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PHYLOGENETIC RELATIONSHIPS OF THE ATOPOSAURIDAE (ARCHOSAURIA, CROCODYLOMORPHA)

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A systematic revision of the family Atoposauridae is presented, interpreting and reviewing their relationships. The seventy-one characters have been divided into cranial, postcranial and metric which have been used in three separate cladistic analyses in order to discuss their concordance. Polarities, in each case, have been deduced from distinct outgroups. We have used a PHYLIP program (version 2.9). There are five valid taxa of Atoposauridae: *Alligatorellus beaumonti* (rejecting the two subspecific taxa) *Alligatorium meyeri, Theriosuchus pusillus, Alligatorium depereti* (which is transferred to a new genus *Montsecosuchus*) and *Atoposaurus* (discussed as a *nomen dubium*). The three cladograms are not fully concordant. The relative level of derivation in postcranial and cranial characters suggests congruence. The metric traits seem to retain, in general, a primitive condition. The final proposed cladogram clusters *Alligatorium* + *Alligatorellus* as the sister group of *Montsecosuchus* + *Theriosuchus*.

KEY WORDS: Phylogenetic analysis, archosauria, crocodylomorpha, mesoeucrocodylia, atoposauridae.

INTRODUCTION

The first atoposaurids were found in the Jurassic lithographic limestones of Bugey (Cerin, Department of Ain, France) (Thiollière, 1849). Almost at the same time, in the Jurassic lithographic limestones of Kelheim (Bavaria, Germany) a specimen similar to one of the French forms, was found, and it was described by Meyer in 1850. The familiar denomination (Atoposauridae), clustering the genera *Atoposaurus, Alligatorellus* and *Alligatorium,* was proposed by Gervais (1871), and Zittel (1890) placed the family within the Crocodylia. The first accurate description was given by Lortet (1892). Nearly a century later, in 1971, three new specimens from the Solnhofen Formation were reported by Wellnhofer (1971), and Clark (1985) reviewed the relationships of the Atoposauridae.

Besides the original genera, *Alligatorium* (type species *A. meyeri* Gervais 1871), *Alligatorellus* (type species *A. beaumonti* Gervais 1871) and *Atoposaurus* (type species *A. oberndorferi* Meyer 1850), new genera and species were added to the Atoposauridae. These were *Alligatorium franconicum* (Ammon, 1906), *Alligatorium depereti* (Vidal, 1915), *Alligatorium paintenense* (Kuhn, 1961), *Atoposaurus jourdani* (Meyer, 1851), *Hoplosuchus kayi (sensu* Huene, 1933), *Shantungosuchus chuchsienensis* (Young, 1961), *Karatausuchus sharovi* (Efimov, 1976) and *Theriosuchus pusillus (sensu* Joffe, 1967). Several of them have occupied different taxonomic positions as was the case with *Hoplosuchus* (Gilmore, 1926; Huene, 1933; Mook, 1934) and *Theriosuchus* (Owen, 1879; Kalin, 1955; Joffe, 1967). Some other taxa have been considered doubtful, such as *Karatausuchus* or *Shantungosuchus*.

No systematic revision of the Atoposauridae has been carried out, with the exception of several short discussions on a few genera or species. The rare proposals on atoposaur relationships have probably been due to peculiarities such as their tiny size (170–500 mm length), their limited and temporarily short record (Kimmeridgian, Berriasian/Valanginian), and ignorance of important anatomical details, even though most specimens are whole.

Consequently, our aim is to interpret and to review the relationships of each taxon composing the family and to propose a more probable cladogram according to their character-state distribution. The demarcation of each taxon is one of our main goals, especially regarding the Spanish species *Alligatorium depereti* (Fig. 1). This last taxon is transferred to a new genus, *Montsecosuchus* (Buscalioni & Sanz, in prep.).

The polarities deduced from 71 cranial, postcranial and metric characters, have been summarized in Appendices 1 to 3 and the data matrices are in Tables 1 to 3. The three analyses allow us to discuss the concordance between cranial and postcranial characters.

In Table 1 the closest outgroup to the clade *Alligatorium* + *Theriosuchus* has been selected according to the proposed cladogram of Mesoeucrocodilia by Clark (1986). Although the congruence in the chronological record of *Araripesuchus*, *Notosuchus* and *Uruguaysuchus* (all of these are later than the atoposaurs) is small, their phylogenetic position is nevertheless congruent. On the one hand, the atoposaurs are more primitive than the rest of the Metamesosuchia (*sensu* Buffetaut, 1982), Goniopholididae, Bernissartidae, and Paralligator (Buscalioni, 1986), and on the other, the whole of the referred outgroup presents more primitive characters than the Atoposauridae.

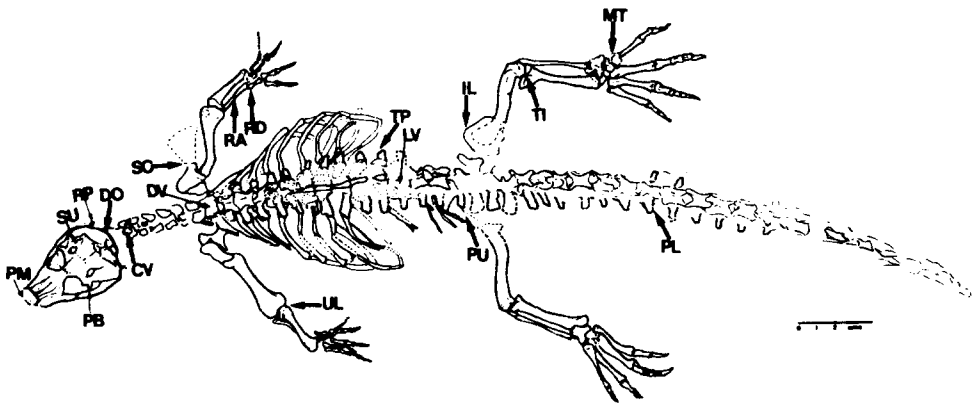

Figure 1 *Montsecosuchus (Alligatorium) depereti* (MMG-512). Letters and arrows indicate the main traits in the specimen. Cranial characters: DO, occipital surface dolichocephalous (21); PB, thickness of postorbital bar (31); PM, anterior outline of premaxillae (25); RP, retroarticular process (5); SU, dorsolateral sulcus in squamosals (18). Postcranial characters: CV, first cervical vertebra; DV, first dorsal vertebra; IL, anterior process of ilium (62); LV, first lumbar vertebra; MT, fifth metatarsal (reduced in *Montsecosuchus*); PL, pleurapophyses; PU, pubis; RA, radius-ulna rate (70); RD, proximal shape of the radiale (54); SC, scapular lamina (48); TI, tibial proximal surface (55); TP, development of the transverse process (39); UL, proximal end of ulna (52). The numbers in brackets correspond to the character definitions in the Appendices (1 to 3).

With respect to the analysis of postcranial characters, protosuchids (*Protosuchus, Hemiprotosuchus, Lesothosuchus* and *Baroqueosuchus*), *Orthosuchus*, as Crocodylomorpha (*sensu* Clark, 1986), have been selected as the outgroup. The chosen outgroup is limited by the scarce postcranial fossil record and the lack of accurate descriptions. The Fruita form (Clark, 1986) and *Uruguaysuchus* (the best postcranial remains known) are also included as reference taxa closer to Atoposauridae than protosuchids or *Orthosuchus*. Nevertheless, *Uruguaysuchus* was described in 1933 by Rusconi, and later by Price (1959), but the specimens are now lost (Gasparini, 1971). There are many unverified and uncertain characters in Table 2, and so this phylogeny is somewhat tentative.

We have used the PHYLIP program (version 2.9) (Wagner and Camin-Sokal mainly) developed by Felsenstein (1986), which has maximum parsimony and compatibility programs, where the outgroup option is considered for a single species. The characters have not been weighted. There is no character discussion for the homoplastic character determination in the data, but some of them have been previously examined in this way (Buscalioni, 1986).

SYSTEMATICS AND CRITICAL ANALYSIS OF THE ATOPOSAURID RECORD

The most frequent features used in the taxonomy of the Atoposauridae are: a) body size (rather small), b) short rostral length, c) paired external nares, d) relatively small supratemporal fenestrae, e) the slenderness of the limbs and the peculiar limb ratios f) the absence or reduction of the dermal armour (see Nopcsa, 1928; Mook, 1934: Kälin, 1955; Kuhn, 1968; Steel, 1973).

The named atoposaurs (see above) could be grouped as follows: forms whose "overall similarity" is high (metric relations included). These are *Atoposaurus jourdani, A. oberndorferi, Alligatorellus beaumonti*, and *Alligatorium meyeri*. Another group could be formed by those new species and subspecies referred to the above-mentioned taxa which have been found in the same formation and adjacent outcrops. These are *Alligatorellus beaumonti bavaricus, Alligatorium paintenense, Alligatorium franconicum* and *Alligatorium depereti* (the Montsec Formation was eventually dated in 1972 as Berriasian/Valanginian by Peybernes & Oertli, but it was previously considered Kimmeridgian). The third group would include some new genera referred to the Atoposauridae by the above mentioned features. These are *Shantungosuchus, Karatausuchus* and *Hoplosuchus*. Thus, we believe that all the attributions to the Atoposauridae, based on classical taxonomic concepts (such as size, preservation and age), suggest a bias on geographical criteria.

The ingroup is established by five of the twelve quoted taxa; we believe that the omitted taxa are either not atoposaurids or *nomina dubia* taxa. Several authors have pointed out the controversial relationships of *Karatausuchus, Hoplosuchus* and *Shantungosuchus* within the Atoposauridae (Buffetaut, 1982; Clark, 1985, 1986; Buscalioni, 1986). We agree with the interpretation of *Hoplosuchus*, by Clark (1986) who considers that it fits well in the "protosuchian grade". *Karatausuchus* is an indeterminate form with an imprecise position within the Metamesosuchia (*sensu* Buffetaut, 1982) (Buscalioni, 1986). *Shantungosuchus* is poorly known, too.

Two of the three species of *Alligatorium, A. paintenense* and *A. franconicum*, are not included, while the third one, *"A.depereti"* is included as *Montsecosuchus*. *A. paintenense* is grouped in the Metamesosuchia close to Goniopholididae, Bernissartidae + Paralligatoridae (Buscalioni, 1986) because of its rostral length, confluent

external nares, wide supratemporal fenestra, and transversely wide osteoderms. Its mandible is posteroventrally projected, as in the *Oweniasuchus minor* specimen (BMNH–48328), a goniopholidid. *A. franconicum* is difficult to evaluate, and we believe that it should be considered as a *nomen dubium*. The single apomorphic trait that it exhibits is the lesser anterior development in the ilium, which is present in *Montsecosuchus* and most of the later Mesoeucrocodilia.

The two subspecies proposed by Wellnhofer (1971) in *Alligatorellus (A. beaumonti beaumonti*, Cerin, and *A.beaumonti bavaricus*, Bavaria) are based on cranial metric divergences and sutures. They were attributed to different geographic habitats. A revision of the Cerin and Bavarian specimens suggest to us that the metric divergences are due to ontogenic and preservational factors (Buscalioni, 1986). The differences found in the skull reconstruction of Wellnhofer (1971) in the lacrimal and prefrontal sutures with the nasal, are not very accurate, as Clark (1985) has also pointed out. *Atoposaurus* consists of two species, *A.jourdani* and *A.oberndorferi* of Meyer (1850–1851). Wellnhofer (1971) justified them according to the following traits: a) the strength of the hind limb in the Cerin specimens, b) the rostral length, c) the tibia/femur ratio, d) the length of the caudal region, e) the length of the precaudal region. We think that some of the divergences are not as pronounced as this author denoted. The tibia/femur ratio is 0.94–1.00 in the *Atoposaurus* specimens. The rostral length divergences are due to the poor preservation of the Bavarian specimens. Finally, the precaudal and caudal regions show some dissimilarities, such as the number of lumbars or caudals, but nevertheless preservation and/or individual variations could modify these two characters.

Valid Taxa

The validity of generic taxa within the Atoposauridae has recently been discussed by Clark (1985, 1986) who proposes that *Atoposaurus* and *Alligatorellus* are synonyms of *Alligatorium* (single valid species *A. meyeri*). This author holds that the observed differences are due to ontogeny. In fact, the atoposaurs have a gradient from *Atoposaurus* (175 mm in size) to *Alligatorium meyeri* (500 mm in size). On the other hand, the Solnhofen Formation is characterized by a high potential of preservation (whole skeletons of juvenile and adult fishes, type A of preservation, Buisonjé, 1985), and it would not be surprising to find other juvenile vertebrates.

In the cladogram proposed by Clark (1986) the family consists of two taxa, *Theriosuchus* and *Alligatorium* alone, but in his discussion on each other taxon, he notes some discordances. We believe that such differences should also be considered in the evaluation of the taxa.

We think *Alligatorellus* (Fig. 2,3) is a valid taxon, and we disagree with Clark (1986) on a number of points. We consider that, unlike the rest of the atoposaurids, either in the Bavarian or French *Alligatorellus* specimens, the postero-lateral lobule of the squamosal is absent, and in both the frontal takes part in the supratemporal fossae. Also, in *Alligatorellus* (SES and MHNL 15639) the ventral surface of the angular descends with respect to that in *Alligatorium* or *Theriosuchus*. In the postcranial skeleton *Alligatorellus* exhibits a peculiar scapular shape, relatively slender, with an uncurved anterior border, and the acromial region is longer than in *Alligatorium, Montsecosuchus*, or *Atoposaurus*.

Atoposaurus (Fig. 4) shows a number of features that could be interpreted as juvenile: absence of scutes, slit-like supratemporal fossae, smooth ornamentation, wide occipital region, and slender postorbital bar (Iordansky, 1973). In fact,

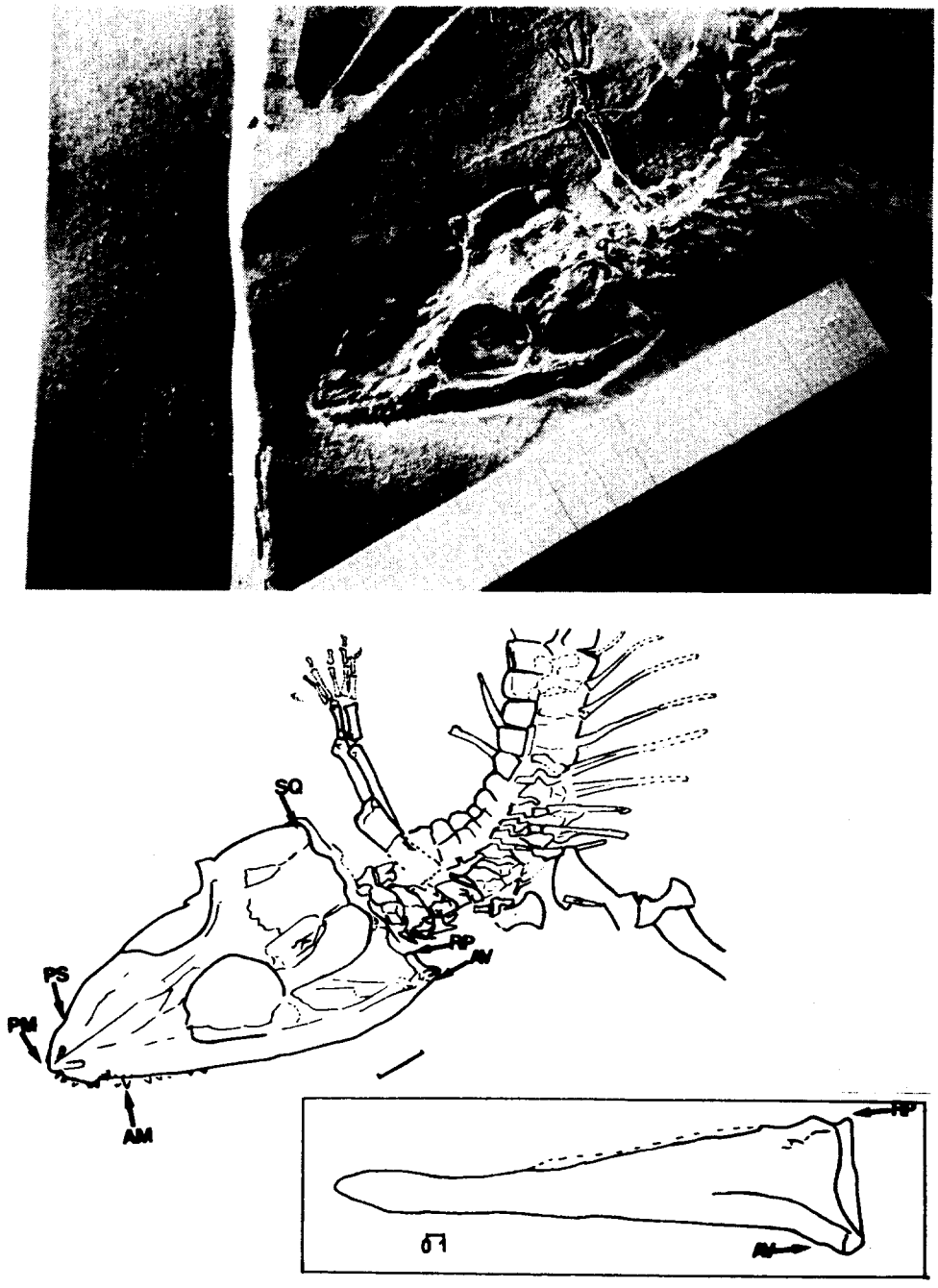

Figure 2 Alligatorellus beaumonti (MNL-15639) AM, anterior maxillary teeth (9); AV, angular ventral outline (6); PS, premaxillo-maxillary space (10); SQ, squamosal posterolateral lobule (absent). Scale equals 5 mm (see Fig. 1 for the remaining abbreviations). The isolated figure represents schema of the mandible of *A. beaumonti* (SES, Obereichstätt), scale in cm.

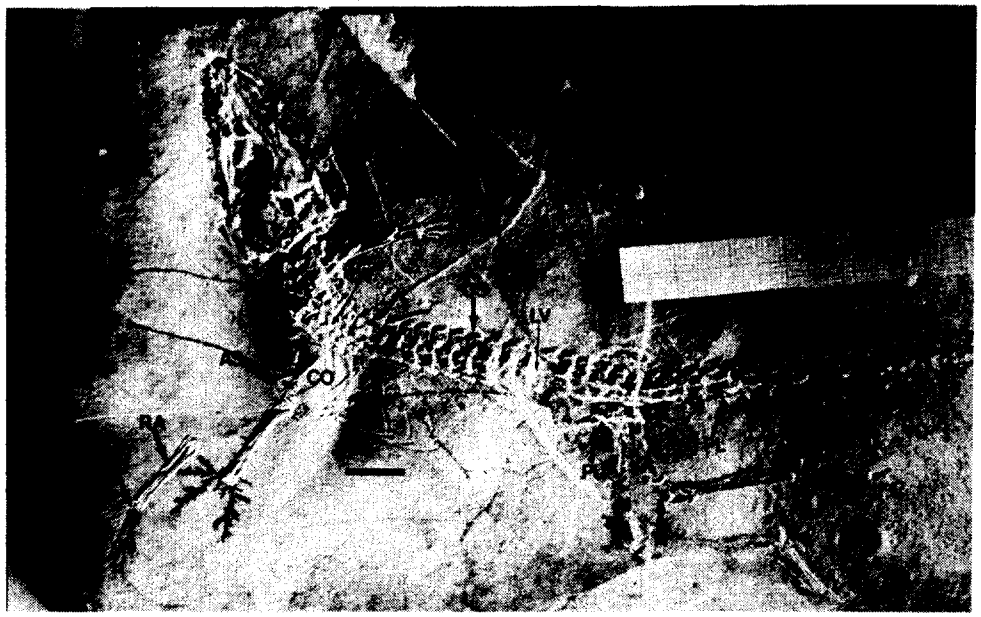

Figure 3 *Alligatorellus beaumonti* (MHNL-15639). AS, acromial region in scapula (47); CO, direction of the glenoid surface of the coracoid (46); OS, osteoderm outline (61); VO, ventral caudal osteoderm. (See caption of Fig. 1 for the remaining abbreviations). Scale bar equals 1 cm.

Atoposaurus is a confusing taxon, since it has no autopomorphic traits, and since it shares with *Montsecosuchus* and *Alligatorellus* (not juvenile forms) some of these features. Among the *Atoposaurus* specimens there are also some discrepancies. The radiale seems to have two conditions. In MHNL 15680 the proximal and distal ends are equally wide, but in BSS 1901I12 the bone impression seems to be hatchet-shaped. On the other hand, if we consider them as juveniles, while osteoderms are absent or costal segments are single, some specimens like MHNL 15680 show strong postcranial ossification. With all the above problems, *Atoposaurus* will be discussed at the end of this paper, after the cladograms.

Alligatorium depereti (Fig. 1) (the Spanish Montsec form) has been discussed as a species related to the genus *Alligatorium* by Wellnhofer (1971) and Buffetaut (1982). We propose to transfer it to the new genus *Montsecosuchus* based mainly on postcranial features and proportions (Buscalioni & Sanz, in prep.). *Montsecosuchus* shows strong fore limbs in comparison to the hind limbs. The humerus has a large distal end, the ulna is robust and the ulna/humerus ratio is also relatively low. The radius/ulna ratio has a different value than in atoposaurs, since the radius is shorter. The radiale in *Montsecosuchus* is hatchet-shaped. The cranial-presacral length ratio differs from atoposaurids (unknown datum in *Theriosuchus*) since presacral length is relatively larger. Metatarsal V is reduced in *Montsecosuchus* but not in *Atoposaurus* or *Alligatorellus*. The pleurapophyses as well as synapophyses are robust (antero-posteriorly wide). In the pelvic girdle, *Montsecosuchus* seems to have three sacral vertebrae, although a further preparation of the specimen is necessary to determine if

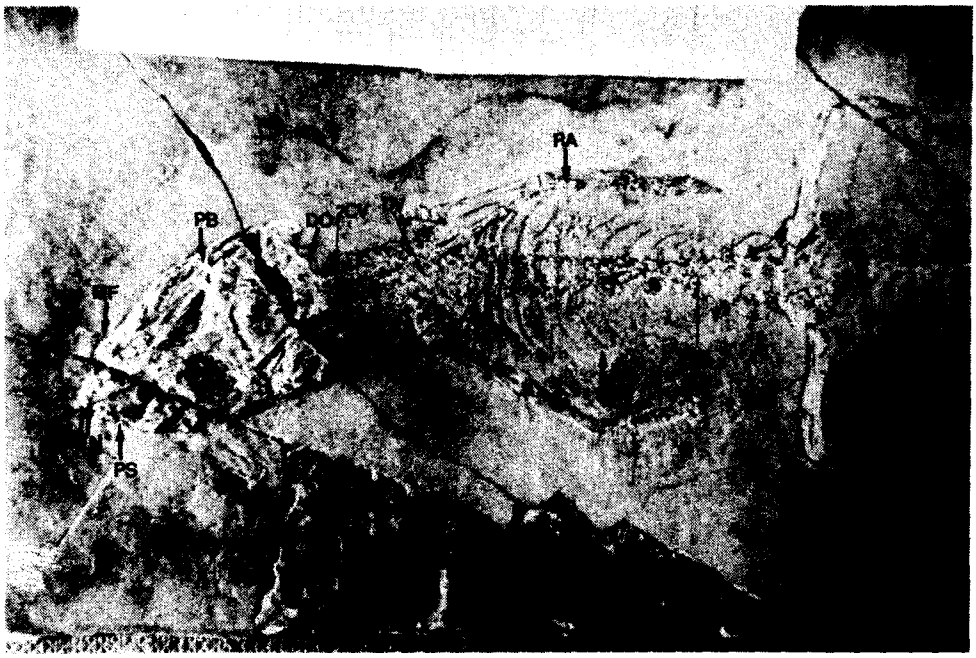

Figure 4 *Atoposaurus jourdani* (MHNL-15679). Cranial characters: EN, external nares (14); MF, maxillary festooning (7); Postcranial characters: 2CV, second cervical vertebra; CT, capitulum and tuberculum (41); SR, single ribs; SV, first sacral vertebra (See the preceeding figure legends for the remaining abbreviations). Scale bar equals 5 mm.

the third probable pleurapophysis is an artefact belonging to the ischium lamina. Finally, the ilium blade has a rounded anterior border without a process.

CORE RESULTS: PHYLOGENETIC PROPOSALS

Cranial Characters (Appendix 1, Table 1, Figure 6)

The monophyly of the Atoposauridae is based on the following apomorphic traits (see Appendix 1): (9) enlarged anterior maxillary teeth, (15) external mandibular fenestrae absent, (16) antorbital fenestrae reduced or absent, (28) squamosals not descendant and (32) dental hypertrophy absent. The next two characters could be considered as probable synapomorphies (data are absent in *Atoposaurus* and *Alligatorium*): (12) five premaxillary teeth, and (13) 12 to 18 maxillary teeth. Atoposaurids share two more traits: (4) maxillary posterior teeth laterally compressed, and (19) short orbito-supratemporal space (but both are also present in *Uruguaysuchus*). The first one (4) is unknown in *Araripesuchus*, so the character should remain unclear in the definition of Atoposauridae. The second (19) is primitive in *Araripesuchus*, the short orbito-supratemporal space in *Uruguaysuchus* may be convergent, as it also occurs in the Fruita form.

The core results deal with two main sister groups, (*Alligatorium* + *Theriosuchus*) + *Montsecosuchus* and *Atoposaurus* + *Alligatorellus*. The clade (*Alligatorium* + *Theriosuchus*) + *Montsecosuchus* shares the features: (22) well developed ornamentation, and

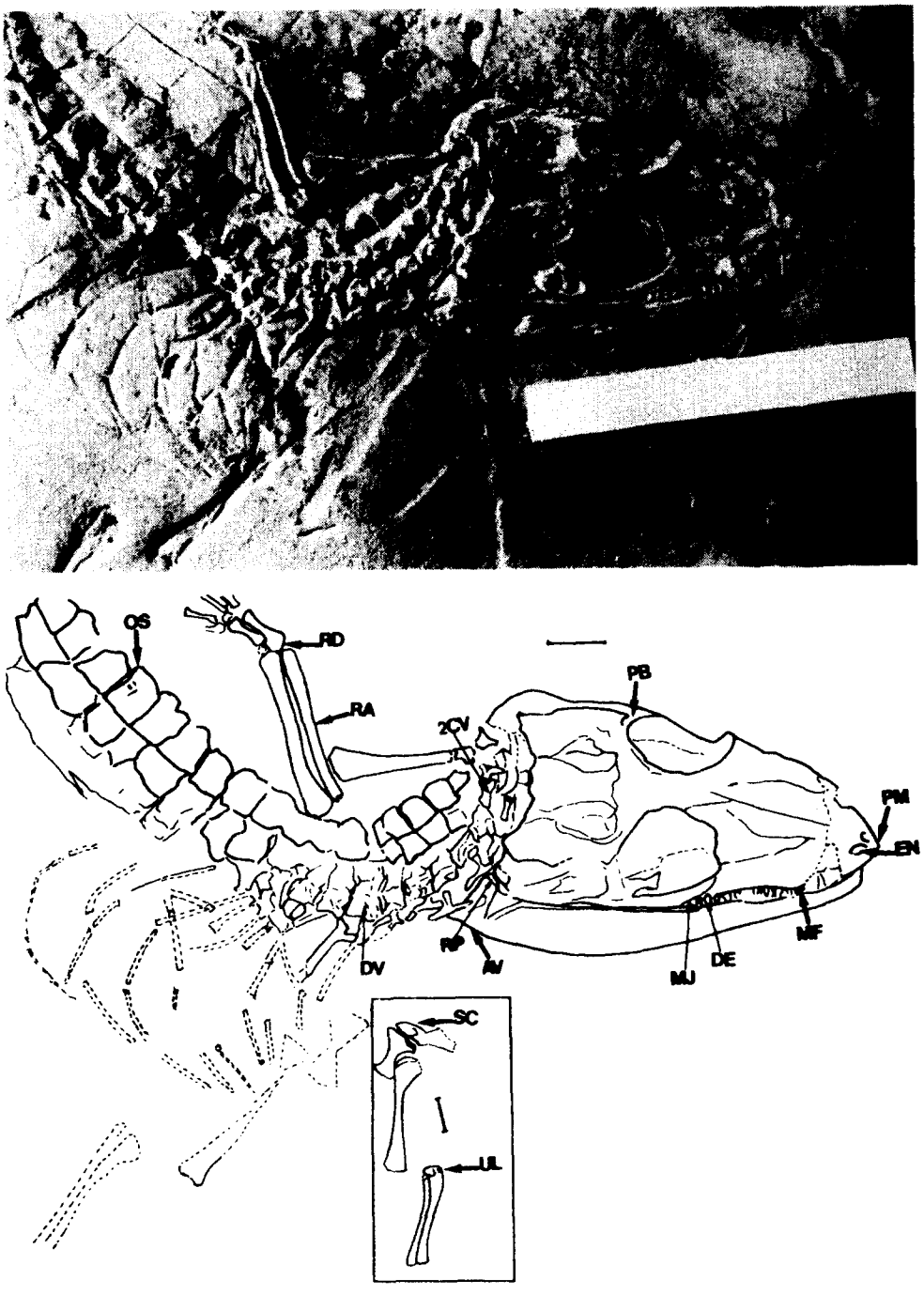

Figure 5 *Alligatorium meyeri* (MHNL-15642/46). Cranial characters: DE, dentition (11); MJ, maxillo-jugal suture. The inset shows the right fore limb in the counterpart (MHNL-15642) (see the preceeding figure legends for the remaining abbreviations). Scale equals 1 cm.

Table 1 Cranial Characters. Data Matrix

Notosuchus	1	0	0	01	1	00	00	0	00	01	0	0	0	1	0	0	0	1	0	1	0	0	1	0	N	0	0	0	0	0	1	0	0	1
Uruguaysuchus	0	?	0	11	1	00	00	0	01	01	1	0	0	?	0	0	0	?	1	0	0	1	1	0	0	1	0	0	1	?	1	0	0	0
Araripesuchus	1	1	1	??	1	01	01	0	01	00	?	0	0	0	0	0	1	1	0	0	0	0	1	0	0	1	0	0	1	?	1	0	?	?
Atoposaurus	0	?	?	??	?	??	01	0	11	01	?	1	?	0	?	1	1	1	1	0	1	0	1	?	0	1	1	1	1	?	0	1	?	?
Alligatorellus	0	1	0	11	0	11	01	0	11	01	1	1	1	0	1	1	1	1	1	0	0	0	B	?	0	1	1	1	1	0	0	1	?	?
Alligatorium	0	1	0	11	0	01	01	1	11	01	1	?	1	0	1	1	1	1	1	0	0	1	1	?	0	1	0	1	1	?	1	1	0	0
Montsecosuchus	?	1	0	??	?	??	00	0	??	01	?	?	?	?	?	1	1	0	1	0	1	1	?	?	?	1	0	1	1	0	1	1	?	?
Theriosuchus	0	0	1	11	?	01	11	1	11	11	1	1	1	0	1	1	1	0	,1	1	0	1	1	0	1	1	0	1	1	0	1	1	0	0
CHARACTER	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34

Table 2 Postcranial Characters. Data Matrix

Protosuchids[+]	0	00	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	?	0	0	1	0	0	00
Orthosuchus	0	00	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	?	1	0	?	0	0	0	0	0	0	00
Atoposaurus	1	01	?	1	1	1	1	1	0	0	1	?	0	0	1	0	1	?	1	B	?	1	0	1	0	N	N	??						
Alligatorellus	1	??	0	1	1	1	0	1	0	B	1	1	1	1	1	?	1	?	1	1	1	1	0	0	0	1	1	01						
Alligatorium	1	01	?	?	?	1	1	?	0	?	1	1	0	0	?	?	?	1	1	1	?	?	?	0	0	1	1	??						
Montsecosuchus	?	??	?	1	1	1	1	1	0	1	1	1	0	?	?	?	?	?	1	1	1	1	?	0	0	1	1	11						
Theriosuchus	1	11	?	1	1	1	1	?	?	?	1	1	?	?	?	?	?	?	?	1	?	?	1	0	0	0	0	??						
CHARACTER	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62						

Character-states: (0) primitive, (1) derived, B Both, N not applicable
Protosuchids : source of data: *Protosuchus*, Colbert and Mook, 1951 : Clark, 1986, *Hemiprotosuchus*, Bonaparte, 1971, *Lethosuchus*, Whetstone and Whybrow, 1983, *Baroqueosuchus*, Busbey and Gow, 1984.

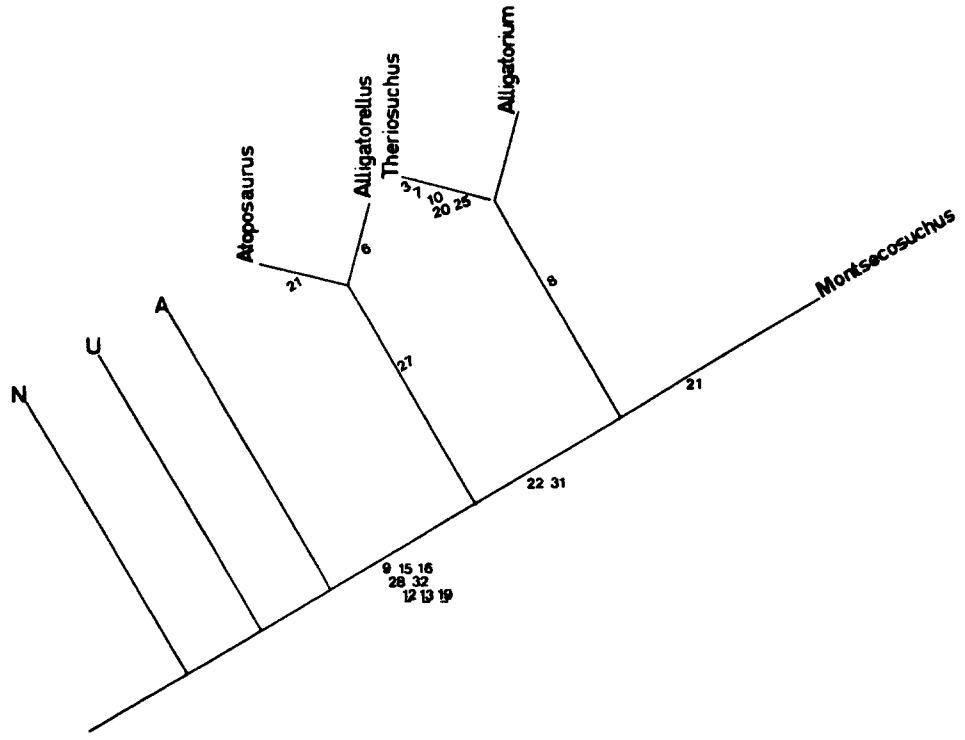

Figure 6 Cladogram of atoposaurid relationships based on cranial characters. The outgroup is N. *Notosuchus*; U, *Uruguaysuchus*; A, *Araripesuchus*.

(31) postorbital bar thick. *Theriosuchus* and *Montsecosuchus* also show a reversion in the trait (18), presence of a sulcus in the dorsolateral edge of the squamosals. *Alligatorium* and *Theriosuchus* share the concave dorsal outline of the snout (8). *Atoposaurus* and *Alligatorellus* share the slit-like supratemporal fenestrae (27).

The taxon *Theriosuchus* is the best defined, since it shows five apomorphic traits: (3) maxillo-jugal suture forward of orbit, (7) strong maxillary festooning, (10) premaxillo-maxillary space with a diastema, (20) parieto-frontal surface with a sagittal ridge, and (25) premaxillae anteriorly wide. *Alligatorium* (fig. 5) is poorly defined, except for those traits proposed for the clade (see Fig. 6). *Montsecosuchus* and *Atoposaurus* are defined by: (21) occipital surface dolichocephalous. *Alligatorellus* has the apomorphy: (6) retroarticular process ventrally incurved.

Postcranial Characters (Appendix 2; Table 2; Figure 7)

The cladogram resolution on the postcranial data is not as clear as for the cranial features. This is due mainly to some poorly known data, so that character states are replaced in the cladogram (see Fig. 7). The main apomorphic traits of atoposaurs are: (35) vertebral centra rounded, (36) absence of anterior keels or hypapophyses in the cervicals, (38) fusion of the para-diapophysis at the level of vertebrae 18–20, (39) transverse process anteroposteriorly developed, (40) posterior costal uncinate process, (41) capitulum-tuberculum widely open (probably except in *Alligatorellus*), (42)

lumbar region with more than two centra, (46) coracoid glenoid fossa in dorsal position. Although the next trait is not fully represented in atoposaurids (lack of data in *Theriosuchus* and *Alligatorium*), this could be shared by all the taxa: (49) shallow supracetabular rim. Among the above features, some (35, 36) are also present in early mesoeucrocodiles (Fruita form). One other trait, (62), reduction in the anterior process of the ilium, may be placed at the base, since it is shared by some further mesoeucrocodiles.

The resulting cladograms deal with two basic nodes. Node A represents *Theriosuchus*, and B the rest of the atoposaurids. *Theriosuchus* has the apomorphies: (36) anterior keels in the cervicals, and (57) procoelous centra. The indeterminate node B shares the characters (60), scutes without anterior "peg", and (61), subtrapezoidal scutes (not valid in *Atoposaurus* because of the total absence of dermal armour). The characters (53), radius articulating on the anterior part of the radial condyle of the humerus, and (55), proximal surface of the tibia with two concavities, could be shared by this clade. The proximal surface of the tibia in Eusuchia shows the primitive condition. There are no strong features that support any sister group. *Alligatorellus* is based on: (47) large acromial region in scapula, and (48) straight and narrow scapular lamina. *Alligatorium* has no autopomorphies. *Montsecosuchus* is defined by: (44), sacral region with three vertebrae, and (62), the total absence of an anterior ilium process. *Atoposaurus* is defined by the total absence of dorsal scutes. Perhaps *Atoposaurus* could share a reversion in: (54), radiale not hatchet-shaped proximally. This reversion is based on *Orthosuchus*, since the character is expressed in protosuchids.

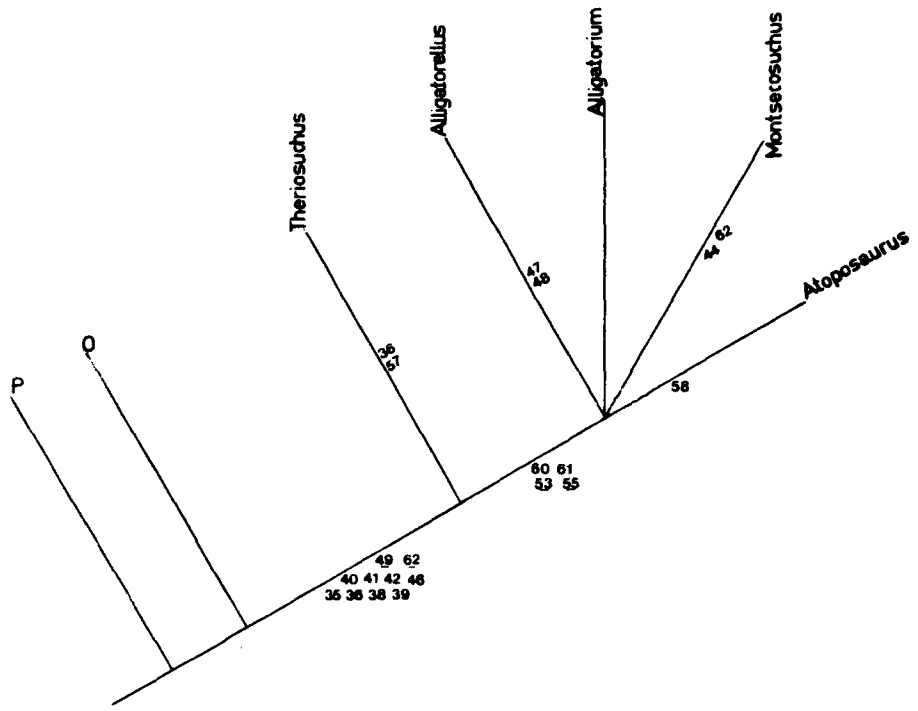

Figure 7 Cladogram of atoposaurid relationships based on postcranial characters. The outgroup is P, protosuchids; O, *Orthosuchus*.

Table 3 Metric Characters. Data matrix

Orthosuchus	0	0	0	0	0	0	0	0	0
Atoposaurus	1	1	1	1	1	0	0	0	0
Alligatorellus	1	1	1	1	1	0	0	0	0
Alligatorium	1	1	1	1	1	0	0	0	0
Montsecosuchus	0	1	1	1	0	1	0	1	1
Theriosuchus	?	1	1	1	?	0	0	0	1
CHARACTERS	63	64	65	66	67	68	69	70	71

Metric Characters (Appendix 3, Table 3, Figure 8)

The ranges proposed for the metric features have been set by comparing a large sample of crocodiles (*Bernissartia*, several *Goniopholis*) and we believe that they are significant. The monophyly of the Atoposauridae is based (with respect to *Orthosuchus*) on: (64), the relative width of the rostrum, as long as wide or wider than long, (65), the buccal index with values over 100, subquadrangular in shape, (66), the supratemporal ratio, supratemporal fossae smaller than orbits (see Appendix 3 for all characters, and Table 4 for the metric values).

Table 4 Metric values of cranial and Postcranial ratios

Orthosuchus	ca.37	56	94	110	102	74	94	—	95
Atoposaurus	52	114	197	40	55	70	95	99	94
Alligatorellus	51	148	250	53	48	70	95	97	85
Alligatorium	50	103	146	53	47	69	90	92	85
Montsecosuchus	27	121	192	46	77	46	82	65	75
Theriosuchus	—	103	162	70	—	63	93	93	76
CHARACTERS	63	64	65	66	67	68	69	70	71

Ratio enuntiations in Appendix 3. *Orthosuchus* : source of data, Nash, 1975

The cladogram deals with two clades, *Theriosuchus* + *Montsecosuchus* and the rest of the atoposaurs as indeterminate. The first clade shares, (71), ulna/humerus relation, ulna much shorter than humerus. *Montsecosuchus* has two autopomorphies: (68), radius/tibia ratio, radius 1/3 of tibia length, and (70), radius/ulna ratio, radius less than ulna. The next clade shares the (63), cranial-presacral ratio, cranial one half the presacral length, and the (67), scapula/humerus relation, scapula one half the humerus length. The cranial-presacral ratio is considered as a primitive feature in *Montsecosuchus*, with respect to the reconstructed proportions proposed by Nash (1975) in *Orthosuchus*. The above traits (63) and (67) are unknown in *Theriosuchus*.

DISCUSSION

The cladograms from cranial, postcranial, and metric data, are not fully concordant. The cranial one has the best resolution since postcranial and metric data have some unknown values. The conclusions may be considered in two ways, globally and by taxa.

The metric data seem to keep primitive characteristics in general. The relative cranial length in atoposaurids is comparable to *Notosuchus*, *Uruguaysuchus* and *Araripesuchus*, with the supratemporal fossae shorter than the orbits, and short wide rostra.

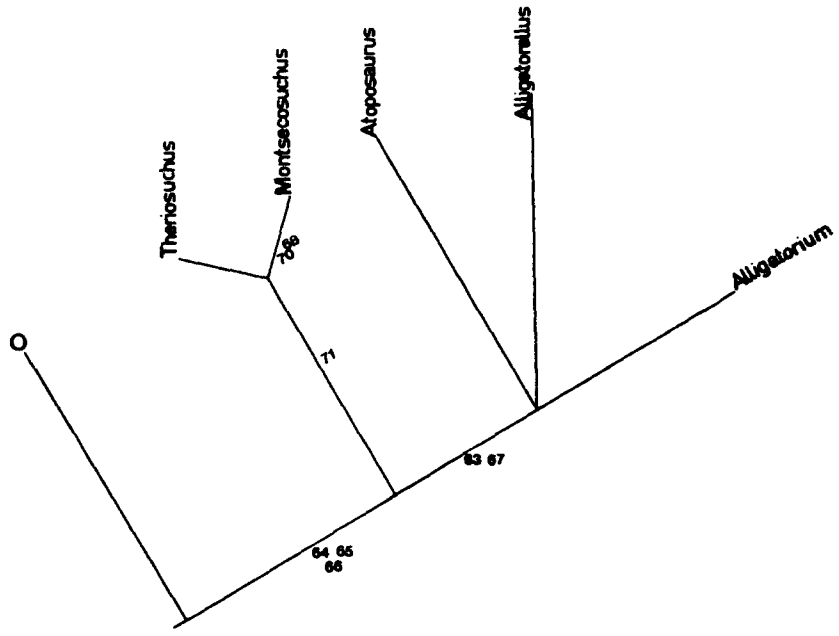

Figure 8 Cladogram of atoposaurid relationships based on metric characters. The outgroup is O, *Orthosuchus*.

The postcranial data are derived in atoposaurids, as a whole. Nevertheless, if we compare *Uruguaysuchus* with the atoposaurs, the latter taxon has more derived traits in the postcranial than in the cranial characters.

Concerning the taxa, *Theriosuchus* is the best defined. The relative level of derivation in postcranial and cranial data suggests congruence (procoelous vertebrae, anterior dorsal vertebrae keeled, absent or reduced antorbital foramen, premaxillo-maxillary space, anterior outline of premaxillae). In *Montsecosuchus*, proportions are very peculiar; the radius/humerus ratio is close to the Eusuchia (*Crocodylus*). *Alligatorium* and *Alligatorellus* are more primitive forms. *Alligatorium* has no autopomorphies, while *Alligatorellus* shows a number of them in the cranial (retroarticular process) and postcranial skeletons (scapula lamina shape). *Atoposaurus*, as we have noted, is a confusing form, with no clear apomorphy. *Atoposaurus* may be a *nomen dubium* and its interpretation as a juvenile (perhaps of *A.meyeri*) can neither be confirmed nor rejected.

We propose two synthesis cladograms (fig. 9) and classifications. The difference within the final cladograms is based on the position of *Montsecosuchus*. In 9B, *Montsecosuchus* is the sister group of *Alligatorellus* + *Alligatorium*, where characters (60) and (61) on the osteoderm shape, and probably (53) and (55), are shared by all the three taxa. Nevertheless, osteoderms are not as well known in *Montsecosuchus* as in *Alligatorellus* or *Alligatorium*. In the same cladogram the reversion in characters (60) and (61) would not be necessary for *Theriosuchus*, as occurs in 9A. Otherwise, traits (8) and (71) would be convergent: *Alligatorium-Theriosuchus* ((8) in 9A, 9B) and *Montsecosuchus-Theriosuchus* ((71) in 9B). If we consider some of the autopomorphies

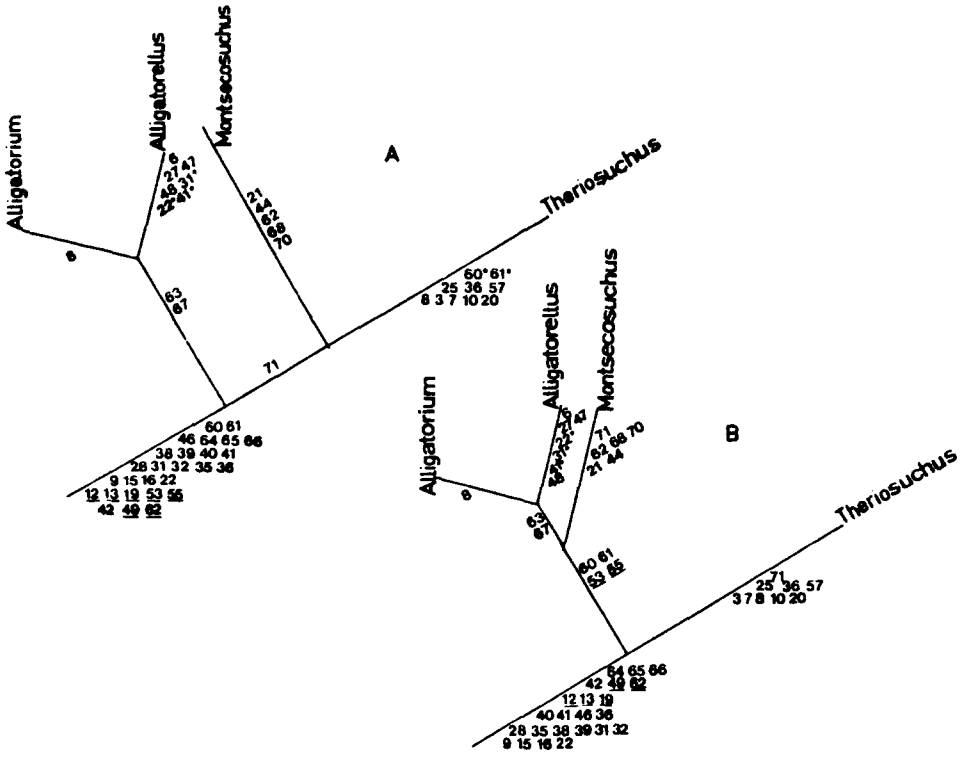

Figure 9 Synthesis cladograms of atoposaurid relationships. A, preferred cladogram.

found in *Montsecosuchus* and the feeble traits that support the clade (*Alligatorium* + *Alligatorellus*) + *Montsecosuchus*, cladogram 9A is preferred.

Abbreviations

BMNH: British Museum Natural History. BSS: Bayerische Staatssammlung für Paläontologie und Historische Geologie, München. MHNL: Musée Guimet d'Histoire Naturelle de la Ville de Lyon. MMG: Museo Martorell de Geologia, Barcelona. SES: Sammlung Eduard Schöpfel, Obereichstätt.

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APPENDIX 1. CRANIAL CHARACTERS

1. Relation of frontal to supratemporal fossae takes part (0)/excluded (1)
2. Lacrimo-nasal suture posterior to nasal (0)/lateral to nasal (1)
3. Maxillo-jugal suture posterior to orbit (0)/anterior to orbit (1)
4. Maxillary posterior teeth conical (0)/laterally compressed (1)/laterally compressed and denticulated (2)
5. Retroarticular process slightly developed (0)/strongly developed (1)
6. Angular, ventral outline straight (0)/dorsally incurved (1)/ventrally incurved (2)
7. Maxillary festooning absent (0)/slight (1)/strong (2)
8. Dorsal outline of snout straight or convex (0)/concave (1)
9. Enlarged anterior maxillary teeth absent (0)/anterior-2nd, 3rd alveoli (1)/middle-4th, 5th alveoli (2)
10. Premaxillo-maxillary space present with a notch (0)/absent or slight (1)/diastema (2)
11. Dentition homodont (0)/heterodont (1)
12. Premaxilla, number of teeth less than five (0)/ five (1)
13. Maxilla, number of teeth less than 12 (0)/12 to 18 (1)
14. External nares paired (0)/single (1)
15. External mandibular foramen present (0)/absent (1)
16. Antorbital fenestrae present (0)/reduced or absent (1)
17. Postorbital pillar exterior (0)/interior (1)
18. Dorso-lateral edge in squamosals with a sulcus (0)/without sulcus (1)
19. Orbito-supratemporal space relatively long (0)/short (1)
20. Parieto-frontal surface smooth (0)/with a ridge (1)
21. Occipital surface arrangement vertical (0)/caudal ("dolichocephalous") (1)
22. Ornamentation tenuous (0)/well developed (1)
23. Pineal foramen present (0)/absent (1)
24. Choana with septum present (0)/absent (1)
25. Anterior outline of premaxillae pointed (0)/wide (1)
26. Quadrate fenestrated (0)/not fenestrated (1)
27. Supratemporal fossae wide (0)/slit-like (1)
28. Postero-laterally descendant squamosals present (0)/absent (1)
29. Direction of external nares frontal (0)/dorsal (1)
30. Basioccipital ventral and anterior present (0)/absent (1)
31. Thickness of postorbital bar slender (0)/thick (1)
32. Dental hypertrophy present (0)/absent (1)
33. Greatest quadrate hemicondyle medial (0)/lateral (1)
34. Quadrate condyle development slight (0)/pronounced (1)

APPENDIX 2. POSTCRANIAL CHARACTERS

35. Morphology of vertebral centra spool-shaped (0)/rounded (1)
36. Keels or/and hypapophuses in cervicals anteroposterior (0)/absent (1) anterior (2)
37. Keels in the anterior dorsals absent (0)/present (1)
38. Para-diapophysis fusion in 23 or 24 vertebrae (0)/18–20 (1)
39. Distal development of transverse process dorsoventral (0)/anteroposterior (1)
40. Costal uncinate process anterior and posterior (0)/posterior (1)

41. Capitulum and Tuberculum slightly separated (0)/widely separated (1)
42. Lumbar region one-two centra (0)/more than two (1)
43. Number of cervicals less than nine vertebrae (0)/nine (1)
44. Number of sacrals two (0)/more than two (1)
45. Posteromedial coracoid process styliform (0)/spatulate (1)
46. Direction of the glenoid surface in coracoid posterior (0)/dorsal (1)
47. Acromial region in scapula not exceeding the coracoid edge (0)/exceeding (1)
48. Scapular lamina relatively short, dorsally spread and anteriorly curved (0)/ relatively tall, narrow, dorsally spread and straight (1)
49. Supracetabular rim prominent (0)/shallow (1)
50. Anterior descendant process of the ilium single (0)/bifurcated (1)
51. Pubis in the acetabular cav. takes part (0)/excluded (1)
52. Ulna proximal end anterolaterally expanded absent (0)/present (1)
53. Radius-humerus articulation in the radial condyle (0)/anterior to the radial condyle (1)
54. Proximal shape of radiale proximal and distal ends equally wide (0) hatchet-shaped (1)
55. Proximal surface of tibia flat or with one concavity (0)/two concavities (1)
56. Maximum proximal diameter of tibia anteroposterior equal to lateromedial (0)/ lateromedial larger (1)
57. Vertebrae amphicoelous (0)/procoelous (1)
58. Dorsal scutes present (two rows) (0)/absent (1)
59. Ventral trunk scutes absent (0)/present (1)
60. Anterior "peg" in scutes present (0)/absent (1)
61. Osteoderm outline Transversely larger (0)/subtrapezoidal or quadrangular (1)
62. Anterior process of ilium long (0)/relatively short (1)/absent (2)

APPENDIX 3. METRIC CHARACTERS

63. Cranial/presacral length ratio cranial length less than half the presacral length (0)/about one half (1)
64. Relative rostral width (Rostral width/length, Kälin, 1933) longer than wide (0)/ as long as wide or wider than long (1)
65. Buccal Index (Ayarzagüena, 1984) (Pmx. width + 10th tooth width/rostral length) buccal shape trapezoidal (0)/quadrangular (1)
66. Supratemporal relation (Fossa/orbita length) supratemporal fossae larger than orbits (0)/shorter or equal (1)
67. Scapulo-humerus length ratio about the same length (0)/scapula half the humerus length (1)
68. Radius/Tibia length ratio radius about ½ of tibia length (0)/radius about ⅓ of tibia length (1)
69. Tibia/Femur length ratio about the same length (0)/Tibia much shorter than femur (1)
70. Radius/Ulna length ratio radius as long as ulna (0)/shorter than ulna (1)
71. Ulna/Humerus length ratio ulna about the same length (0)/ulna much shorter than humerus (1).

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