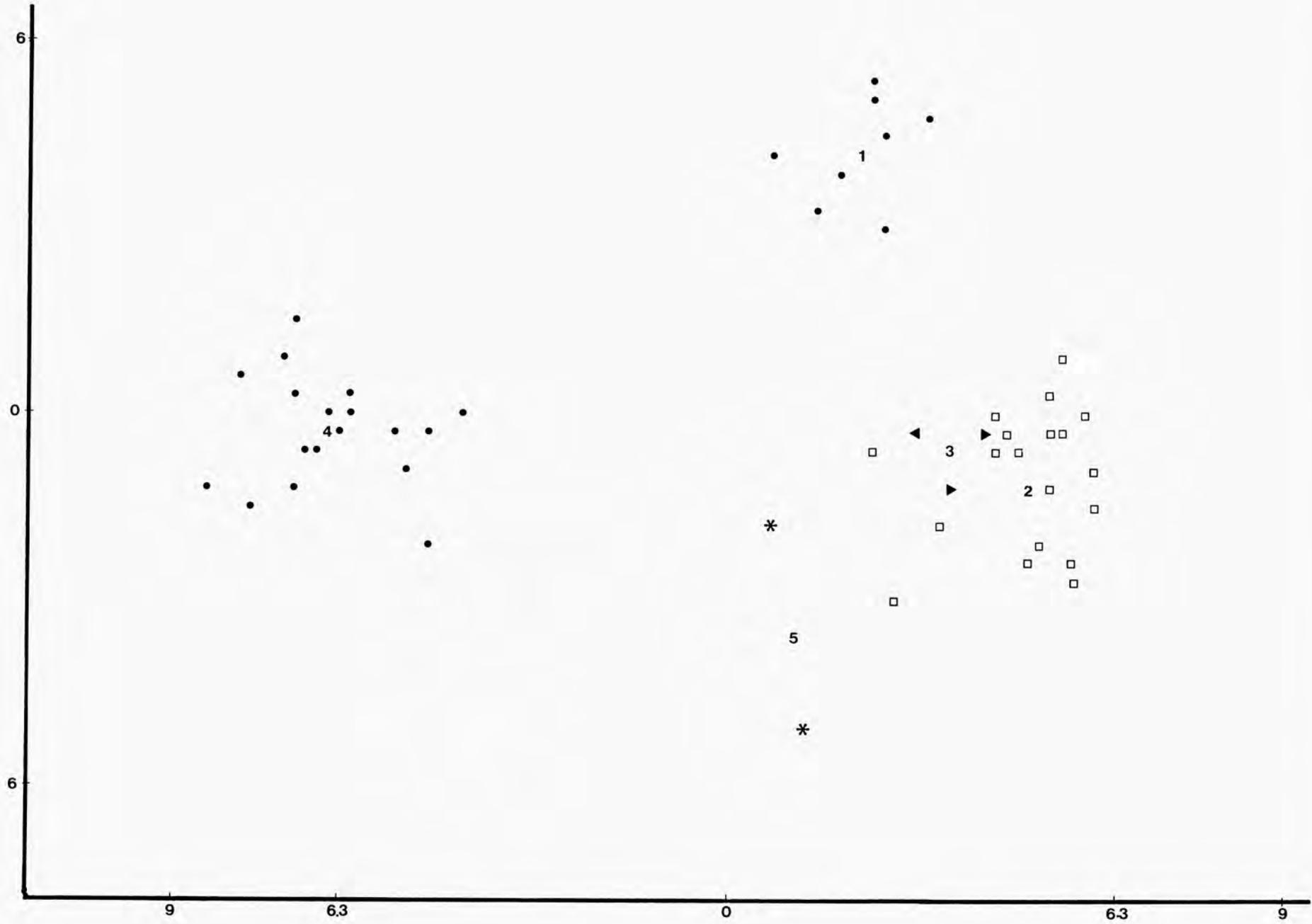
Lamellar or pseudolamellar tissue type is related to a slow rate of growth, so probably the individual may belong to a small-sized species. The *cortex* is scarcely vascularized and the medullary cavity is rather small in relation to the *cortex*. Both characters are unusual in freshwater or marine crocodiles (RICQLÈS, 1976; BUFFRENIL *in litt.*), but are more frequent with terrestrial forms. This suggest that *Bernissartia* was most probably a terrestrial crocodile.

The skeletochronology method suggests that the individual was no more than 6 years old (BUSCALIONI & SANZ, 1987b). In Recent crocodiles the growth rate is fastest during the first 4 years (BUFFRENIL, 1980b), some species apparently reaching sexual maturity shortly after 5-6 years of age (CHABRECK & JOANEN, 1979 for *Alligator mississippiensis*).

Because there are few data on ontogeny of the bone in Recent crocodiles, it is difficult to interpret the information from one fossil specimen. Nevertheless it seems likely that the Galve specimen was an immature individual.

The morphometric analysis is based on the statistical stepwise discriminant analysis (BMDP-7M, BROWN, *et al.*, 1985). We have used ten cranial indices as variables (Table 2; Figure 14), as defined by KÁLIN (1933). The data concern four Recent genera and six species: *Alligator mississippiensis*, *Caiman latirostris* DAUDIN, 1802, *Caiman crocodilus* LINNE, 1758, *Osteolaemus tetraspis* COPE, 1860, *Crocodylus siamensis* SCHNEIDER, 1801 and *Crocodylus niloticus* DAUDIN, 1802, and the *Bernissartia fagesii* specimens from Galve and Bernissart.

The plotted points (Figure 15) represent the values of the canonical variables that discriminate the genera. There is no overlapping between *Alligator* and *Crocodylus* or of either of these genera with *Caiman* SPIX, 1825 or *Osteolaemus* COPE, 1860. However, an overlapping area is seen for *Caiman* and *Osteolaemus* and for these and *Bernissartia* (according with the vertical axis). The cranial indices that composed the discriminant canonicals



- ◁ Fig. 15 - Plotted points are the values of the canonical variables resulting from the statistical stepwise discriminant analysis (BMDP-7M). The discriminate genera are: 1. centroid of *Alligator*; 2. centroid of *Caiman*; 3. centroid of *Osteolaemus* (black arrows); 4-centroid of *Crocodylus* and 5-centroid for *Bernissartia* (asterisks). Source of data for Recent crocodiles, KÄLIN (1933). From the total introduced cranial indices (see Table 2), the ones that composed the discriminant canonicals are: LC, CI, RII, EOI, TCI, TC4, TC5 and OCI ( see caption of Table 2 for definitions).

TABLE II

LC	CI	RI	RII	EOI	TCI	TCIV	TCV	OCI	OCII	
115	59	65	54	23	78	63	78	17	63	Bernissart specimen
74	49	78	45	29	71	60	90	20	68	Galve specimen

Cranial indices and values of *B. fagesii* (IRScNB-R46) from Bernissart (Belgium) and CR-82 from Galve (Spain). LC, cranial length; CI, length/width skull ratio; RI, width/length rostrum ratio; RII, rostrum/skull length; EOI, interorbital space width/orbital length; TCI, length/width of the cranial table; TCIV, cranial table /skull width; TCV, cranial table width; OCI, orbital skull length; OCII, orbital length/width ratio. Cranial indices are defined as in KÄLIN (1933).

(LC, CI, RII, EOI, TCI, TC4, TC5 and OCI) group *Bernissartia* with the smaller species. This result is consistent with that of the skeletochronology method. There is no evidence on the size/age curve for small Recent species from which we can extrapolate data for *Bernissartia*. With the available metric data it is impossible to infer anything about the probable individual age neither of the Spanish specimen, nor of the Belgian specimen, which would be even more interesting. With only two specimens of *B. fagesii* any fit of the available data to a bivariate graph of cranial variables for Recent species would be suitable, and thus of no significance.

From the above results we conclude that the adult size of *Bernissartia fagesii* must be small. The bone histology and the morphometric comparison are consistent with

each other. Moreover, on the evidence of the number of growth rings in the immature specimen from Spain, we consider it as a small species.

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#### APPENDIX 1

##### Postcranial characters

1. Morphology of vertebral *centra*: amphicoelous (0); procoelous (*centra* with low condyles are included in the term) (1).
2. Neural spine of the *axis*: tall (0); low (1).
3. First caudal vertebra: without anterior condyle (0); biconvex (1).
4. Vertebral hypapophyses: low and tubercular (0); high (1).
5. Cervical hypapophyses: extending most of the length of the *centrum* (0) (In dyrosaurs from the last cervicals to the first thoracics hypapophyses extend the full length of the *centra*, LANGSTON *in litt.*); anterior part of the *centrum* only (1).
6. Neural spines of the last cervicals: anteroposteriorly wide (0); narrow (1).
7. Number of cervical vertebrae: less than nine (0); nine (1).
8. Odontoid process: wide, being slightly wider than the *axis* (0); less than or similar to the width of the *axis* (1).
9. Scapular blade: anteriorly concave and posteriorly straight (0); both outlines straight (1).
10. Ventral width of the coracoid: narrower than the dorsal end (0); wider or about the same size as the dorsal end (1).
11. Proximal shape of the radiale: hatchet shaped (0); spool shaped (1).
12. Iliac blade: Posterior part as high as the anterior one (0); taller in the posterior part (1).
13. Ischiadic lamina: without caudal prolongation at its medial end (0); caudally prolonged (1).
14. *Pubis* distal end: slightly expanded (0); medio-ventrally expanded (spatulated) (1).
15. Proximal articulation of the *tibia*: with two facets (0); one facet (1).
16. Greater dimension of the proximal end of the *tibia*: lateromedial longer than anteroposterior (0); about equidimensional (1).
17. Nuchal scutes: no gap between nuchal and trunk armor (0); nuchal and trunk armor separated by a gap (1).
18. Dorsal scutes: with an anterolateral peg (0); without peg (1).
19. Osteoderms dorsal rows: two (0); more than two (1) (Dyrosaurs probably present the derived condition).
20. Proximal articulation of the *ischium*: double (dorsal and anterior independent) (0); single (a single facet anterodorsal) (1).
21. Nuchal scutes: imbricated anteroposteriorly (0); sutured or adjacent (1).

#### APPENDIX 2

##### Cranial characters

22. Anterolateral outline of the postorbital: squared (0); curved (1).
23. Lacrimo-jugal suture: jugal reaching the lacrimal before the orbital edge (0); jugal advanced with a long lacrimal suture (1).
24. Jugal width in its infratemporal region: ventral side of the jugal in continuity with its anterior portion (0); "stepped" with respect to the anterior part (1).
25. Frontal with an interorbital transverse ridge: absent (0); present (1).
26. Splenial: taking part of the symphysis (0); absent from the symphysis or barely forming part of it (1).
27. External mandibular *fossae*: absent (0); present (1). In some goniopholidids from North America the mandibular external *fossa* is present.
28. Frontal, between the orbits: flat and wide (0); narrower than its anterior and posterior ends (1).
29. Anterior frontal process in its dorsal contacts with the nasals; quadrangular and wide (0); triangular and acute (1).

30. Exoccipitals in the paroccipital processess: with a lateral outline curved overlaying the quadrates (0); with a stepped lateral contour (1).
31. Fronto-parietal suture: frontal broadly exposed in edge of temporal *fossa* (0); frontal barely entering the temporal *fossa* (1).
32. Maxillo-palatine suture (on ventral surface): quadrangular (0); triangular with an acute anterior end (1).
33. Orbital edge of the jugal: straight (0); convex (1).
34. Medial processess of the maxillary: excluded from the anteromedial edges of the palatine cavities (0); backwardly projecting, reaching the palatine laterally (1).
35. Ectopterygoids with a short anterodorsal projection (0); long projection running along the maxillary (1).
36. Dorsal laterosphenoid emplacement in relation to the quadrate in the temporal passage: posterior to central (0); quadrates advanced and medially well developed, the laterosphenoid anteriorly placed (1).
37. Long posterolateral projections of the squamosals: lobulated (0); triangular (1).
38. Medial descending process of the prefrontal: transversely wide (0); anteroposteriorly wide (1).
39. Distance between the orbit and the supratemporal edges *fossa*: short, as a bar (0); wide (1).
40. Quadratojugal spine: absent (0); present (1).
41. Quadratojugal dorsal ornamentation: profuse (0); scarce or absent (1).
42. Jugal posterior length: short (0); long, jugal ending in a sharp apophysis (1).
43. *Choana*: lacking a complete median septum (0); divided by a *septum* (1).
44. Preorbital *foramen*: present (0); absent (1).
45. Mandibular teeth: without two (3rd-4th) mandibular caniniforms (0); with two developed caniniforms (1).
46. Tympanic recessus: anteroposterly developed (0); dorsoventrally developed (1).
47. Basisphenoid: not hidden (0); hidden (1).
48. Medial flange of the retroarticular process: with the maximum curvature at mid-length of the retroarticular process (0); anteriorly disposed (1).
49. Retroarticular dorsal curvature: not much incurved, its tip does not extend beyond the dorsal margin of the mandible (0); extends above the dorsal margin of the mandible (1).
50. Premaxillomaxillary ventral suture: orthogonal to the axial plane (0); oblique (ascendent or descendent) to the axial plane (1). The North American goniopholidids show the derived condition.
51. Lacrimo-nasal suture: present (0); absent (1).