For the family pets:

Sandy, who, despite being blind and lacking any functional dentition, has continued to laugh in the face of natural selection for almost two decades;
And Shaft, who, despite reminders too numerous to count, considers himself to be in complete control at all times.
May I never cease to be amazed.

UNIVERSITY OF ALBERTA

THE TAXONOMY AND SYSTEMATICS OF THE GENUS *AIGIALOSAURUS* (SQUAMATA: AIGIALOSAURIDAE)

by

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ABSTRACT

Aigialosaurus dalmaticus and *A. bucchichi* are redescribed and the genus *Opetiosaurus* is shown to be a junior synonym of *Aigialosaurus*. These redescriptions highlight morphological data that have been overlooked by, or were unavailable for, previous studies. A systematic analysis of anguimorph lizards finds *Aigialosaurus* to be closely allied with *Paravaranus* to form the sister group to varanids. A further analysis of all mosasauroids finds no support for a recent hypothesis postulating three separate evolutionary occurrences of paddle-like limbs within the clade. The results indicate that paddle-like limbs likely evolved twice among mosasauroids although the interrelationships of the basal taxa, including both *A. bucchichi* and *A. dalmaticus*, remain poorly resolved. The genus *Aigialosaurus* is not found to be the most basal mosasauroid as previously hypothesized, but is instead located amongst a series of consecutive sister taxa to Natantia.

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GENERAL INTRODUCTION

The family Aigialosauridae was erected by Kramberger (1892) for two semi-aquatic squamate specimens: *Aigialosaurus dalmaticus* and *A. novaki* from the Cenomanian-Turonian of Hvar, Croatia. Many new taxa have been added to the family, but over a century after the erection of Aigialosauridae, *A. dalmaticus* and a specimen described by Kornhuber (1901) as "*Opetiosaurus*" *bucchichi* from the same Croatian island, remain the most complete, and informative, representatives of the group.

While the taxonomic status of aigialosaurs has changed little in the past century, the interfamilial relationships have been modified considerably making the phylogenetic relationships between aigialosaurs, mosasaurs, dolichosaurs, coniasaurs, varanids and other squamates a topic of much debate. *Aigialosaurus dalmaticus* and *O. bucchichi* have been widely recognized as the most basal mosasauroids due to their derived mosasaurian skull characters but relatively conservative terrestrial limb structure. Recent systematic analyses (Bell 1993 and 1997, Bell and Polcyn in press) have indicated that the taxa commonly referred to as aigialosaurs form a non-monophyletic group within Mosasauroidea. The relationships hypothesized in the most recent analysis (Bell and Polcyn in press) suggest new scenarios for the evolution of the paddle-like limb in different mosasaurian groups in addition to several interesting new ideas regarding the bio-geographic origins of mosasaurs.

As *A. dalmaticus* and *O. bucchichi* are widely assumed to represent basal mosasauroids they are excellent representatives to use in studies of mosasauroid relationships within anguimorph lizards. Numerous anguimorph studies (Norell et al. 1992, Lee 1997, Gao and Norell 1998) have resolved different anguimorph tree topologies, but the relationships of aigialosaurs (and by association mosasaurs) within

Anguimorpha remain relatively poorly tested. The descriptive literature available for *A. dalmaticus* and *O. bucchichi* (Carroll and deBraga 1992) contains erroneous anatomical information that makes accurate character coding for phylogenetic analyses impossible.

In order to accurately assess the positions of *A. dalmaticus* and *O. bucchichi* within both Mosasauroidea and Anguimorpha it is essential that detailed redescriptions of both specimens be undertaken. Redescription will allow for more accurate character codings within the systematic analyses than has been previously possible and will also allow for detailed comparison between the two specimens. This detailed comparison will test the suggestion of previous authors (Carroll and deBraga 1992, Caldwell et al. 1995) that *A. dalmaticus* and *O. bucchichi* represent congeneric specimens.

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CHAPTER ONE

A REVIEW OF THE TAXONOMY AND SYSTEMATICS OF THE AIGIALOSAURS

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INTRODUCTION

The conventional characterization of 'aigialosaurs' is that they are semi-aquatic squamates that lived in marginal marine habitats during the early stages of the Upper Cretaceous. The first described aigialosaurs were found in the Cenomanian-aged rocks along the coast of the Adriatic Sea; more recently, Bell (1997) reported on the presence, though without any description of the animal, of an aigialosaur from North America (this characterization is now revised in this volume). Recent taxonomic and systematic questions of aigialosaur nomenclature and phylogenetic relations have focused on which taxa are valid, who is their closest sister group within Squamata, and whether of not there is a monophyletic Aigialosauridae (Caldwell et al. 1995; Bell 1997), all of which harkens back to a similar debate between Kornhuber (1873) and Kramberger (1892).

There are currently six published descriptions of putative aigialosaurs: *Aigialosaurus dalmaticus* Kramberger, 1892, *A. novaki* Kramberger, 1892, *Carsosaurus marchesetti* Kornhuber, 1893, *Opetiosaurus bucchichi* Kornhuber, 1901, *Proaigialosaurus hueni* Kuhn, 1958, and *Haasiasaurus gittelmani* Polcyn et al., 1999. In addition to the specimens properly described in the historical literature there are two more important taxa that have played integral roles in recent discussions of aigialosaur taxonomy and phylogeny. *Dallasaurus turneri* Bell and Polcyn, in press (previous literature as "the Dallas aigialosaur" although the most recent systematic analysis places it as the sister group to clidastine mosasaurs), has just recently been described and "the Trieste aigialosaur," erroneously referred to the genus *Opetiosaurus* (Calligaris 1988) and then left unnamed by Carroll and deBraga (1992) and later researchers, which is in the process of being described (A. Palci pers. comm.). These eight specimens represent the complete dataset upon which our understanding of aigialosaurs is based.

It is the goal of this study to review the literature describing and interpreting these eight specimens from the first publication (Kramberger 1892) through the most recent systematic analyses (Bell and Polcyn in press and Polcyn and Bell in press). This review will identify gaps in the current knowledge of aigialosaurs and, by association, weaknesses in current systematic hypotheses. By analyzing the strengths and weaknesses of previous taxonomic and systematic interpretations it will be possible to determine the best starting points for future research and the directions that this research should take.

REVIEW

The family Aigialosauridae was erected by Kramberger (1892) to contain the previously described *Acteosaurus* von Meyer, 1860, and *Adriosaurus* Seeley, 1881, his newly described specimens from the island of Lesina, Italy (now Hvar, Croatia), *A. dalmaticus* and *A. novaki*, and the renamed *Pontosaurus* (=*Hydrosaurus*) *lesinensis* originally described in 1873 by Kornhuber (for a review of *P. lesinensis* and dolichosaur systematics see Pierce and Caldwell 2004). Kramberger grouped the Aigialosauridae with the Dolichosauridae (including only *Dolichosaurus longicollis* Owen, 1850) in the new Suborder Ophiosauria (Fig.1-1a; this name was actually preoccupied and was emended to Dolichosauria at a later date). Kramberger hypothesised that the Aigialosauridae were ancestral to modern lacertilians, dolichosaurs, and pythonomorphs (=snakes and mosasaurs).

Kramberger's classification scheme was reviewed by Kornhuber (1901) who determined that the members of the Family Aigialosauridae did not differ significantly from extant monitors and thus did not merit removal from the family Varanidae. Kornhuber (1901) argued that the "completely different shape" of the quadrate in *A. dalmaticus* was not sufficient cause to erect a new family, suggesting instead that quadrate shape was extremely variable across Varanidae and that the differences seen in *A. dalmaticus* were not exceptional. Kornhuber (1901) went on to point out that if any specimen were to be used to illustrate a transitional form between varanids and pythonomorphs it should be not Kramberger's *A. dalmaticus*, but instead his new specimen *O. bucchichi* based on its "special, outstanding dentition" (the cone-shaped dentition of *O. bucchichi* appears to have been crushed, giving the teeth a more leaf-like appearance [pers. obs.]). It should be noted that in addition to contradicting Kramberger's (1892) classification scheme, Kornhuber (1901) also refused to acknowledge the renaming of *Pontosaurus*, repeatedly referring to the specimen as *Hydrosaurus* throughout his paper.

With two totally different classification schemes in the literature, Nopcsa (1903) was the next to review the "*Varanus*-like lizards of Istria." While agreeing with Kramberger (1892) that the Aigialosauridae were sufficiently different from extant varanids to merit a familial distinction, Nopcsa (1903) proposed a different distribution of genera amongst the families. It was Nopcsa (1903) who recognised that the lengthy neck and tail and reduced limbs of *Acteosaurus*, *Adriosaurus* and

Pontosaurus were much more similar to characteristics seen in *Dolichosaurus*, thus meriting their placement in the family Dolichosauridae (Fig.1-1b). The remaining lizards (*Aigialosaurus*, *Carsosaurus*, *Opetiosaurus* and *Mesoleptos zendrini*) were grouped together in an emended Aigialosauridae.

Nopcsa (1908, 1923) again reviewed the relationships of fossil lizards, with the latter paper being his final word on the subject. Rejecting his earlier (Nopcsa 1903) suggestion that dolichosaurs and aigialosaurs were distantly related, Nopcsa determined that they should be placed in the same family. After some taxonomic juggling (see Nopcsa 1923 for details) the family Dolichosauridae was emended to include three subfamilies: Dolichosaurinae (*Acteosaurus*, *Adriosaurus*, *Pontosaurus*, *Dolichosaurus* and the newly named *Eidolosaurus*), Aigialosaurinae (*Aigialosaurus*, *Carsosaurus* and *Opetiosaurus*) and the newly erected, monogeneric Mesoleptinae (*Mesoleptos*). Nopcsa (1923) also went to great lengths to disagree with earlier arguments by Féjérváry (1918), who suggested that the cranial similarities seen in aigialosaurs and mosasaurs were a result of convergence, and to state that the subfamily Aigialosaurinae contained the ancestors of the mosasaurs. In addition to supporting the aigialosaur-mosasaur relationship, Nopcsa (1923) also suggested an aigialosaurian-like ancestor for snakes, based on similarities in the caudal regions of *A. dalmaticus* and *Pachyophis woodwardi*.

At the same time that Nopcsa (1923) was penning his final thoughts on the subject, Camp (1923) was publishing his classification of lizards. His taxonomic groupings (Fig.1-1c) were in general agreement with earlier works by Dollo (1904), Williston (1904) and Nopcsa (1923), although the details of the taxonomy varied slightly. The families Varanidae, Dolichosauridae and Aigialosauridae were grouped in the Superfamily Varanoidea. Camp (1923) believed that aigialosaurs were descended from "true lizards near the Varanidae" and that they were ancestral to both the mosasaurs and the dolichosaurs (Camp did not think snakes were dolichosaur descendents, instead placing Serpentes as a suborder derived from a common ancestor of aigialosaurs and varanids). The classification scheme devised by Camp (1923) was used by most researchers in the field as the working model until it was thoroughly revised by Estes et al. (1988) using computer-based parsimony methods.

The next to examine aigialosaurs were McDowell and Bogert (1954) in their treatise on *Lanthanotus borneensis*. They concluded that *L. borneensis* was not a highly derived varanid but instead a relict aigialosaur. This claim was based on the similarities in the hinge of the lower jaw (while superficially similar, the hinges differ significantly upon closer examination), reduced phalangeal number (their count of four phalanges on the fourth digit of the aigialosaur pes has been shown to be erroneous; *Opetiosaurus* and *Aigialosaurus* both show five phalanges in this position), and shortened limbs seen in aigialosaurs and *L. borneensis*. McDowell and Bogert (1954) placed *Lanthanotus* in a clade with dolichosaurs, aigialosaurs and mosasaurs but did not hypothesise any sister group relations within this clade.

After McDowell and Bogert (1954) mentioned aigialosaurs, Kuhn (1958) described *Proaigialosaurus hueni* from skull fragments found at Solnhofen in southern Germany. The description is not very thorough and the specimen has since been lost. Thus *Proaigialosaurus* made an extremely brief, and not terribly useful, appearance in the aigialosaur literature. Should the specimen ever be relocated, a thorough redescription and detailed drawings and photographs should serve to verify the original diagnosis and allow the specimen to be placed in a systematic context.

When Camp and Allison (1961) revised the earlier classification of lizards (Camp 1923) the general arrangement remained the same with two new families being added to the Superfamily Varanoidea: the Helodermatidae and the Lanthanotidae (the authors obviously disagreed with the classification of *Lanthanotus* as an aigialosaur by McDowell and Bogert [1954]). Russell (1967) used Camp and Allison's (1961) taxonomic scheme in his landmark publication which focused on the Mosasauridae but also mentioned basal mosasauroids. While discussing mosasaurian ancestors, Russell suggested that they likely passed through a body-form similar to that of aigialosaurs, reaffirming the close evolutionary relationship of the two groups. Russell also took issue with the suggestion by McDowell and Bogert (1954) that *Lanthanotus* had its origin within the mosasauroids and instead placed them in a polytomy with helodermatids, varanids and "saniwinines" as "tertiary varanoids" (Russell 1967, p.200).

Russell (1967) covered the subject of mosasaurs so thoroughly that few new studies appeared on the subject, save various new species descriptions, for the following two decades. Aigialosaurs were left unmentioned in the literature during this period.

The year before Russell (1967) published his manuscript, the first English translation of Hennig's (1966) 'Grundzüge einer Theorie der phylogenetischen Systematik' (Phylogenetic Systematics) appeared. While the method was set out in the 1950s, the use of Hennig's parsimony analysis of phylogeny did not become popular until personal computers became available to run large analyses. The first large squamate phylogeny to be analysed using computers was that of Estes et al. (1988). The paper was a first attempt to put all lizard families in a systematic context using both osteological and soft tissue characters. This study resulted in a sizeable departure from the classification of Camp (1923) on the familial level. Unfortunately, fossil squamates, such as mosasaurs, dolichosaurs and aigialosaurs, were not included in the analysis.

Despite being excluded from the Estes et al. (1988) analysis, aigialosaurs did reappear in the literature in the form of a survey of Adriatic lizards by Calligaris (1988). This review added little information to that already known from much earlier in the century with the exception of mentioning a new specimen from Komen, Slovenia. The new specimen was casually referred to the genus *Opetiosaurus* but was not formally described. The conclusions that Calligaris (1988) drew from his review were that the taxonomy proposed by Nopcsa (1903) was sufficient (Calligaris refers to Nopcsa [1923] instead of Camp [1923] who emended the familial groupings and whose classification scheme was more widely accepted) and that there was little to be done with the group until further specimens were discovered.

The following descriptive and interpretive studies are all cladistic studies of phylogeny, the data of which are all explicitly available for criticism in each publication.

Carroll and deBraga (1992)

Carroll and deBraga (1992) published general descriptions of *O. bucchichi*, *A. dalmaticus* and Calligaris' (1988) Komen specimen, which they referred to not as *Opetiosaurus* but instead as "the Trieste aigialosaur." Carroll and deBraga (1992) assumed that the three specimens were closely related and shared similar ways of life. This meant that they were describing a generalised "aigialosaurian-grade" body-plan. Carroll and deBraga (1992) used the information from their descriptions to code a fifteen-character matrix for "Aigialosauridae" (a composite of characters from the three specimens in the study, in effect an assumed monophyletic group) and nine other terminal taxa in an attempt to determine aigialosaur relationships within Anguimorpha. The resulting tree (the first published phylogenetic analysis to include aigialosaurs) placed aigialosaurs in a polytomy with the *Lanthanotus*/*Varanus* and *Cherminotus*/*Saniwa* clades. This grouping was supported by several characters including: the shape of the pterygopalatine suture, the degree of contact between the supraoccipital and the parietal, the presence or absence of a notched dentary, and the size of the supratemporal process of the parietal, of which only the latter two are visible on known aigialosaur specimens. It should be noted that, while the systematic analysis was relatively cursory by some standards, this study represents the first computer generated systematic analysis of aigialosaur relationships.

deBraga and Carroll (1993)

DeBraga and Carroll (1993) proceeded to publish a larger-scale analysis of mosasauroid and lizard systematics. Aigialosaurs were again coded as a single terminal taxon, negating any possibility of testing their monophyly. The analysis (142 characters and 17 taxa) was designed primarily to study the internal relationships of the family Mosasauridae but the Aigialosauridae were found to nest as the sister group to the Mosasauridae, and the Varanidae were determined to be the sister group to the mosasauroids (aigialosaurs and mosasaurs). DeBraga and Carroll (1993) concluded that mosasauroids were descended from ancestral varanids and proposed 39 character shifts that had occurred in aigialosaurs following the speciation event that separated them from the lineage of modern varanids. Many of these characters were visible on only a single aigialosaur specimen and some of the characters for which state changes are described are not visible in any of the aigialosaur specimens (premaxillary tooth count, premaxillary bar length, ossified tympanum, anteromedial and posteromedial processes of the coronoid, and strength of coronoid/prearticular suture). This lack of information and variation among character states within Aigialosauridae was not deemed to be a problem as they were assumed to represent a monophyletic assemblage.

DeBraga and Carroll (1993) have received less attention than another data set produced around the same time (Bell 1993, see below) due in part to the characters chosen by the authors. In many cases the characters are redundant, resulting in higher weighting of certain morphological changes, or are vaguely worded (e.g., character 62: posteromedial process of coronoid tightly/weakly sutured to prearticular; the "strength" or "weakness" of a suture is impossible to interpret without quantifying the mobility of the elements involved). For example, deBraga and Carroll's (1993) characters 1, 2, 6, 9, 17, and 21 are all associated with a lengthening of the snout region. Characters 24 and 25 both deal with the shape of the orbital margin of the frontal (25 is scored as straight versus concave and 26 as straight versus convex). These characters could easily be condensed into a single multi-state character. Both *Globidens* (strongly convex) and *Plotosaurus* (slightly concave) were scored for the shape of the frontal orbital margin when in both of these genera the frontal is excluded from the orbit by the prefrontal and postorbitofrontal (Bell 1997). Numerous problems with character definition and weighting have led to the analysis of deBraga and Carroll (1993) being passed over in favour of Bell's (1993) study of mosasauroid interrelationships.

Bell (1993, 1997)

Bell (1993) produced the most complete systematic analysis of mosasauroids to date (151 characters for 37 taxa) as a part of his PhD dissertation (this was pared down to 142 characters for 37 taxa by the time it was published [Bell 1997] although the modifications did not change the preferred tree topology). Once again the focus of the analysis was not on aigialosaurs but instead on mosasaurs, but the analysis represented the first test of the monophyly of the Aigialosauridae (although it was not the first analysis to test this in press –the study was not published for four years [Bell 1997; Fig.1-2a] - it was chronologically the first to test the hypothesis). Bell (1993, 1997) did not include *Carsosaurus marchesetti* or any dolichosaurs, but did include "the Dallas aigialosaur" (recently described as *Dallasaurus turneri* [Bell and Polcyn in press]). The results of the analysis showed aigialosaurs to be a paraphyletic group with *Opetiosaurus* being the sister taxon to all other mosasauroids and *Aigialosaurus* grouping with the basal mosasaur *Halisaurus*. These results were poorly supported by bootstrapping tests, but this may have been a result of large amounts of data missing from the aigialosaurian taxa. Bell (1993, 1997) represented the first rigorous test of the monophyly of the family Aigialosauridae since the erection of that taxon. It should also be noted that Bell (1993) did not find any support for a varanid/mosasauroid sister-group relationship, contradicting the finding of Carroll and deBraga (1992) and deBraga and Carroll (1993).

Bell (1993, 1997) included all mosasauroids with the exception of *O. bucchichi* in the family Mosasauridae on the basis of seven unequivocal characters. Two of these characters deal with the premaxilla and snout and a third characterises the width of the internarial process of the frontal. These areas are poorly preserved in *A. dalmaticus* and are absent from the Trieste specimen (A. Dutchak pers. obs.). The split deltopectoral crest of the humerus with two insertion areas is listed as a character that unequivocally supports the family Mosasauridae (Bell 1993) despite the fact that *Dallasaurus* is listed as showing the primitive characterisation of a single crest. Of the three remaining characters listed as giving unequivocal support to Bell's (1993) diagnosis of Mosasauridae, the midline dorsal keel of the frontal appears similar in *Opetiosaurus* and *Aigialosaurus*, although it is coded differently, and *Opetiosaurus* cannot be coded for either the presence or absence of zygosphenes and zygantra or the shape of the dorsal ridge of the vertebral synapophysis. However, despite several questionable character codings and a heavy bias in the matrix towards quadrate characters (20 of the 142 published in Bell [1997]), Bell (1993, 1997) was a good starting point for further investigations into mosasauroid interrelationships by later researchers.

Caldwell et al. (1995)

Bell's (1993) hypothesis of a paraphyletic Aigialosauridae was countered when *Carsosaurus marchesetti* was redescribed by Caldwell et al. (1995). While the focus of the paper was on limb mechanics and growth, aigialosaur systematics were also discussed, and the analysis (66 characters and ten taxa; Fig.1-2b) represented the first published phylogenetic test of aigialosaur monophyly (two years prior to the publication of Bell's thesis dissertation [Bell 1997]). The results of this test were less than spectacular, with *Aigialosaurus*, *Opetiosaurus*, *Carsosaurus* and the Trieste aigialosaur nesting in a polytomy with the Mosasauridae (defined in this case as mosasauroids with paddle-like appendages). Caldwell et al. (1995) pointed out that the basal polytomy with mosasaurs was caused by a single character (relatively short ribs in the posterior portion of the rib cage) whereas the aigialosaurs were united (and differentiated from the mosasaurs) by eight characters including absence of contact between the postorbital and postfrontal, presence of a premaxillary foramen, and number of presacral vertebrae. This state of affairs indicated to Caldwell et al. (1995) that aigialosaurs probably represented a monophyletic assemblage. It should also be noted that, like Bell (1993), Caldwell et al. (1995) found no support for the varanid/mosasauroid sister group relationship recovered by Carroll and deBraga (1992) and deBraga and Carroll (1993).

Caldwell (1996)

With several different mosasauroid phylogenies available, Caldwell (1996) reviewed the hypotheses and published a data set (91 characters and 15 taxa) constructed by taking Bell's (1993) matrix, removing a number of taxa and then deleting any characters that were phylogenetically uninformative for the remaining taxa. Caldwell (1996) did make some small adjustments to the character codings for *O. bucchichi* (which he considered congeneric with *A. dalmaticus*). In addition to these changes, Caldwell (1996) referred the Trieste aigialosaur (Carroll and deBraga 1992) to *C. marchesetti* and used the new specimen to fill in some gaps in the data set. The phylogeny recovered by Caldwell (1996) contradicted his earlier findings (Caldwell et al. 1995) by supporting a paraphyletic Aigialosauridae; hardly a surprise considering the characters were taken from Bell (1993).

Caldwell (1999a)

Caldwell (1999a) used a matrix that had been further pared-down from Caldwell (1996) to examine coniasaur-mosasauroid relationships. Some of the 73 characters were reworded and the analysis included only 11 taxa (three of which were aigialosaurs) and once again a paraphyletic Aigialosauridae was recovered. As the matrix was still based on Bell's (1993) characters and codings, and no additional aigialosaur data were added, this result was to be expected.

Caldwell (2000)

Caldwell (2000) published a further modification of the Bell (1993) matrix that recovered a monophyletic Aigialosauridae. This tree topology was a result of further changes to the matrix used in Caldwell's earlier publications (Caldwell 1996, 1999a). Eight characters from Caldwell (1999a) were removed (these characters dealt with the fronto-parietal suture, the posterodorsal process of the maxilla, the shape of the scapula-coracoid suture and the composition of the appendicular epiphyses among other features) and a single character was added (the number of cervical vertebrae). The resulting matrix had 66 characters and twelve terminal taxa (with *Dolichosaurus longicollis* added to the taxa from Caldwell [1999a]). Only two characters supported a monophyletic Aigialosauridae to the exclusion of all other taxa: the lack of a constricted internarial process of the frontal, and narrow pterygoid processes on the basisphenoid. These characters proved sufficient to maintain a monophyletic Aigialosauridae even when a strict consensus of the 27 most parsimonious cladograms was constructed. It should be noted that the cranial morphology of *C. marchesetti* is unknown so the strict consensus was effectively supporting the congeneric grouping of *O. bucchichi* and *A. dalmaticus* suggested by Caldwell et al. (1995).

Bell and Polcyn (in press) and Polcyn and Bell (in press)

The most recent analyses of the mosasauroid ingroup are found in this volume (Bell and Polcyn in press, Polcyn and Bell in press). The systematic analysis in each publication is the same, with Bell (1997) being the source of all but two of the characters. This most recent analysis is the first to insert *Haasiasaurus gittlemani*, which was suggested to have aigialosaurian affinities (Polcyn et al. 1999). Not surprisingly, the tree topology recovered by Bell and Polcyn (in press) is similar to that found in Bell (1997), although halisaurines were moved from the basal position to a sister group relationship (along with the Trieste aigialosaur) with russellosaurines. The major difference in the recent study is that the basal polytomy has been resolved. *Opetiosaurus* and *Aigialosaurus* are found to be sequential sister taxa to the rest of the mosasauroids whereas *Haasiasaurus* is found to be the sister taxon to the clade of (halisaurines (russellosaurines)), the Trieste aigialosaur is the sister taxon to halisaurines and *Dallasaurus* (still referred to as "the Dallas aigialosaur" in the data matrix) is the sister taxon to mosasaurines.

Because the purpose of their studies was to analyze the relationships of mosasaur taxa in detail, the authors (Bell and Polcyn in press, Polcyn and Bell in press) may be excused for not reducing the number of taxa used in the matrix. However, if the goal of the study is to examine relationships among taxa, then only diagnosable taxa should be included. One cannot make an informative statement about the relationship of any taxon to "Taxon novum YMP" (Polcyn and Bell in press) if this specimen lacks diagnosable characters. In addition to the presence of several superfluous taxa, the authors do not explain why the character scoring changes for aigialosaurian taxa suggested by Caldwell (1996) have not been added or addressed in the text.

Bell and Polcyn (in press) argue that paddle-like limbs may have evolved twice or more in mosasauroids. This implies that paddles cannot be used as a synapomorphic character uniting mosasaurs. Instead, the synapomorphies uniting all aigialosaurs and mosasaurs would be features of the skull as found in *Aigialosaurus dalmaticus* and *Opetiosaurus bucchichi*. These features, which are clearly plesiomorphic for the entire ingroup of Bell and Polcyn (in press), might include quadrate morphology, dental morphology, and the morphology of the intramandibular joint. Following this reasoning, it is not aigialosaurs that are subsumed within the Mosasauridae, but rather that all mosasauroids are subsumed within the Aigialosauridae, leaving the Mosasauridae as a polyphyletic taxon. Mosasaurs are then nothing more than aigialosaurs that evolved paddle-like limbs at least three times in their history. Bell and Polcyn's (in press) phylogeny supports the monophyly of traditional mosasauroid subfamilies, e.g., Halisaurinae, Russellosaurinae, and Mosasaurinae (although the families have been rearranged), but finds no support for a paddle-bearing common ancestor, distinct from an aigialosaur, that was by diagnosis of possession of paddles plus 'aigialosaur' cranial characters, a mosasaur. This is an important perspective that influences the interpretation of phylogenetic results but is not discussed by Bell and Polcyn (in press) or Polcyn and Bell (in press).

Bell and Polcyn's (in press) phylogeny provides two nomenclatural possibilities for re-naming the clearly polyphyletic Mosasauridae. The difference depends on the naming convention applied. For Node-Based taxonomy: Aigialosauridae are monophyletic inclusive of all descendent taxa, and the name Mosasauridae should be discarded in favour of Aigialosauridae with descendent clades bearing new names at the respective nodes. For Stem-Based taxonomy: a new name, Aigialosauroidea, inclusive of the most recent common ancestor of

Opetiosaurus bucchichi (the most basal mosasauroid in the phylogeny) and all of its descendants, and the Mosasauridae inclusive of the most recent common ancestor of (*Haasiasaurus* + ((the "Trieste aigialosaur" + Halisaurus) + Russellosaurinae)) and (*Dallasaurus* + Mosasaurinae).

Global Analyses Including Aigialosaurs

While the series of mosasauroid ingroup analyses failed to yield a definite answer as to the monophyly or paraphyly of the Aigialosauridae, several larger-scale squamate analyses were undertaken to investigate the relationships of various taxa within Squamata (Lee 1997; Caldwell 1999b; Lee and Caldwell 2000; Lee and Scanlon 2002; Pierce and Caldwell 2004). In no case were aigialosaurs the focus of these studies, but the results are nonetheless informative.

Lee (1997)

Lee (1997) used previous studies of squamate systematics (Pregill et al. 1986; Estes et al. 1988; Rieppel 1988; deBraga and Carroll 1993) to construct a data matrix of 144 osteological characters for 15 terminal taxa. The study focused on the relationships within Platynota and, unlike previous studies, included numerous fossil taxa (10 of the 15 taxa). The results of the systematic analysis indicated strong support (40 characters and a bootstrap score of 100) for a pythonomorph clade of mosasauroids and snakes. Lee (1997) determined that varanids were the sister group to pythonomorphs. While this placement appears to contradict Carroll and deBraga (1992) and deBraga and Carroll's (1993) suggestion that mosasauroids were the sister taxon to varanids, snakes were not included in either of the earlier studies so the pythonomorph clade could not be tested.

Lee (1998)

Lee (1998; Fig.1-3a) built upon his previous study (Lee 1997) and produced a much larger data set (230 osteological characters for 22 taxa) including all squamate groups. Once again, when mosasauroids were included in the matrix they formed a well-supported pythonomorph clade with snakes. The mosasauroid-snake relationship is supported by 43 characters (about 30 of which deal with the braincase, tooth replacement and the mandible and intramandibular hinge), most of which are diagnosable only on mosasaurian taxa.

Caldwell (1999b)

Caldwell (1999b; Fig.1-3b) also determined that the varanoid relationships of mosasauroids proposed by Carroll and deBraga (1992) were not supported (based on 95 osteological characters and 21 terminal taxa), and that mosasauroids together with coniasaurs formed the sister group to snakes (Caldwell 1999b, Fig. 6). Caldwell's (1999b) study was also based upon the previous work of Estes et al. (1988) with the differences being the addition of fossil taxa to the matrix and the removal of soft-tissue characters. The ((Mosauroidea, *Coniasaurus*) Serpentes) clade was supported by five unequivocal and four equivocal characters. The majority of these characters deal with the intramandibular hinge, although the presence of zygosphenes and zygantra also supports the clade. The clade of mosasauroids, coniasaurs and snakes was found to be the sister group to Scleroglossa (all other squamates except iguanians).

Lee and Caldwell (2000)

Lee and Caldwell (2000) again recovered a well-resolved Pythonomorpha, this time using a modified version of Lee's (1998) data matrix. Lee and Caldwell (2000) used 258 characters coded for 32 terminal taxa. This matrix was further modified by Lee and Scanlon (2002) who reduced the number of characters (248) and added *Mesoleptos zendrinii*, the focal point of the paper. A third study (Pierce and Caldwell 2004) reduced Lee and Caldwell's data set to 15 anguimorph taxa and coded them for 159 characters (the reasons for the reduction in characters are not explicitly stated but it can be assumed that the change is due at least in part to the reduction of terminal taxa that made many characters autapomorphic and uninformative). Pierce and Caldwell (2004) were focused on the relationships of the dolichosaur *Pontosaurus lesinensis* within anguimorphs and thus paid little attention to the placement of the mosasauroid clade other than to note that it fell out as the sister group to the dolichosaur-snake assemblage (thereby retrieving a monophyletic Pythonomorpha).

Rieppel and Zaher (2000)

While the findings of Caldwell (1999b) and Lee (1997) and the studies that stemmed from that data set (Lee 1998; Lee and Caldwell 2000; Lee and Scanlon 2002; Pierce and Caldwell 2004) appear to indicate a solid relationship between mosasauroids and snakes, not everyone was convinced. The findings of Lee (1998) (and consequently all the studies that utilized variations of this matrix) were challenged by Rieppel and Zaher (2000), who suggested that the dentition, braincase and intramandibular joint characters (about 30 of the 43 characters suggested by Lee [1998]) that link snakes and mosasauroids together as pythonomorphs may be the result of convergence. By modifying the character set and ingroup taxa from Lee (1998), Rieppel and Zaher (2000) retrieved results that placed mosasauroids as the sister group to an amphisbaenian/dibamid/snake clade within Anguimorpha; this contradicted the findings of Lee (1998) who found that, when all squamates are tested together, dibamids and amphisbaenians group well outside of Anguimorpha and instead form a monophyletic sister group to a gekkonid/pygopodid clade. By further manipulating the ingroup taxa and ordering of characters, Rieppel and Zaher (2000) were able to retrieve a tree topology that grouped mosasauroids as a sister taxon to varanids (supporting the findings of Carroll and deBraga [1992] and deBraga and Carroll [1993]). This hypothesis requires acceptance that amphisbaenians and dibamids are nested within Angiumorpha, a relationship that requires further investigation. The numerous modifications to character scoring, weighting, and ordering by Rieppel and Zaher (2000) serve as an excellent reminder that selective manipulation of ingroup taxa and characters can allow a researcher to obtain almost any tree topology.

CONCLUSIONS

The monophyly of the aigialosaurs is again being questioned (Bell and Polcyn in press, Polcyn and Bell in press), though what is clear now is that this is a matter of taxonomic definition. Clearly, redescriptions of the key taxa (*Aigialosaurus dalmaticus*, *Opetiosaurus bucchichi* and "the Trieste aigialosaur") are essential to further investigations of the most recent hypotheses. Bell's (1993) data matrix has proven to be the most popular tool for hypothesizing mosasauroid phylogenies and the many modifications to the characters and taxa included in the matrix have resulted in a very robust data set. While the most streamlined versions of Bell's (1993) matrix (Caldwell 1999a, 2000) may not be optimal for testing relationships within Mosasauridae, it is essential that the modifications to character scoring among the basal taxa be utilized or discussed by later researchers so as to continue improving the understanding of mosasauroid systematics. The next step in this process is to insert the information gained from redescriptions of *Opetiosaurus bucchichi* and *Aigialosaurus dalmaticus* and the description of the "Trieste" aigialosaur alongside the data from *Dallasaurus* and *Haasiasaurus* to get the most inclusive hypothesis of mosasauroid interrelationships to date.

The question of where mosasauroids fit within Squamata remains a hotly debated topic, with all of the recent analyses tracing their roots back to Estes et al. (1988). The close relationship of mosasauroids with snakes remains uncertain, but the sister group relationship between varanoids and mosasauroids has been poorly supported in most recent studies. Lee's (1998) matrix will continue to provide a source of informative characters and is a good starting point for future studies. The problems inherent in squamate systematics stem in large part from a lack of fossil data for numerous groups (not the least of which are amphisbaenians and dibamids). Until this problem is rectified it is unlikely that squamate relationships will be distilled to a single robust hypothesis.

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FIGURE 1-1 A. The original arrangement of aigialosaurs and dolichosaurs according to Kramberger (1892), B. the modified taxonomic scheme proposed by Nopcsa (1903) separating the long necked dolichosaurs from the larger aigialosaurs, C. the systematic relations of anguimorph lizards, modified from Camp (1923).

A

Suborder Dolichosauria

Aigialosauridae	**Dolichosauridae**
Acteosaurus	*Dolichosaurus*
Adriosaurus	
Pontosaurus	
Aigialosaurus	

B

Order Squamata

Suborder Lepidosauria

Aigialosauridae	**Dolichosauridae**
Aigialosaurus	*Dolichosaurus*
Carsosaurus	*Acteosaurus*
Opetiosaurus	*Pontosaurus*
?Mesoleptos	*Adriosaurus*

C

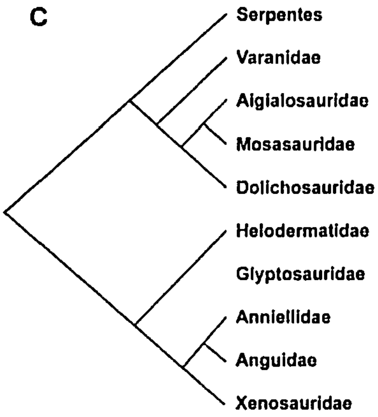


FIGURE 1-2. A. The interrelationships of the mosasauroids, modified from Bell (1997) showing a paraphyletic aigialosauridae B. 50% majority rule consensus tree from Caldwell et al. (1995) showing a monophyletic Aigialosauridae.

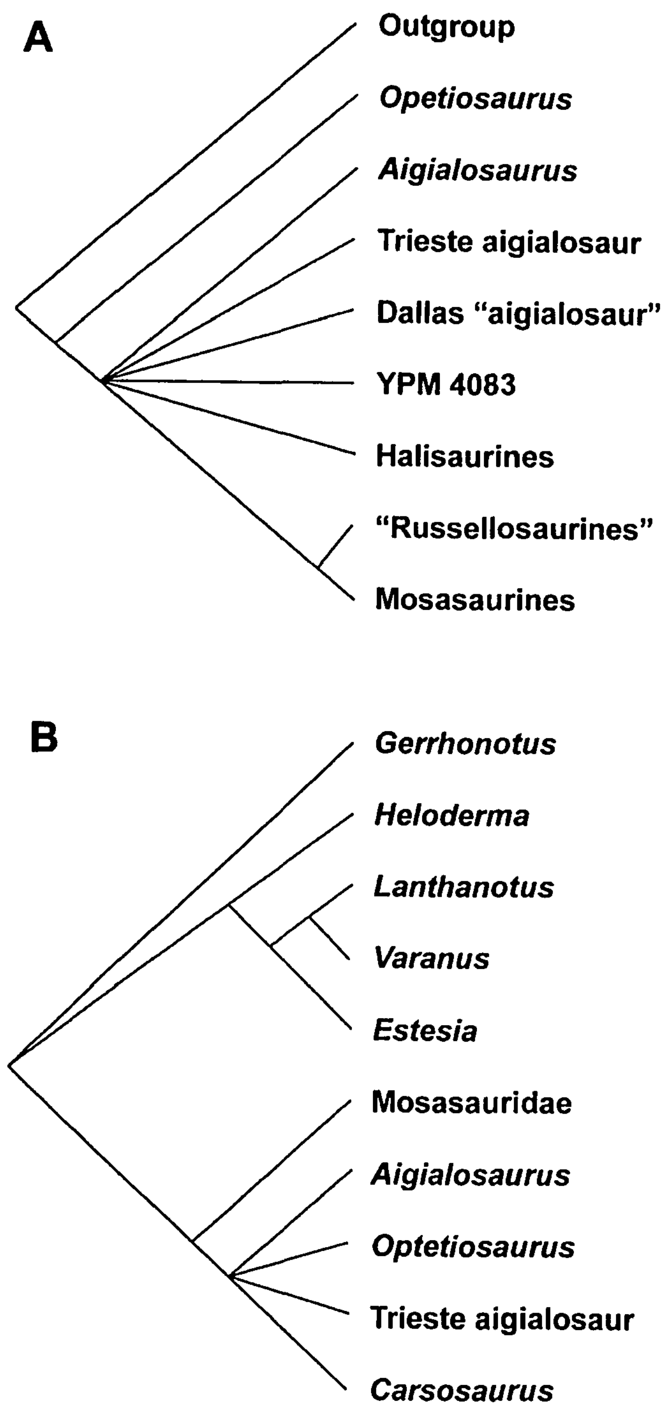
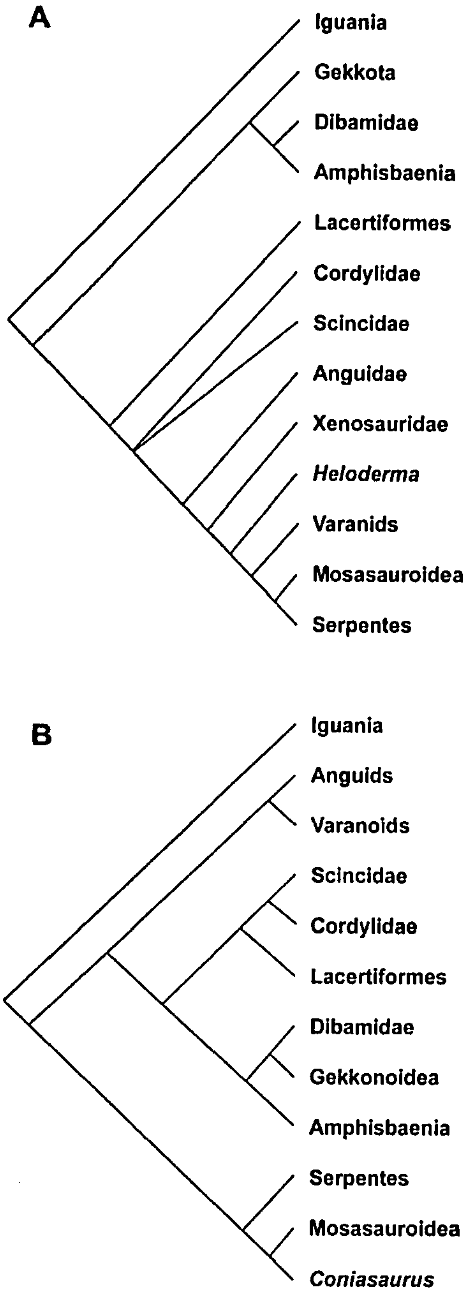

A
Outgroup
Opetiosaurus
Aigialosaurus
Trieste aigialosaur
Dallas “aigialosaur”
YPM 4083
Halisaurines
“Russellosaurines”
Mosasaurines
B
Gerrhonotus
Heloderma
Lanthanotus
Varanus
Estesia
Mosasauridae
Aigialosaurus
Optetiosaurus
Trieste aigialosaur
Carsosaurus

Figure 1-3. A. The systematic relationships of squamates, modified from Lee (1998) showing mosasauroids as the sister group to Serpentes, B. squamate relationships modified from a majority rule consensus tree (Caldwell 1999b) showing mosasauroids and coniasaurs as the sister group to Serpentes.


A
Iguania
Gekkota
Dibamidae
Amphisbaenia
Lacertiformes
Cordylidae
Scincidae
Anguidae
Xenosauridae
Heloderma
Varanids
Mosasauroidea
Serpentes
B
Iguania
Anguids
Varanoids
Scincidae
Cordylidae
Lacertiformes
Dibamidae
Gekkonoidea
Amphisbaenia
Serpentes
Mosasauroidea
Coniasaurus

CHAPTER TWO

A REDESCRIPTION OF *AIGIALOSAURUS DALMATICUS* (SQUAMATA: AIGIALOSAURIDAE) WITH COMMENTS ON EVOLUTIONARY PATTERNS WITHIN MOSASAUROIDEA

Submitted as: Dutchak, A.R., and Caldwell, M.W. A redescription of *Aigialosaurus dalmaticus* (Squamata: Aigialosauridae) with comments on evolutionary patterns within Mosasaroidea. Canadian Journal of Earth Sciences.

INTRODUCTION

Kramberger (1892) diagnosed the taxon Aigialosauridae to include a single genus and species of fossil lizard, *Aigialosaurus dalmaticus*, followed by Nopcsa (1908, 1923) who added a number of taxa and specimens to bring the composition of the group to its current status (Dutchak in press). Recent phylogenetic analyses of the Aigialosauridae (e.g., Carroll and deBraga 1992, Caldwell et al. 1995, Bell 1997, Bell and Polcyn in press) and the closely related Mosasauridae have for the most part concluded that the former are a paraphyletic assemblage. Additionally, Bell and Polcyn's (in press) phylogeny suggests that the Mosasauridae are not monophyletic as they are conventionally diagnosed to include only halisaurines, mosasaurines, tylosaurines and plioplatecarpines. Recognizing all these phylogenetic uncertainties and suggestions of aigialosaurid paraphyly, we will continue to use the informal term "aigialosaur" throughout this study until new informal terms are derived from an as-yet non-existent formal nomenclature.

Current understanding of aigialosaurs is that they are extinct semi-aquatic squamates whose remains are found along the shores of the Mediterranean in rocks dating from the lower part of the Upper Cretaceous (e.g., Kornhuber 1901; Kramberger 1892), and from similar aged rocks in the southern United States (e.g., Bell 1997, Bell and Polcyn in press). Only four relatively complete aigialosaur specimens are known worldwide, but these specimens are, for the most part, well preserved. *Aigialosaurus dalmaticus* (Kramberger 1892) and *Opetiosaurus bucchichi* (Kornhuber 1901) are from the island of Hvar, Croatia; while *Carsosaurus marchesetti* (Kornhuber 1893), and a soon-to-be-described (A. Palci pers. comm.

2005) specimen currently known as "the Trieste aigialosaur" (Carroll and deBraga 1992), were found in Komen, Slovenia. In addition to these specimens a number of partial specimens have been assigned to the "Aigialosauridae" including *Haasiosaurus (=Haasia) gittelmani* (Polcyn et al. 1999), and *Dallasaurus turneri* (Bell and Polcyn in press).

Despite a number of synthetic works on the subject of aigialosaurs, mosasaurs and fossil lizards (Calligaris 1988, Carroll and deBraga 1992, Bell 1997, Caldwell 2000, Lee and Scanlon 2002), aigialosaurs remain poorly described. The original descriptions of the Hvar and Komen specimens are now well over 100 years old. *Carsosaurus marchesetti* has recently been re-described (Caldwell et al. 1995), but the Hvar specimens and the "Trieste" aigialosaur have not been reviewed in detail. Numerous systematic analyses have been performed using various aigialosaurs (see Dutchak [in press] for an overview) but the data matrices have relied on generalized descriptions or previous studies that include incorrectly scored morphological characters. Thorough descriptions will allow for more detailed systematic analyses and a better understanding of aigialosaur, mosasauroid, and squamate relationships.

Aigialosaurus dalmaticus was the first aigialosaur described and was placed in the (then) monogeneric family Aigialosauridae Kramberger, 1892. The specimen was collected from the Cretaceous sediments of Hvar, but no stratigraphic details were mentioned in the original description. The island of Hvar has a narrow band of platy limestones across its northern peninsula, running from the town of Starigrad in the west to the village of Vrboska in the east (Fig. 2-1). These platy limestones are known to be fish bearing (Bassani 1882), and are the only sediments on the island similar to those in which *A. dalmaticus* is preserved. These limestones have been dated as Upper Cenomanian by Gušić and Jelaska (1993) using relative dating of Foraminiferans, rudist corals and *Chondrodonta* 'oysters'. It is not known if *Aigialosaurus dalmaticus* and *Opetiosaurus bucchichi* (the latter of which was also found on Hvar and described with no stratigraphic information [Kornhuber 1901]) were found at the same locality, though there is no doubt that they were excavated from the same sediments. Prospecting on Hvar, conducted by the author in the summer of 2004, revealed that multiple quarries have been opened and back-filled over the centuries during mining operations conducted for platy limestone as a roofing material.

Several authors have suggested *Opetiosaurus* to be a junior synonym of *Aigialosaurus* (Carroll and deBraga 1992; Caldwell et al. 1995; Caldwell 2000), although Polcyn et al. (1999) support a continued generic differentiation of the two species (following Bell [1997]). The phylogeny of Bell (1997) recovers *O. bucchichi* as the sister taxon to all other mosasauroids, but this topology may be related to the questionable coding of several characters and will be explored further in this study. Once both *A. dalmaticus* and *O. bucchichi* have been re-described in detail, the question of synonymy will be more readily answered. In this study, a detailed and focused redescription of the type specimen of *A. dalmaticus* is presented in addition to a review and discussion of the anatomical evidence claimed to support the phylogenetic position of *A. dalmaticus* as hypothesized by Carroll and deBraga (1992), Bell (1997), and Bell and Polcyn (in press).

MATERIALS AND METHODS

The holotype of *Aigialosaurus dalmaticus* was observed under a light microscope, digitally photographed, and drawn using a camera lucida apparatus. A latex cast of the holotype was also used to help verify the identity of structures when the holotype was no longer available to us for prolonged study.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

AIGIALOSAURIDAE Kramberger, 1892

Genus *Aigialosaurus* Kramberger, 1892

Type species- *Aigialosaurus dalmaticus* Kramberger, 1892

Diagnosis- As for species

Aigialosaurus dalmaticus Kramberger, 1892

Revised Diagnosis- Moderately large squamate with seven or eight cervical, 19 or 20 presacral trunk, and at least 15 caudal vertebrae. Tail is laterally compressed with elongate, posteriorly angled neural arches on caudal vertebrae. Limbs are those of a terrestrial varanoid, with well developed digits. Frontal makes up entire dorsal rim of orbit. Parietal process of postorbitofrontal contacts parietal laterally. Quadrate rami of parietal extend posterior to foramen magnum. Extensive suprastapedial process creates rounded quadrate morphology. Moderately deep tympanic bulla.

Range- ?Upper Cenomanian – Lower Turonian (Upper Cretaceous).

Type Locality- A limestone quarry located on a transect between Starigrad and Vrboska on the island of Hvar, Croatia (Fig. 2-1).

Holotype- BSP 1902II501, housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich. The specimen is encased in a large block of platy limestone that preserves the articulated skull and most of the postcrania of a single individual (Fig. 2-2). The skull is largely complete, missing only the tip of the snout. The postcranial elements are articulated, with the right fore and hindlimbs preserved. The tail is truncated after the 15th caudal centrum. The specimen lies on its left side with the skull exposed in right dorsal view. The ventral side of the skull has been prepared but very little detail is visible as the bone and surrounding matrix are almost identical in color and texture.

DESCRIPTION

Skull

Premaxilla: The tip of the snout of *Aigialosaurus dalmaticus* has been broken off and a number of the remaining elements are badly eroded. Carroll and deBraga (1992) suggest that the posterior process of the premaxilla extends to reach the anterior process of the frontal. We note that there is a thin sliver of bone near the edge of the slab (Fig. 2-3) and conclude that this is the only remnant of the premaxilla; due to the high degree of erosion there is no visible premaxillary-frontal suture.

Maxilla: The posterior two thirds of the right maxilla are visible in dorsal view. The anterior third is very poorly preserved, making it difficult to determine whether the bone bends medially to support the nasal capsule, as in varanids (Carroll and deBraga 1992), or remains vertical, as in mosasaurs. The medial edge of the maxilla contacts the frontal. The extent of this contact is unknown due to the fragmentary preservation of the anterior extension of the frontal. The maxilla contacts the prefrontal posteromedially and the lacrimal posterolaterally. Carroll and deBraga (1992, Fig. 6A) illustrate a clear contact between the lacrimal and maxillary, but no such contact could be discerned due to poor preservation. There are at least three teeth preserved in the right maxilla (Fig. 2-3) although the five illustrated by Carroll and deBraga (1992) are not immediately obvious. The teeth are slender and recurved but no surface detail is preserved and there is no evidence of the bulbous tooth root seen in mosasaurs (Russell 1967).

In addition to the portion of the right maxilla preserved in dorsal view, there is a significant portion of the left maxilla preserved on the ventral side of the slab (Fig. 2-4). However, due to the extremely poor preservation of both the bone and the few preserved teeth, nothing other than general outlines can be discerned.

Frontal: The frontals of *Aigialosaurus dalmaticus*, as in mosasaurs, are fused. The frontals are well preserved from the contact with the parietal to the anterior edge of the prefrontals, at which point they have been broken, eroded, or destroyed by preparation. The frontals have a triangular base posteriorly and a lengthy narrow anterior process which starts where the frontals enter the orbital margin. In many mosasauroids the frontals are excluded from the orbital margin (Bell 1997) but in *A. dalmaticus* they make up the entire dorsal rim. There is an extensive contact with the frontal ramus of the postorbitofrontal. The frontal also contacts the entire medial side of the prefrontal. The fronto-parietal sutural contact is relatively straight compared to that of other mosasauroids (but similar to contacts found in extant varanids) with no embayments; this suture makes no contribution to the margin of the parietal foramen.

There is no sign of nasals in *Aigialosaurus dalmaticus*, although this may be due to the poor preservation of the snout.

Prefrontal: Both prefrontals are intact and preserved in dorsal view. The bones are roughly trapezoidal with the longest edge being along the medial contact with the frontal. The relationships of the surrounding elements are best seen on the right prefrontal as taphonomic processes have obscured the left side of the skull. The posterior margin of the prefrontal is incorporated into the anterior border of the orbit. The prefrontal does not contact the postorbitofrontal as it does in many mosasaurs (Bell 1997); instead there is a wide gap between the dorsal extremities of the two bones. Anteriorly, the prefrontal is bordered by the maxilla and ventrally it contacts the lacrimal, although in this case the lacrimal is not preserved well enough to get a good look at the suture.

Lacrimal: The right lacrimal of *Aigialosaurus dalmaticus* is preserved in dorsal view. The preservation is poor in this portion of the skull so that the sutures with surrounding bones are indistinct. The bone appears to be small and oblong, roughly half the length of the prefrontals and wider posteriorly than anteriorly. The lacrimal contributes to the anterior orbital margin and appears to have a lengthy contact with the jugal. The anterior extent of the lacrimal is not visible due to poor preservation.

Jugal: The right jugal is preserved in dorsal view and forms the ventral half of the orbital margin. The bone is long and slender and is broken halfway along the anterior ramus which extends just beyond the margin of the orbit to contact the lateral edge of the lacrimal. The angle where the anterior and postorbitofrontal rami of the jugal meet is just slightly more than 90 degrees. The details of both the jugal-postorbitofrontal and jugal-lacrimal contacts are obscured by poor preservation.

Postorbitofrontal: The right postorbitofrontal is partially preserved in lateral view. Three of the four processes that make up the bone are visible, with the jugal process and suture being obscured by poor preservation. There is a fracture between the narrow, elongate frontal process and the main body of the postorbitofrontal. The parietal process is short and varanid-like (Carroll and deBraga 1992) in that it contacts the parietal laterally, as opposed to vertically in mosasaurs (Carroll and deBraga mention *Clidastes sternbergi* as the exception to this rule; members of the genus *Prognathodon* should also be included as in this genus the parietal has expanded to the width of the frontals, almost eliminating the parietal process of the postorbitofrontal). The squamosal ramus of the postorbitofrontal is lengthy. Although Carroll and deBraga (1992 Fig. 6A) illustrate a clear suture between the postorbitofrontal and squamosal, it appears as though the bones have fractured at the suture and are slightly displaced from each other. The squamosal ramus of the postorbitofrontal does not appear to be as well developed as in most mosasaurs where it extends as far posterior as the quadrate rami of the parietal (Bell 1997).

The left postorbitofrontal is relatively well preserved in dorsal view, but does not present any additional anatomical information.

Parietal: The parietals of *Aigialosaurus dalmaticus* are fused to form a single relatively well-preserved structure with the only fracture being at the base of the right parietal ramus. The anterior portion of the parietal is broad and flat, forming the entire margin of the large parietal foramen, which is in the same relative position as in most varanids. The quadrate rami of the parietal are robust and extend posteriorly past the foramen magnum, as in most mosasaurs (Bell 1997). The nature of the contact between the quadrate ramus of the parietal, the squamosal and the supratemporal is obscured by poor preservation.

Carroll and deBraga (1992) suggest that a portion of the parietal is visible on the underside of the specimen, but the nature of the preservation makes this identification questionable.

Epipterygoid: The right epipterygoid is preserved as a thin element on the dorsal side of the *Aigialosaurus dalmaticus* slab. The bone extends laterally from the midpoint of the right margin of the parietal and appears to extend underneath the postorbitofrontal-squamosal complex towards the lower jaw. The ventral tip of the bone likely became disarticulated from the pterygoid under taphonomic stress.

The fractured left epipterygoid is preserved in two pieces on the ventral side of the slab (Fig. 2-4). The pterygoid process of the left epipterygoid appears to have remained in contact with the left pterygoid but the joint is obscured.

Squamosal: The right, and possibly a fragment of the left, squamosal bone are preserved in dorsal view. The right squamosal is recurved, relatively robust and in contact with the right quadrate, which has rotated roughly 60 degrees clockwise during preservation. The details of the contacts with the postorbitofrontal, supratemporal, quadrate and parietal are not visible due to poor preservation.

Supratemporal: Due to the completeness of the rest of the skull the right supratemporal is assumed to be present, but it is indistinguishable from the surrounding squamosal and parietal.

Quadrate: The right quadrate is preserved in lateral view, but the left quadrate is missing or obscured from view. The quadrate of *Aigialosaurus dalmaticus* has a typical mosasaurian shape due to the presence of a well-developed suprastapedial process and extensive tympanic ala. The rounded shape of the mosasaurian quadrate is not seen in any extant lizards with the exception of the snail-crushing teiid *Dracaena* (Dalrymple 1979). The right quadrate of *A. dalmaticus* appears to have been crushed and broken as the jaw disarticulated under taphonomic stresses, meaning that some details of the bone surface are not visible. The anterior alar rim is intact, running from the peak of the quadrate process to the articular process along the anterolateral edge of the quadrate. The articular process of the quadrate appears intact in the shape of a knob at the base of the bone, slightly displaced posteriorly from its contact with the articular. As stated by Carroll and deBraga (1992), it is not possible to determine whether the articulating surface of the quadrate is a double condyle similar to that of many extant varanoids or flat, similar to that of most mosasaurs. Ideally one would be able to get some indication as to the shape of the articular condyle of the quadrate from the glenoid fossa; unfortunately the glenoid has been covered by the quadrate during preservation. The suprastapedial process is broken and folded over the stapedial notch so that the posterior face of the process is exposed laterally. The shape and extent of the suprastapedial process is a diagnostic character for most mosasaur genera (Bell 1997), but these details are obscured on *A. dalmaticus*.

The quadrate surface details that Carroll and deBraga (1992) discuss are, for the most part, not visible in *Aigialosaurus dalmaticus*. There is no evidence within the tympanic bulla of "a thin disk of bone beneath the level of the tympanum"; a structure referred to by Camp (1942) as an "ossified tympanum," nor are there any roughened surfaces along the suprastapedial process for the attachment of the depressor mandibulae (although there is no doubt this is the origin of the muscle [Russell 1967]).

Basioccipital: The basioccipital is poorly preserved in palatal view. Contrary to Carroll and deBraga (1992) it is not possible to see the suture between the basioccipital and basisphenoid. All that can be said with certainty is that the basioccipital is present and that its proportions cannot be discerned.

Basisphenoid: The basisphenoid is also poorly preserved in palatal view. The basipterygoid processes described by Carroll and deBraga (1992) may be visible (Fig. 2-4) but the preservation is such that only a rough outline of the bone can be identified. Little or no surface detail is visible.

Pterygoid: The quadrate ramus of the left pterygoid is visible in palatal view reaching posterolaterally from beneath the basioccipital-basisphenoid complex. There is no sign of any other parts of the pterygoids, and no evidence of pterygoid teeth.

Prootic-Opisthotic: The paroccipital process composed of the prootic-opisthotic complex may be preserved in ventral view as the posterior of two thin extensions of bone reaching posterolaterally from the basioccipital, as suggested by Carroll and deBraga (1992).

Additional cranial structures: The frontal and parietal are identified in ventral view by Carroll and deBraga (1992, Fig. 6B). Given the state of preservation of the underside of the skull of *Aigialosaurus dalmaticus*, additional preparation is needed to verify the identities of these structures. There are no traces of the epipterygoids, parasphenoid or palatines.

Mandible

Articular, Angular and Surangular: The posterior half of the lower jaw of *Aigialosaurus dalmaticus* is crushed, twisted, and generally poorly preserved. On the dorsal side of the slab the right mandible is preserved in lateral view. The only suture visible is that between the angular and surangular; this suture trends posterodorsally before disappearing in front of the quadrate. The quadrate has rotated clockwise and has been crushed on top of the articular surface so that the alar rim covers the glenoid fossa (Fig. 2-3). The angular extends anteriorly to contact the dentary below the midpoint of the orbit. The details of the angular-dentary joint are not discernible due to poor preservation. The jugal and coronoid have been crushed on top of the anterior extension of the surangular so that the nature of the contact at the intramandibular hinge is obscured from view.

The ventral side of the slab bearing the specimen of *Aigialosaurus dalmaticus* appears to have more complete preservation of the posterior lower jaw (the left mandible in lateral view this time), but the preservation is so poor that very little detail is visible. It appears as though the right prearticular has been folded around the left mandible, with the right articular appearing in medial view just above the left articular (Fig. 2-4). As on the dorsal side of the slab, the right articular-angular joint is not visible. The right splenio-angular articulation appears to be preserved in ventral view although identification of the elements is tentative at best. It is not possible to determine whether the angular fits into a "cup-shaped excavation in the posterior end of the splenial" as in mosasaurs (Russell 1967), but the orientation of the elements appears more similar to the intramandibular hinge of mosasaurs than to the more rigid articulation found in extant varanids. The left postdentary bones are preserved in lateral view and appear to be articulated and almost intact. The left retroarticular process has broken off the end of the mandible, with the fracture appearing to be in the area of the glenoid fossa. While it is possible that this fracture occurred at the articular-surangular suture, it is not possible to definitively determine the relationships of the left postdentary bones relative to each other due to poor preservation.

The jaw articulation of a generalized aigialosaur is reconstructed by Carroll and deBraga (1992). They suggest that the glenoid fossa was composed of both the articular (posteromedially) and the surangular (anterolaterally). This study of *Aigialosaurus dalmaticus* neither supports nor refutes this conclusion. The left surangular cannot be reliably differentiated from the angular and articular on the ventral side of the slab and, as mentioned previously, the area around the glenoid fossa of the right mandible has been covered by the quadrate. Because details of the relationships of the elements are obscured, this specimen of *A. dalmaticus* cannot be used as evidence for the jaw articulation suggested by Carroll and deBraga (1992).

Coronoid: The right coronoid of *Aigialosaurus dalmaticus* is preserved as a crushed mass underneath the jugal. No details of size, shape or contacts with other bones can be determined. There may be a portion of the left coronoid preserved on the ventral side of the slab, as is suggested by Carroll and deBraga (1992), but the identification is tentative at best.

Splenial: The right splenial is visible on the ventral side of the slab. The joint with the angular is vaguely visible, but the details of the contact are obscured by poor preservation. The general shape of the contact suggests a relatively loose joint, more similar to that of mosasaurs than extant varanids. The splenial extends anteriorly to the edge of the slab. It is not possible to determine at what point the splenial is overlapped medially by the dentary although there do appear to be several teeth preserved along the anterior third of the jaw (indicating an overlap somewhere posterior to this point). The right splenial is not visible in dorsal view but it is instead present as a thin splint on the ventral side of the slab. In most mosasauroids, the splenial is visible laterally as a thin bulge at the base of the dentary as it approaches the intramandibular hinge. In this case the right splenial appears to have been folded underneath the dentary by taphonomic processes.

Dentary: Both the right and left dentaries are preserved (the left is visible in lateral view on the ventral side of the slab; the right is visible in lateral view on the dorsal side of the slab and in medial view on the ventral side of the slab). The skull has been crushed in such a way that the nature of the contacts between the dentary, splenial, angular and surangular are obscured. The right dentary is long and slender, with little surface detail preserved. The anterior tip of the dentary has been broken off along with the tip of the snout. There are several teeth preserved in situ on the right dentary but the nature of their attachment to the mandible is unclear. The left dentary is extremely poorly preserved, with even a general outline being difficult to determine. There may be one or two dentary teeth preserved near the tip of the snout, but it is not possible to determine whether or not they are in situ. Once again there is no visible surface detail.

Teeth: There are a number of maxillary teeth preserved on both the ventral and dorsal sides of the slab. Poor preservation negates the possibility of getting a tooth count, and the nature of the tooth root is not visible. There is not enough information to say anything meaningful about tooth replacement. The teeth appear to be recurved but no striations are visible on their surface. There is no evidence to indicate either the presence or absence of pterygoid teeth in *Aigialosaurus dalmaticus.*

Postcranial Skeleton

Vertebrae: Between 45 and 47 vertebrae are preserved in right lateral view on the dorsal side of the specimen, with the vertebrae near the posterior of the specimen having indistinct outlines and the better part of the caudal series missing. The cervical region of *Aigialosaurus dalmaticus* is crushed and twisted, making the fifth through eighth vertebrae difficult to differentiate. The ribs associated with these vertebrae are broken and folded on top of one another, making their length and termination relative to the sternum (which is not visible) impossible to determine. The relatively intact ribs that undoubtedly contacted the sternum can be seen starting around the ninth vertebrae. It remains uncertain whether *A. dalmaticus* had seven cervicals (Carroll and deBraga 1992) or possibly eight, which would place it between *Varanus*, which has nine cervicals, and mosasaurs, which have seven (Russell 1967).

The atlas is not visible on the dorsal side of the specimen. Carroll and deBraga (1992) suggest that the atlas intercentrum is visible on the ventral side of the skull. While this is a possibility, the postcranial elements visible on the ventral side of the *Aigialosaurus dalmaticus* slab are extremely poorly preserved and cannot be reliably identified.

The axis is well preserved on the dorsal side of the slab, clearly identifiable by the anteroposteriorly elongate neural spine. The fourth and fifth cervicals are well preserved, showing the peduncles fused to the centrum and the loosely attached posterior hypapophyses. The neural spines of the posterior cervical vertebrae are anteroposteriorly elongate, with the posterior limit being above the leading edge of the following vertebrae. Short zygapophyses are visible on the right side of most of the cervicals, but the crushing of the vertebral column is such that zygosphenes are not preserved.

The vertebrae of *Aigialosaurus dalmaticus* are procoelous, although the details of the condyle-cotyle articulations are not visible. The trunk vertebrae (presacral but post-cervical) are massive. Much of the surface detail has been destroyed, but the zygapophyses and neural spines are preserved in most cases. The neural spines are thick, appear relatively squared, and extend the entire length of each vertebra. The zygapophyses are wide and robust, but not elongate. There are 19 or 20 presacral trunk vertebrae with the 14 or 15 anteriormost bearing long, robust ribs that may be pachyostotic. The ribs on the final four or five presacral vertebrae are shorter and more gracile than their predecessors. Carroll and deBraga (1992) state that the "lower margin of the centrum angles posteriorly so that the condyle of the centrum is widely exposed ventrally." At no point does this appear to be the case on *A. dalmaticus* as the vertebral column is preserved in dorsolateral view with the condyle-cotyle articulations obscured. The two sacral vertebrae of *A. dalmaticus* are badly crushed. They appear similar in size and shape to the trunk vertebrae, with large, squared neural arches.

Only the first four caudal vertebrae of *Aigialosaurus dalmaticus* are preserved in any detail, although there are portions of as many as fifteen caudals on the slab. The transverse processes of the first four caudals are large and robust, and appear to narrow slightly posteriorly. The neural arches are angled posteriorly starting at the first caudal and appear to be narrower on the sixth and eighth vertebrae, but there is no sign of any haemal arches. The lack of haemal arches may be due to the pygal vertebrae of *A. dalmaticus* being similar to mosasaurs in lacking haemal arches (Russell 1967), or it may simply be due to poor preservation throughout the caudal region. There do appear to be the remnants of several haemal spines on the last four caudal vertebrae (caudals 11-15).

Appendicular Skeleton

Pectoral Girdle: Most of the pectoral girdle of *Aigialosaurus dalmaticus* is not preserved. There appears to be a small portion of the scapulocoracoid preserved just anterior to the proximal tip of the humerus. The bone is badly eroded and no surface detail is visible.

Forelimb: The right forelimb of *Aigialosaurus dalmaticus* is relatively well preserved. The humerus is robust and similar in shape to that of a large varanid. There is no shortening of the shaft or widening of the epiphyses to indicate *A. dalmaticus* was approaching the mosasaurian condition. The epiphyses are separate from the main shaft of the humerus, which is suggested by Carroll and deBraga (1992) to represent skeletal paedomorphosis. While the radius and ulna may not support this conclusion, the long bones of the hind limb also appear to have separate epiphyses. The preservation of the proximal and distal ends of the humerus do not allow for identification of surface detail.

The ulna appears marginally longer than the radius (although the exact length of each bone cannot be determined due to poor preservation of the epiphyses) and has a significantly expanded proximal head. There is a large chunk of the shaft missing in the proximal half of the bone and the distal head appears to contact several carpals. At the joint between the ulna and humerus there is a triangular piece of bone; this is most likely the tip of the ulnar condyle. The radius is more slender than the ulna and is preserved with its distal head slightly dislocated from the carpal region. The radius too is broken, with a large piece of the shaft missing from the middle of the bone.

The only recognizable carpal is the ulnare. It is small, squared and closely associated with the distal tip of the ulna. The ulnare appears to contact the fourth and fifth metacarpals. Carroll and deBraga (1992) suggest the phalangeal count of their generalized aigialosaur manus is 2-3-4-5-3, the count on *Aigialosaurus dalmaticus* is ?-?-4-5-3 because the first two digits are so poorly preserved as to be almost invisible. The fourth digit is the longest by a significant margin and is tipped by a small, slightly recurved claw. This is the only digit of the *A. dalmaticus* manus that has a claw preserved, although it can be assumed that all of the digits were clawed, as in extant varanids.

The overall forelimb structure of *Aigialosaurus dalmaticus* shows no signs of modification for an aquatic lifestyle. The limb proportions appear very similar to those of extant varanids and it is likely that they functioned in much the same manner for terrestrial propulsion (Landsmeer 1983).

Pelvic Girdle: The pelvic girdle of *Aigialosaurus dalmaticus* is incompletely preserved. The most obvious portion is the large iliac crest that extends posteriorly from the acetabulum; the latter element is incompletely preserved and partially obscured by the head of the right femur. The full extent of the iliac crest cannot be determined as it is hidden beneath the zygapophyses of the first two caudal vertebrae but it appears to be significantly longer than those of extant terrestrial lizards such as large monitors or iguanas. The anterior extension of the pelvic girdle is suggested by Carroll and deBraga (1992) to be a portion of the pubis; however, as no suture is visibl,e we suggest that what has been preserved is a well-developed anterior iliac process. Many lizards possess a small pointed tip on the anterior edge of the ilium (Romer 1956) although none of these tips are developed into the large crest present in *A. dalmaticus*. This increased surface area would allow space for attachment of larger iliotibialis, iliofibularis and iliofemoralis muscles, lending greater adduction power to the hindlimb. This condition is suggestive of the bizarre iliac configuration of mosasaurs.

Hind limb: The right femur is a long and robust bone preserved with the anterior surface exposed. The head of the femur is broken off from the shaft and dislocated from the acetabulum. The distal tip of the femur remains in contact with the tibia and fibula, clearly showing the nature of the knee joint. The distal tip appears to have epiphyseal ossifications that have not yet fused to the shaft of the bone. Because the proximal tip of the femur is slightly broken and displaced it cannot be determined if the gap at the proximal epiphysis is due to simple taphonomic stress or if the epiphysis was unfused to begin with.

The tibia and fibula are preserved in situ although both bones are heavily fractured at their midpoints. Both lower hind-limb bones appear to have unfused epiphyses at both their proximal and distal tips. There may be a portion of the left tibia preserved behind the posterior iliac crest, partially hidden beneath the zygaphophyses of the caudal vertebrae. This area is heavily eroded.

The tarsals are heavily eroded, as are the metatarsals and phalanges. It is possible to determine a partial phalangeal formula of 2-3-4-5-?, which coincides with Carroll and deBraga's (1992) generalized aigialosaur formula of 2-3-4-5-3 taken from

Opetiosaurus bucchichi. The fourth digit is significantly longer than the other digits, as in the forelimb. The short, hooked fifth metatarsal mentioned by Carroll and deBraga (1992) is not visible.

DISCUSSION AND CONCLUSIONS

Phylogenetic relationships

Aigialosaurs get their name from the family Aigialosauridae (Kramberger 1892) which was erected to include *Aigialosaurus dalmaticus* (for a complete review of aigialosaur taxonomy see Dutchak in press). However, the modern usage of the term "aigialosaur" usually refers to a semi-aquatic lizard of Upper Cenomanian age that possesses some skull (intramandibular hinge and circular quadrate among others) and caudal vertebral (elongate neural and haemal spines) features seen in mosasaurids, but retains trunk and limb characteristics similar to those of terrestrial anguimorphs. Many "aigialosaurs" are referred to the group on the basis of apparent semi-aquatic morphologies, and not because they possess shared characteristics with *A. dalmaticus* that are suggestive of a close evolutionary relationship. In this sense, the term "aigialosaur" should be considered an ecological grade as opposed to a term recognizing closely related taxa (i.e., monophyletically).

The supposed monophyly of aigialosaurs (Carroll and deBraga 1992, deBraga and Carroll 1993) has been questioned by the results of several systematic analyses (Bell 1997, Bell and Polcyn in press, Polcyn and Bell in press). These analyses included several incorrectly scored characters for basal mosasauroids such as *Aigialosaurus dalmaticus* and *Opetiosaurus bucchichi.* As these taxa lie at the base of the mosasauroid tree and lack many characters visible in mosasaurs, small changes in character scoring can have a demonstrable effect on the resulting trees and their subsequent implied evolutionary scenarios. When the group in question is composed of relatively few specimens (as aigialosaurs are in this case) it is vital that all data be as accurate as possible to prevent skewed results supporting monophyly or even polyphyly of such higher-level taxa.

The strength of the evolutionary scenario of Bell and Polcyn (in press) is weakened by the inclusion of numerous undescribed taxa in their data matrix. "Taxon novum YMP" appears to be the sister taxon to the clade of *Dallasaurus turneri* and Mosasaurinae (Fig. 2-5). Thorough understanding of the basal taxa is required as they are key in the construction of evolutionary hypotheses such as the one discussed above. Once the poorly known basal taxa (*Opetiosaurus bucchichi*, the Trieste aigialosaur, and "Taxon novum YMP") have been detailed in the literature discussions of evolutionary relationships will be much more useful.

Palaeobiogeography and Origins

The phylogeny (Fig. 2-5) of Bell and Polcyn (in press) has very interesting and important evolutionary and palaeobiogeographic implications. For example, the phylogenetic relationships of the terrestrial to semi-aquatic 'aigialosaurs' suggests very strongly that speciation may have been driven by a vicariant and perhaps relictual distribution occurring prior to the evolution of semi-aquatic habits. This scenario is similar to that proposed for the marine and non-marine species of iguana currently extant on the Galapagos Islands (Pianka and Vitt 2003); the evidence for later semi-aquatic evolution in 'aigialosaurs' is based on their distributions from the northern Tethys to the Western Interior Seaway.

More problematic in terms of palaeobiogeographic and origin scenarios are the phylogenetic relationships of these varied "aigialosaur" sister groups to their respective mosasaur subfamilies. The tree supported by Bell and Polcyn (in press) suggests that halisaurine and russellosaurine ("Russellosaurina") mosasaurs originated in the Mediterranean, whereas mosasaurine mosasaurs originated in North America. Again, as noted previously, this question is only problematic as long as the informal term 'mosasaur' is used to refer to Bell and Polcyn's (in press) non-monophyletic Mosasauridae.

Limb Evolution: Terrestrial to Aquatic

Building on the palaeobiogeography and origins issues, we also note that a dispersed origins model, as implied by Bell and Polcyn's (in press) phylogeny, is difficult to accept due to the great dispersal abilities associated with fully aquatic lifestyles. The probability of separate groups (ie: two groups of plesiopodal aigialosaurs) in close proximity successfully converging on the same ecological niche at the same time (as the results presented by Bell and Polcyn [in press] appear to suggest that halisaurine and russellosaurine mosasaurs did) would seem to be low. The hypothesis of Bell and Polcyn (in press) also suggests that semi-aquatic descendants of *Opetiosaurus bucchichi* and *Aigialosaurus dalmaticus* managed to get from the Mediterranean to southern North America without developing fully aquatic morphologies. Should this be the case, one would expect more discoveries of aigialosaur-like lizards similar to that mentioned by Buchy et al. (2004) along the paleo-shores of North Africa and South and Central America.

The tree presented by Bell and Polcyn (in press) indicates that no fewer than three different types of paddle-like limbs evolved within the mosasauroids and that there are two separate origins of this limb (Fig. 5); halisaurs and russellosaurs share a common ancestor but evolved very different paddle anatomies (see Caldwell 1996). This situation is indicated by the presence of the plesiopedal Trieste specimen as the sister taxon to halisaurs, and *Haasiasaurus gittlemani* as the sister taxon to all other russellosaurines. The only way for this relationship to occur within Russellosaurina through a single derivation of hydropedal limbs, according to the tree topology preferred by Bell and Polcyn (in press), is for the Trieste specimen to have re-evolved terrestrial limbs from a mosasaurian paddle.

Aigialosaurus dalmaticus

The placement of *Aigialosaurus dalmaticus* near the base of the mosasauroid tree makes it an extremely important specimen with regard to dispersal theories, patterns of limb development, and phylogenetic relationships. Bell and Polcyn (in press) have demonstrated that new information, such as that gained from the addition of numerous new taxa to an existing systematic data set, can have profound effects on the resulting evolutionary hypotheses. A better understanding of *A. dalmaticus* and other basal mosasauroids (*Opetiosaurus bucchichi*, the Trieste aigialosaur, Taxon novum YMP) will allow modification and refinement of the scenarios implied by Bell and Polcyn (in press), and generate a clearer picture of mosasauroid relationships within Squamata.

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FIGURE 2-1. Map of the island of Hvar, Croatia; inset box shows detail of probable quarry localities on the northern peninsula of the island.

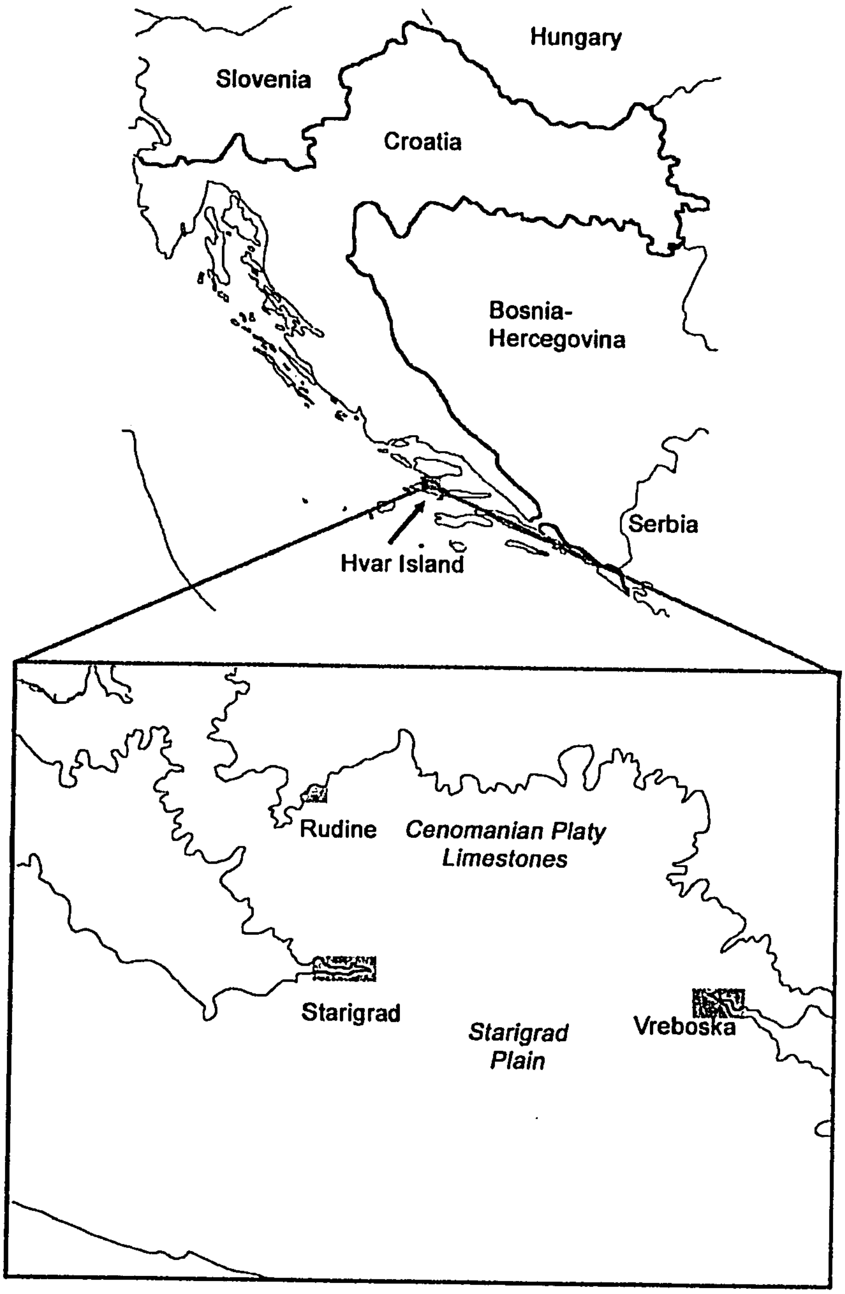

Hungary
Slovenia
Croatia
Bosnia-
Hercegovina
Serbia
Hvar Island
Rudine
Cenomanian Platy
Limestones
Starigrad
Starigrad
Plain
Vreboska

FIGURE 2-2. The holotype of *Aigialosaurus dalmaticus*, BSP 1902II501, housed in the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich.

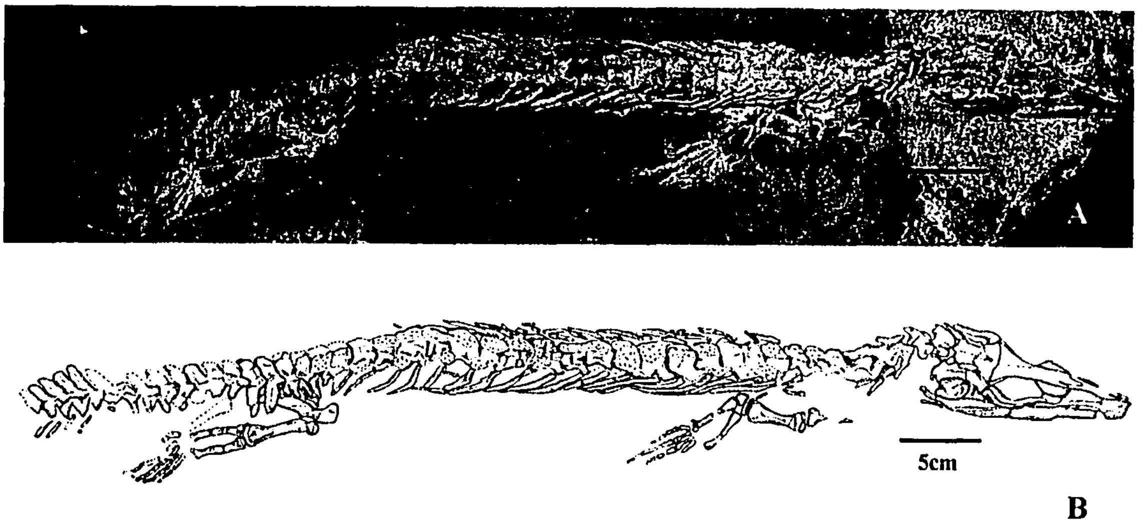
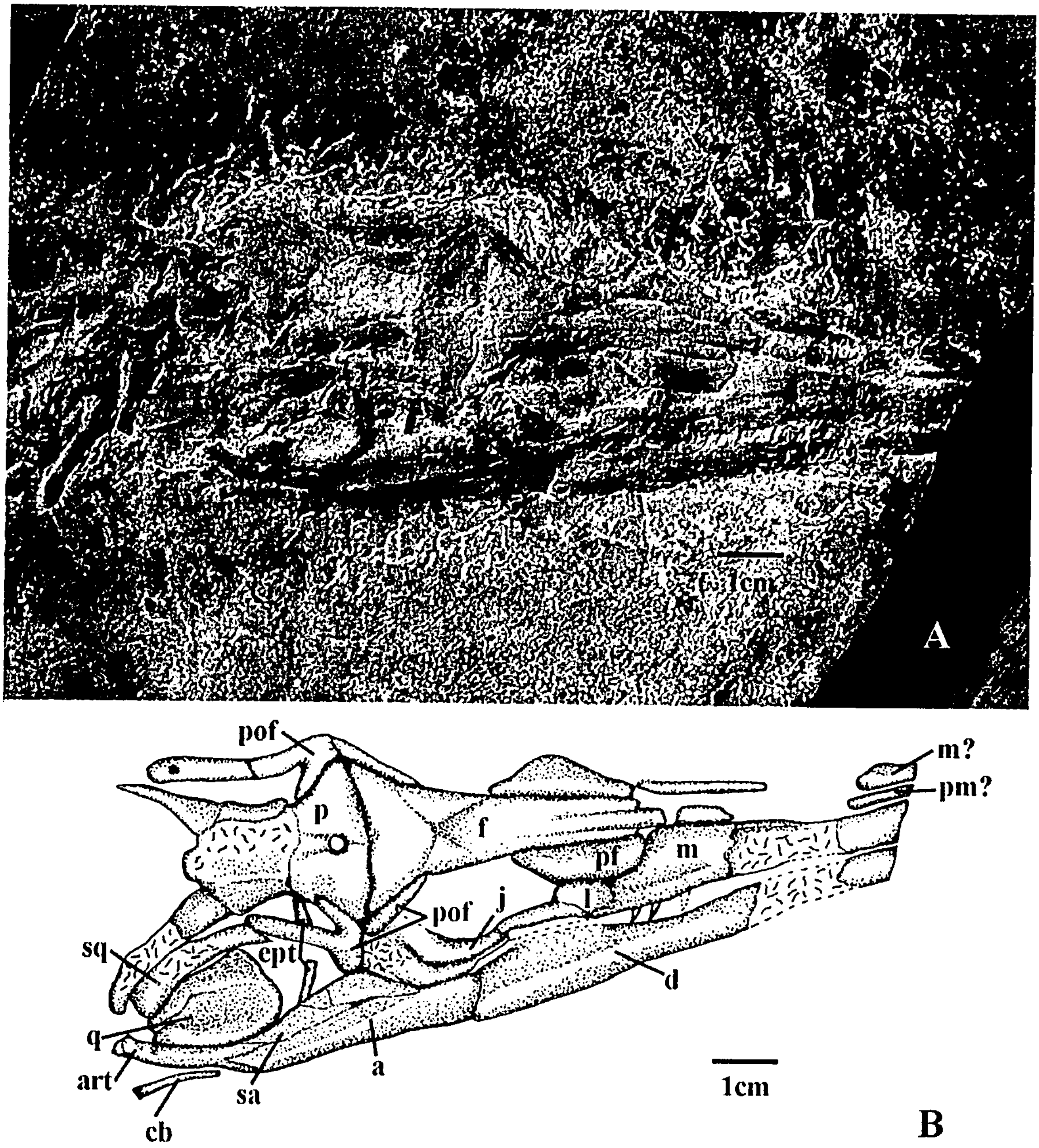

A
5cm
B

FIGURE 2-3. The skull of *Aigialosaurus dalmaticus* in dorsal view. Abbreviations: a, angular; art, articular; cb, ceratobranchial; d, dentary; ept, epipterygoid; f, frontal; j, jugal; l, lacrimal; m, maxilla; p, parietal; pf, prefrontal; pm, premaxilla; pof, postorbitofrontal; q, quadrate; sa, surangular; sq, squamosal.



1cm
A
pof
m?
pm?
p
f
pf
m
l
pof
j
sq
ept
d
q
art
sa
a
cb
1cm
B

FIGURE 2-4. The skull of *Aigialosaurus dalmaticus* in ventral view. Abbreviations: art, articular; bo, basioccipital; bs, basisphenoid; lc, left coronoid; ld, left dentary; lept, left epipterygoid; lpt, left pterygoid; lsa, left surangular; lsp, left splenial; m, maxilla; pof, postorbitofrontal; rd, right dentary; rpa, right prearticular; rsp, right splenial.

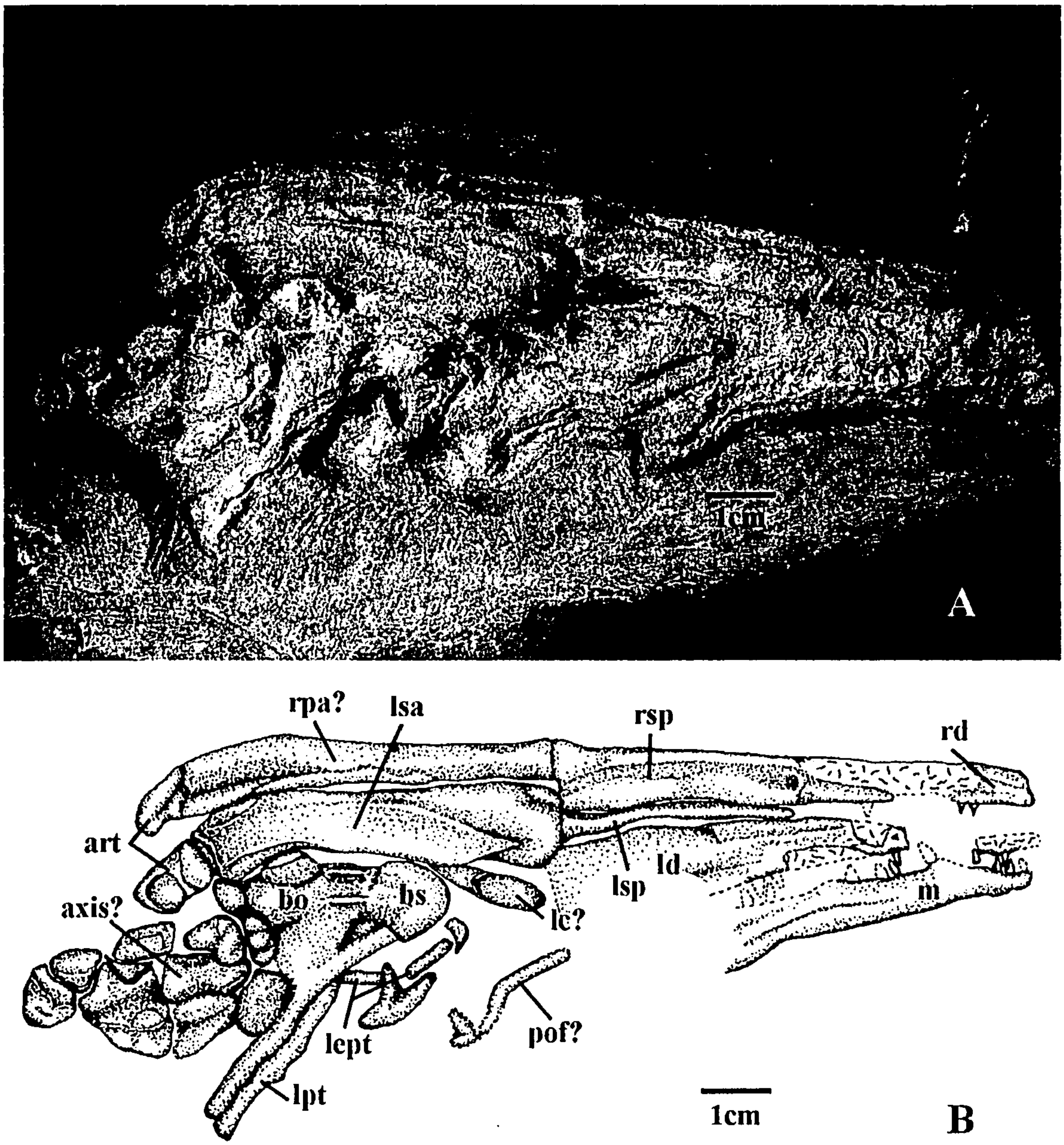
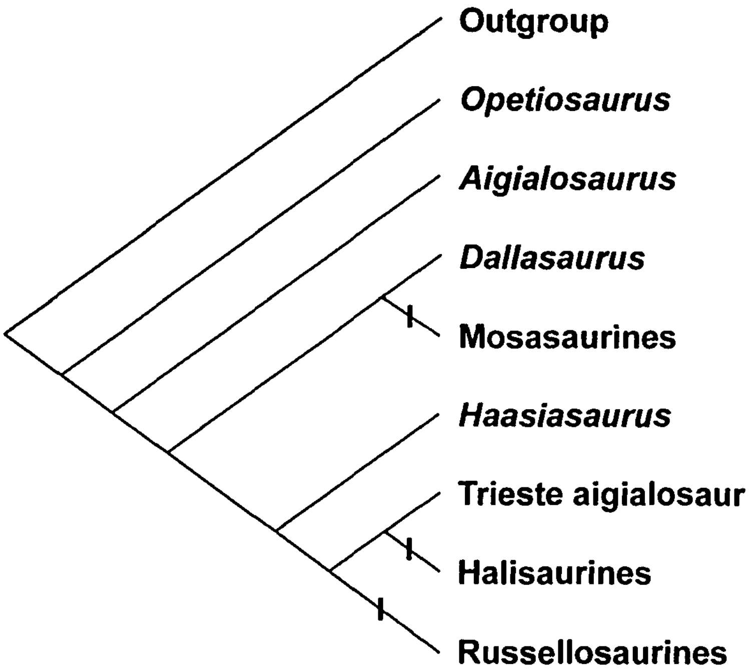

1cm
A
rpa?
lsa
rsp
rd
art
axis?
bo
bs
lc?
lsp
ld
m
lept
pof?
lpt
1cm
B

FIGURE 2-5. Systematic relationships of mosasauroids modified from Bell and Polcyn (in press). Bars on branches indicate putative evolution of paddle-like limbs.


Outgroup
Opetiosaurus
Aigialosaurus
Dallasaurus
Mosasaurines
Haasiasaurus
Trieste aigialosaur
Halisaurines
Russellosaurines

CHAPTER THREE

A REDESCRIPTION OF *AIGIALOSAURUS* (=*OPETIOSAURUS*) *BUCCHICHI* (SQUAMATA: AIGIALOSAURIDAE) WITH COMMENTS ON AIGIALOSAUR TAXONOMY

INTRODUCTION

It has been suggested by several authors (Carroll and deBraga 1992, Caldwell et al. 1995, Caldwell 2000) that *Opetiosaurus bucchichi* and *Aigialosaurus dalmaticus* are congeneric, if not conspecific. This suggestion was countered by Bell (1997), Polcyn et al. (1999), Bell and Polcyn (in press), and Polcyn and Bell (in press). All of these taxonomic suggestions were made without the benefit of a detailed comparison of the two specimens. Given the recent publication of a new scenario for the evolution of the paddle-like limb in mosasaurs (Bell and Polcyn in press, see Dutchak and Caldwell submitted for analysis) it has become apparent that *O. bucchichi* and *A. dalmaticus* are extremely important taxa with regard to mosasaurian systematics. To this end, detailed morphological descriptions of basal mosasauroids are essential to testing this new hypothesis. It is the goal of this study to redescribe *O. bucchichi*, complete a detailed comparison of *A. dalmaticus* and *O. bucchichi*, and show that *Opetiosaurus* is a junior synonym of *Aigialosaurus*.

MATERIALS AND METHODS

The large specimen mounted on the museum wall in Vienna was observed visually and photographed through the glass case with a digital camera. The Austrian Geological Survey slabs were observed under a light microscope. The slab containing cranial material was prepared from the ventral side to expose the palate and casts were made of both the dorsal and ventral sides of the slab for use in photography.

SYSTEMATIC PALEONTOLOGY

SQUAMATA Oppel, 1811

AIGIALOSAURIDAE Kramberger, 1892

Genus *Aigialosaurus* Kramberger, 1892

Synonymy: *Opetiosaurus* Kornhuber, 1901 (Caldwell et al. 1995:526)

Type Species- *Aigialosaurus dalmaticus* Kramberger, 1892

Included Species- *Aigialosaurus dalmaticus* Kramberger, 1892; *Aigialosaurus bucchichi* Kornhuber, 1901

Revised Generic Diagnosis- Moderately large squamate with seven or eight cervical, 19 or 20 presacral trunk, and at least 80 caudal vertebrae. Tail is laterally compressed with elongate, posteriorly angled neural and haemal spines on the caudal vertebrae. Limbs are those of a terrestrial anguimorph, with well developed digits and a phalangeal count of 2-3-4-5-3 on both manus and pes. Frontal makes up entire dorsal rim of orbit. Parietal process of postorbitofrontal contacts parietal laterally. Quadrate rami of parietal extends posterior of foramen magnum. Extensive suprastapedial process creates rounded quadrate morphology. Pterygoid teeth present. Trilobate coronoid.

AIGIALOSAURUS BUCCHICHI Kornhuber, 1901

(Figs. 3-1, 3-2, 3-3)

Opetiosaurus bucchichi Kornhuber, 1901:14, figs. 1-3 (original description)

Aigialosaurus bucchichi (Kornhuber): Caldwell et al. 1995:526 (new combination)

Diagnosis- Lacks premaxillary rostrum. Uniform curvature of quadrate tympanic ala. Dentary teeth with conical, recurved tips rapidly expanding to broad cylindrical bases. Splenial contacts coronoid at intermandibular hinge. Final three or four caudal vertebrae have sharp downward curvature.

Type Locality- A limestone quarry between Starigrad and Vrboska on the island of Hvar, Croatia

Range- Upper Cenomanian of Hvar, Croatia

Holotype- Unnumbered specimen housed at the Naturhistorisches Museum Wien (Vienna) and with four unnumbered counterpart slabs housed at the Austrian Geological Survey. The museum specimen preserves most of the postcranium with the exception of some caudal regions and the better part of both hindlimbs. This specimen also preserves the anterior half of the right mandible and the left jugal as well as a natural mold of the dorsal surface of the skull. The Geological Survey counterparts contain three sections of caudal vertebrae and the posterior half of the skull in dorsal view. The snout and portions of the right and left mandibles have been lost (probably when the slab of platey limestone was originally split). The ventral side of the skull counterpart has been prepared to show details of the palate.

DESCRIPTION

Skull

Premaxilla: The snout of *Aigialosaurus bucchichi* is only preserved as dorsal and palatal impressions. Contrary to Carroll and deBraga (1992), in neither case is the impression detailed enough to determine the nature of the premaxillary-maxillary sutures, nor is there any indication of the degree of posterior extension of the premaxillary towards the frontal. The impression on the Vienna Museum specimen indicates the snout is broader than in most mosasaurs, and *A. bucchichi* does not appear to have had a premaxillary rostrum. Bell (1997) noted that the internarial bar of *A. bucchichi* is "distinctly less than half of the maximum width of the rostrum in dorsal view"; in the absence of a rostrum this statement is rendered meaningless.

The snouts of *A. bucchichi* and *A. dalmaticus* are not comparable as the elements of the former are missing and the snout of the latter is extremely poorly preserved.

Maxilla: The maxilla is preserved for the most part in the form of casts of the general outline of the snout in dorsal and palatal view. The posterior-most extension of the right maxilla is preserved both in dorsal and ventral view on the Geological Survey slab. The maxilla is overlapped posteriorly by the jugal and there appears to be a tight interlocking joint with the lacrimal postero-medially. The snout is broken where the prefrontal-maxillary contact would start, but the impression of the snout indicates that *Aigialosaurus bucchichi* does not differ substantially from *A. dalmaticus* in this feature. The ventral aspect of the maxilla reveals seven teeth (Fig. 3-2), although they do not appear to be in situ as the palate is relatively poorly preserved.

Frontal: The frontal of *Aigialosaurus bucchichi* is well preserved, in dorsal view, on the Geological Survey slab from the posterior contact with the parietal to the anterior tip of the prefrontals where it has been fractured and lost with the rest of the snout (Fig. 3-3). The frontals are fused (unlike those of modern varanids) and elongate. The frontal tapers quickly from the broad, relatively straight contact with the parietal to the dorsal rim of the orbit, from which point it narrows anteriorly at a much shallower angle to the fracture point. There is a lengthy contact postero-laterally with the postorbitofrontal, but the frontal still contributes significantly to the dorsal rim of the orbit (as it does in *A. dalmaticus*). The lateral contacts with the slightly raised prefrontals are relatively straight. The dorsal surface of the bone is well preserved and there is a small pit along the centerline of the bone 6 mm anterior to the fronto-parietal contact.

As with *A. dalmaticus*, the presence or absence of nasals in *A. bucchichi* cannot be determined due to the fracturing of the skull through the snout region.

Prefrontals: Both prefrontals are well preserved in dorsal view on the Geological Survey slab (Fig. 3-3). The left prefrontal appears to be almost completely intact, while the right is slightly broken at its anterior tip. Both prefrontals have slightly damaged dorsal surfaces, likely from the original splitting of the slab or preparation. The prefrontals have the same general shape as those of *Aigialosaurus dalmaticus*; however, as they are better preserved more details are visible. The posterior margins of the bones contribute to the orbital rims and are slightly concave, unlike those of *A. dalmaticus* which appear relatively straight. The posterior tips of both prefrontals narrow to a fine point. The lateral contact between the right prefrontal and lacrimal is poorly defined. The two bones appear to have been slightly offset by taphonomic processes. There is a tiny sliver of palatine visible beneath the posterior tip of the right prefrontal but the nature of the contact cannot be discerned.

Lacrimal: The right lacrimal is preserved in dorsal view on the Geological Survey slab (Fig. 3). The bone is small and triangular with the base of the triangle forming a contact with both the jugal and the maxilla. The lacrimal also contributes slightly to the anterior rim of the orbit, as in both varanids and mosasaurs (Russell 1967). The maxillary-lacrimal suture appears to be a very tight, interlocking joint. The lacrimal process of the palatine, a fragment of which is preserved along the anterior rim of the orbit, extends to contact the lacrimal posteriorly. The anterior orbital portion of the skull of *Aigialosaurus dalmaticus* is poorly preserved, preventing any comparison between the two specimens.

Jugal: The right jugal is preserved in dorsal view on the Geological Survey slab (Fig. 3-3) and the anterior half of the left jugal is preserved in ventral view on the Vienna Museum slab (Fig. 3-1). The right jugal appears to overlie the maxilla at the contact between the two bones, whereas the lacrimal abuts directly against the antero-medial tip of the jugal. The postorbitofrontal ramus of the right jugal joins the anterior ramus at an angle slightly greater than 90 degrees. The contact of the jugal with the postorbitofrontal is poorly preserved thanks in most part to the extremely gracile tip of the postorbitofrontal ramus of the jugal appearing to be broken. The portion of the left jugal preserved in the Vienna Museum slab does not provide any additional details. While the jugal in *Aigialosaurus dalmaticus* is in considerably poorer condition, it has the same general shape and appears to have the same contacts with other elements as the jugals of *A. bucchichi.*

Postorbitofrontal: The right postorbitofrontal is preserved in dorsal view on the Geological Survey slab (Fig. 3-3). The jugal process is splayed out laterally and appears robust and rounded. It is closely associated with the postorbitofrontal process of the jugal, but the two elements are not articulated. The frontal process of the postorbitofrontal extends antero-medially along the dorsal orbital rim. This process in particular appears almost identical in *Aigialosaurus bucchichi* and *A. dalmaticus*. The squamosal process extends posteriorly into the temporal arcade. The squamosal-postorbitofrontal contact is vaguely visible on the right side of the skull in ventral view and in dorsal view on the left side. The contact extends from the base of the jugal process of the postorbitofrontal past the midpoint of the temporal arcade. In many mosasaurs the postorbitofrontal extends posteriorly almost to the contact between the supratemporal and quadrate (Russell 1967), whereas *Varanus* has a comparatively short squamosal process. Unlike the situation in *A. dalmaticus*, the parietal process of the postorbitofrontal is mostly obscured. It appears as though the process has been folded underneath the parietal by taphonomic processes. This prevents any comment on whether the process contacted the parietal laterally (as in *Varanus* and *A. dalmaticus*) or vertically (as in most mosasaurs). The postorbitofrontals of *A. dalmaticus* and *A. bucchichi* are nearly identical in all visible features.

Parietal: The parietal of *Aigialosaurus bucchichi* is almost intact in dorsal view on the Geological Survey slab (Fig. 3-3), with only the tip of the left quadrate ramus missing. The parietal expands anteriorly to the full width of the frontal and then tapers significantly posteriorly. Unlike many mosasaurs (i.e., *Clidastes*, *Halisaurus*, *Ectenosaurus* [Bell 1997]) the parietal table of *A. bucchichi* remains relatively broad and flat as it extends posteriorly. This is similar to the condition in *Varanus* and *A. dalmaticus*, although the descending flanges of the parietal appear to extend further ventrally in both aigialosaurs than in extant varanids. The relatively small parietal foramen is located 3 mm posterior of the parietal-frontal contact. The quadrate rami are robust and show the mosasaurian condition by extending posterior of the foramen magnum (Bell 1997). The contact between the right parietal and supratemporal is obscured as the surface detail of the bones has been stripped away.

Epipterygoid: The right epipterygoid is clearly visible on the ventral side of the Geological Survey slab (Fig. 3-2). The ventral end of the bone is still in contact with the right pterygoid whereas the dorsal end of the bone has been dislocated and lies crushed underneath the temporal arcade. The dorsal end of the right epipterygoid can be seen in dorsal view projecting laterally from underneath the postorbitofrontal-squamosal complex towards the quadrate. Interestingly, the right epipterygoid of *Aigialosaurus dalmaticus* is preserved in an almost identical position.

Squamosal: The anterior half of the left and the entire right squamosal are preserved on the Geological Survey slab. As in varanids and mosasaurs the squamosal forms the lateral and posterior portion of the temporal arcade. The contact with the postorbitofrontal is lengthy, starting anteriorly just behind the jugal process and extending posterior past the midpoint of the temporal bar. The right squamosal remains in contact with the parietal and quadrate, although the latter bone appears to have been slightly dislocated anteriorly.

Supratemporal: There may be a portion of the right supratemporal preserved in ventral view on the Geological Survey slab (Fig. 3-2), but the identification of this structure is questionable. The thin sliver of bone lies medial to the posterior tip of the squamosal, and lateral to the crushed paroccipital process of the exoccipital. In both mosasaurs and varanids the supratemporal has a significant dorsal process that extends dorso-medially along the quadrate ramus of the parietal (Russell 1967). There is no evidence of this structure in *Aigialosaurus bucchichi*, likely due to poor preservation.

Quadrate: The right quadrate of *Aigialosaurus bucchichi* is preserved in lateral (Fig. 3) and medial (Fig. 3-2) views on the Geological Survey slab. The suprastapedial process and tympanic ala are well developed, giving the quadrate a rounded morphology that is found only in mosasauroids and *Dracaena*, an extant teiid. Carroll and deBraga (1992) describe "a thin crest of bone beneath the level of the tympanum" in both *A. dalmaticus* and *A. bucchichi*, a structure referred to by Camp (1942) as the ossified tympanum. The quadrate of *A. bucchichi* is better preserved than that of *A. dalmaticus*, and after close examination of both specimens it is apparent that in neither case is the ossified tympanum preserved.

The quadrate of *A. bucchichi* appears more rounded than that of *A. dalmaticus* but this may be a result of differential preservation of the two specimens, with *A. dalmaticus* experiencing more dorso-ventral crushing compared to *A. bucchichi*, which probably avoided this fate through dislocation of the jaw during preservation. The stapedial notch is well developed and clearly visible in lateral view, but the notch is not visible in medial view. There is a triangular structure covering the stapedial notch medially that may represent part of the cartilaginous extracolumella or, alternately, it could simply be matrix. The medial surface of the quadrate is relatively flat and featureless. The dorsal rim of the tympanic ala shows roughened areas for muscle attachment, but there are no other features of note. The articular condyle of the quadrate of *A. bucchichi* has a roughened surface that makes details of the articulation with the mandible difficult to discern.

Basioccipital: The basioccipital is visible in ventral view on the Geological Survey slab. The entire surface of the bone is roughened and very little detail is visible and there are no obvious basioccipital tubercles. The contact with the basisphenoid is not apparent. The bone appears to have the same general features as that found in *Aigialosaurus dalmaticus*, although the poor preservation of the basicranial region in both animals prevents a detailed comparison.

Basisphenoid: The basisphenoid is also present in ventral view on the Geological Survey slab, and while the contact with the basioccipital is obscured (possibly indicating the animal was an adult as opposed to a juvenile) the parasphenoid process is visible. The groove for the internal carotid arteries is well preserved. The right basipterygoid process is short, as in mosasaurs (Russell 1967), as opposed to the relatively lengthy structures found in *Varanus*. Both prootics appear to have been crushed and partially folded underneath the basisphenoid by taphonomic processes.

Prootic: The right and left prootics appear to be visible in ventral view on the Geological Survey slab (Fig. 3-2). Both bones have been crushed down on top of the basisphenoid, exposing the rounded basipterygoid processes. There may also be portions of the prootics visible in dorsal view, crushed beneath the descending flanges of the parietal. No surface or structural details are visible on either side.

Parasphenoid: The parasphenoid in *Varanus* and most mosasaurs (Russell 1967) is a tiny sliver of bone that extends dorsally from the contact with the anterior extremity of the basisphenoid. The extremely delicate nature of this structure is the probable reason for its absence in *Aigialosaurus bucchichi.*

Pterygoid: Almost the entire right pterygoid and a minute tooth-bearing portion of the left pterygoid are preserved in ventral view on the Geological Survey slab (Fig. 3-2). The body of the pterygoid is long and slender, with the basisphenoid process obscured by matrix. The quadrate process of the pterygoid is long and thin and has been crushed into the exoccipital. The contact with the quadrate is not preserved. The ectopterygoid process of the pterygoid is dorsoventrally flattened and extends laterally from the body of the bone at almost a right angle. The ectopterygoid process is preserved in dorsal view in the posteriormost portion of the right orbit. Unfortunately the pterygoid-ectopterygoid suture is not preserved. The anterior extent of the palatine process of the pterygoid cannot be determined as there is no obvious suture between the two bones; however, it appears that the palatine process is more similar to the elongate structure found in mosasaurs (Russell 1967) than to the shortened process of varanids. Unlike that of varanids, the body of the pterygoid of *Aigialosaurus bucchichi* bears teeth. Eight pterygoid teeth are visible on the right pterygoid and two teeth are visible on the left pterygoid but complete tooth counts cannot be determined for the bones on either side. The pterygoid teeth are smaller than the maxillary teeth but whether or not they are more recurved, as suggested by Russell (1967), cannot be determined due to the poor state of preservation of the maxillary teeth. The anterior portion of the body of the right pterygoid is covered by an unknown element that extends laterally towards the right maxilla. This element may represent a portion of the right ectopterygoid, although a positive identification is not possible.

Ectopterygoid: The Geological Survey slab bears a portion of the right ectopterygoid preserved in dorsal view along the inside of the lateral rim of the right orbit (Fig. 3-3). The ectopterygoid is displaced anteriorly from its contact with the ectopterygoid process of the pterygoid. As in mosasaurs (Russell 1967) the jugal process of the ectopterygoid of *Aigialosaurus bucchichi* is more sharply recurved than in extant varanids.

Palatine: There appears to be a portion of the right palatine preserved in ventral view on the Geological Survey slab (Fig. 3-2). The bone is dorsoventrally compressed and the exposed portion is quite short. The contact with the pterygoid is not visible as the two bones appear virtually fused together. The maxillary process of the palatine appears to be broad, although preservation makes identification in this portion of the skull difficult. The prefrontal process of the right palatine appears in the anterior rim of the orbit (Fig. 3). The lacrimal-palatine contact is not well preserved.

Mandible

The jaw articulation of aigialosaurs is dealt with in detail by Carroll and deBraga (1992) using structures seen in *Aigialosaurus dalmaticus* and the Trieste specimen. They conclude that both the angular and surangular contribute to the articulation with the quadrate in aigialosaurs and that the articular condyle of the quadrate is essentially flat, as in mosasaurs, as opposed to the double condyle seen in extant varanids (Carroll and deBraga 1992). Because the sutures between elements are not visible, this specimen of *A. bucchichi* neither supports nor refute these conclusions.

Articular: The posterior tip of the right articular is preserved in lateral view on the Geological Survey slab (Fig. 3-3). The retroarticular process is robust and relatively blunt. This is in sharp contrast to *Aigialosaurus dalmaticus* where the remnants of the retroarticular process appear very gracile (although this may be an artifact of preservation as the elements of the mandible of *A. dalmaticus* are difficult to differentiate from one another). The glenoid fossa of *A. bucchichi* is indistinct as are the articular-angular and articular-surangular contacts. The articular condyle of the right quadrate appears to contact a slight depression in the mandible which may represent the glenoid fossa (although this could also be an artifact of preservation or preparation). If this is the case then position of the surangular and articular may offer some modicum of support to the jaw articulation proposed by Carroll and deBraga (1992).

Prearticular: The prearticular extension of the articular is preserved only as an impression on the Geological Survey slab. The impression indicates that the prearticular extended anteriorly as a broad flange along the medial wall of the mandible to an abutting contact with dentary (anterodorsally) and splenial (anteroventrally). Dorsally the prearticular contacts the surangular and, further anteriorly, the coronoid. The ventral contact is with the angular. The nature of all of these contacts cannot be determined from the impression.

Surangular: The posterior tip of the surangular is preserved in lateral view on the Geological Survey slab and an impression of the rest of the surangular is preserved on the Vienna Museum slab. Very little detail can be discerned other than that the bone extended anteriorly to what appears to be an interlocking suture with the dentary. This feature is not readily comparable with *Aigialosaurus dalmaticus* due to the poor preservation of that specimen.

Angular: The tip of the right angular is preserved on the Geological Survey specimen (Fig. 3-3), and there are impressions of the bone in both medial (Geological Survey slab) and lateral (Vienna Museum slab) aspects. The outline of the angular is triangular in both aspects, similar to that of mosasaurs (Russell 1967), as opposed to the thin sliver of bone that is exposed in extant varanids. The angular is difficult to compare with that of *Aigialosaurus dalmaticus* because the identification of this element is tenuous at best on that specimen.

Coronoid: The right coronoid of *Aigialosaurus bucchichi* is preserved in medial view on the Vienna Museum slab (Fig. 3-1). The bone has a tri-lobate shape with two concave surfaces joining at a rounded peak. This morphology is unlike anything seen in mosasaurs or extant varanids. Instead of sitting in a large groove in the surangular, as is the case in most mosasaurs (Russell 1967), the coronoid appears to have an almost horizontal contact with the surangular as in extant varanids (Carroll and deBraga 1992). However, unlike that of extant varanids, the coronoid does not appear to extend anteriorly past the intramandibular hinge.

Splenial: A portion of the right splenial is preserved in medial view on the Vienna Museum slab (Fig. 1) and there is a partial impression on the Geological Survey slab. The details of the dorsal portion of the intramandibular hinge are obscured due to poor preservation; however, there is an impression of the medial aspect of the splenial-angular joint that indicates the contact was a simple abutment (as in mosasaurs) as opposed to the interdigitating relationship seen in extant varanids. The splenial has been broken off anterior to the end of the tooth row, exposing the medial wall of the dentary. The impression of the splenial on the Geological Survey slab indicates that it extended posteriorly to contact the anterior tip of the coronoid. The splenial-coronoid contact does not appear to have been as extensive as that seen in extant varanids (Carroll and deBraga 1992), but the splenial is much more closely related to the coronoid than in most mosasaurs (Russell 1967). The relation of the splenial and angular in *Aigialosaurus bucchichi* are comparable to the structures seen in *A. dalmaticus*, although the features seen on the ventral surface of *A. dalmaticus* are poorly delineated.

Dentary: The right dentary and the anterior tip of the left dentary (as an impression) are visible in medial view on the Vienna Museum slab (Fig. 3-1). Additionally, a portion of the left dentary can be seen crushed underneath the palate on the

Geological Survey slab. As pointed out by Carroll and deBraga (1992) there is a groove in the anterior portion of the right dentary for the Meckelian cartilage. Contrary to the illustrations of Carroll and deBraga (1992) the splenial has been broken and instead of the lingual wall of the splenial it is possible to see the lingual wall of the dentary. The ventral border of the dentary indicates that, like that of mosasaurs (Russell 1967), the splenial was clearly visible in lateral view, unlike in extant varanids where the splenial is restricted to the medial wall of the mandible. The dentary is not easily compared to that found in *Aigialosaurus dalmaticus* because the mandible of the latter is so poorly preserved.

Teeth: There are numerous teeth preserved in situ on the right dentary, several disarticulated teeth associated with the right maxilla, eight teeth on the right pterygoid and two on the left, and numerous tooth impressions on both the Vienna Museum and Geological Survey slabs. The dentary teeth are the most interesting as they have a very unusual shape. The tips are conical and recurved as in typical mosasaurs or extant varanids. The bases of the teeth are much broader than the tips and appear to form almost cylindrical pedestals. Carroll and deBraga (1992) indicate that this morphology is a result of crushing due to taphonomic stresses and that the teeth were simple conical structures during life. It should be pointed out that the tooth bases appear similar to the bulbous tooth roots seen in many mosasaurs, although this could be, as suggested by Carroll and deBraga (1992), a function of taphonomic processes. While Carroll and deBraga (1992) suggest that the dentary tooth count is 22 in each side, the incomplete preservation of the mandible does not allow for a definitive count. There are at least 14 teeth preserved on the right dentary and because the morphology of the teeth remains uncertain it is not possible to speculate on how many teeth the dentary may have been able to hold.

The maxillary teeth are typically conical but incompletely preserved. There is no indication of the base morphology seen in the dentary teeth but none of the maxillary teeth appear to be preserved in situ.

The pterygoid teeth are conical, recurved, and significantly smaller than the maxillary and dentary teeth. A pterygoid tooth count is not possible due to incomplete preservation of the palate of *Aigialosaurus bucchichi.*

Postcranial Skeleton

The skull and atlas-axis complex of *Aigialosaurus bucchichi* were disarticulated from the remainder of the body pre-burial. The neck and trunk of the animal are well preserved on the Vienna Museum slab (Fig. 3-1), although most of the caudal vertebrae and the better part of both hind limbs are represented only by molds.

Vertebrae: A complete vertebral count for *Aigialosaurus bucchichi* is not possible due to a large number of missing caudal vertebrae, but a conservative estimate is seven or eight cervicals, 18-19 trunk vertebrae, two sacrals, an indeterminate number of pygals, and approximately 80 caudals, giving a total count of around 110 vertebrae. The cervical, trunk, and sacral vertebrae are exposed in ventral aspect on the Vienna Museum slab and the caudals are preserved in right lateral view on the Geological Survey slab and in left lateral view on the Vienna Museum slab.

The atlas is partially preserved and disarticulated from the foramen magnum on the Geological Survey slab, although little detail can be discerned. The axis is preserved on the Vienna Museum slab as an impression just posterior to the skull. Very little detail is visible but it appears that the axis had a large neural spine similar to the one more clearly preserved in *A. dalmaticus.* The rest of the cervical vertebrae are preserved attached to the rest of the vertebral column and the trunk. The third through eighth vertebrae form an arc leading to the pectoral girdle and cervical ribs become apparent associated with the fifth or sixth vertebra. Carroll and deBraga (1992) suggest that there are seven recognizable cervical vertebrae in aigialosaurs although they do not point out which aigialosaurian specimens best demonstrate this feature. Because the sternum is not clearly visible in *A. bucchichi* it is not possible to determine which vertebrae bear ribs that attach to it, although the rib associated with the seventh vertebra appears to be relatively large. Thus, as with *A. dalmaticus*, the exact number of cervicals cannot be determined. As stated by Carroll and deBraga (1992), there are no obvious hypapophyses on the cervicals although there appear to be hypapophyseal peduncles on several of the vertebrae.

Given the uncertain number of cervicals and that the pectoral girdle has been crushed on top of, and is obscuring, several vertebrae it is not possible to determine the exact number of trunk vertebrae in *A. bucchichi.* There are 16-17 trunk vertebrae visible and the area obscured by the pectoral girdle appears to have room for two more giving a total of 18-19. As suggested by Carroll and deBraga (1992), the vertebrae are clearly procoelous, and the condyles of several of the vertebrae are ventrally exposed instead of being completely covered by the following centrum. This feature is only seen in the posterior third of the trunk although this may be due to the poor preservation of the vertebral condyles in the anterior portion of the body.

The ribs on the last five trunk vertebrae are drastically shorter than those anterior to them. This is not the case in *A. dalmaticus* where the ribs appear to shorten much earlier in the vertebral series, a difference that has been used to justify the taxonomic separation of the two specimens. The ribs are extremely robust and may represent a pachyostotic adaptation to a semi-aquatic lifestyle.

The sacral vertebrae are the final two vertebrae preserved on the Vienna Museum slab. They appear slightly smaller than the trunk vertebrae and do not bear ribs, but other than that they are unremarkable. The right side of the pelvic girdle appears to have been crushed into the first sacral vertebrae but the nature of the contact between the vertebra and the girdle is obscured.

Some anterior caudal vertebrae are preserved on several small slabs from the Geological Survey and the posterior caudals are preserved right to the tip of the tail on the Vienna Museum slab. The first dozen or so caudals appear to have been lost when the slabs were split apart, leaving only indistinct impressions on the Vienna Museum slab. The intermediate caudals preserved on the Geological Survey slabs show broad, square, posteriorly slanting neural spines transitioning into narrower and more rounded spines in the space of six or seven vertebrae. The haemal spines of these vertebrae are fractured, but appear relatively narrow. This portion of the tail appears similar to the tail of *A. dalmaticus*, although the preservation of that specimen is poor throughout the caudal region.

Most of the posterior 50 caudals are preserved on either the Geological Survey slab that contains the cranial material or on the Vienna Museum slab. The neural spines are elongate and rounded, and the haemal spines are equally lengthy, if not more so posteriorly, although much more gracile. The final few vertebrae are bent ventrally, although not nearly as prominently as those of many mosasaurs. The lengthy neural and haemal spines gave the tail a greater lateral surface area and would have been useful in anguiliform locomotion. This is one of the primary features that indicate *A. bucchichi* was a semi-aquatic squamate and is one of the few postcranial diagnosable characters for aigialosaurs.

Appendicular Skeleton

Pectoral Girdle: The holotype of *Aigialosaurus bucchichi* has the most complete pectoral girdle of any aigialosaur specimen, with both scapulacoracoid complexes being relatively well preserved. There is no evidence of a sternum, an interclavicle, or clavicles, although the absence of these elements is likely a result of taphonomic stresses or pre-burial scavenging. The right scapulacoracoid has been slightly disarticulated from the trunk, whereas the left scapulacoracoid has been crushed on top of the vertebral column. Both elements remain articulated with their respective forelimbs, with the left forelimb being fully extended and the right forelimb fixed at a ninety degree angle (Fig. 3-1). The right scapulacoracoid is poorly defined, with little visible surface detail. The left scapulacoracoid is relatively undamaged and, as suggested by Carroll and deBraga (1992), the scapula and coracoid appear co-ossified. The scapulacoracoid fenestra is obscured by a cervical rib. Because the scapulacoracoid is imperfectly preserved, it is not possible to determine if there were any further emarginations along the edge of the bone. The coracoid foramen is well preserved as is the glenoid fossa. This area of the skeleton is not comparable to that of *A. dalmaticus* as it is very poorly preserved in the only specimen of that species.

Forelimb: Both the right and left forelimbs of *Aigialosaurus bucchichi* are well preserved on the Vienna Museum slab. The left forelimb preserves the most detail and has been figured well by Carroll and deBraga (1992) and Bell (1997). The humerus is elongate and robust and appears almost identical to the humerus of *A. dalmaticus*; however, there is no evidence of unfused humeral epiphyses in *A. bucchichi*. Contrary to the suggestion of Carroll and deBraga (1992), the capitellum and trochlear groove of the left humerus are not readily apparent, as the distal end of the humerus has been damaged. The left radius and ulna are preserved in articulation with the humerus. Both bones of the forearm are well preserved with the ulna being slightly more robust. The radius and ulna both have relatively slender shafts and broad epiphyses, similar to the condition in extant terrestrial varanids. Both the radius and ulna are almost identical to their counterparts in the *A. dalmaticus* specimen.

While the carpals of the forelimb are relatively well preserved, Carroll and deBraga (1992) illustrate nine carpal elements and an unfused proximal epiphysis on the second metacarpal. The interpretation that the radiale, ulnare, both medial and lateral centrales, a pisiform and four distal carpals are present may be optimistic given the state of preservation of the elements. It is more likely that only the radiale, ulnare, and two or three miscellaneous carpals are present. This interpretation would still indicate that the wrist region of *A. bucchichi* is extremely similar to that of an extant anguimorph.

The five metacarpals of the left manus are well preserved with the first and fifth metacarpals being shorter and more robust than the three medial elements. The phalanges are elongate and terminate in pointed unguals. As stated by Carroll and deBraga (1992) the phalangeal count is 2-3-4-5-3.

The forelimb of *A. bucchichi* is consistent with the features seen in the forelimb of *A. dalmaticus*. Both are very similar to the limbs of extant terrestrial anguimorphs.

Pelvic Girdle: Only a small portion of the right side of the pelvic girdle is preserved in *Aigialosaurus bucchichi*. The head of the right femur is articulating with the acetabular portion of the ilium. No details of the structure of the pelvic girdle can be discerned as the rest of the elements are missing. *A. dalmaticus* appears to have a large anterior iliac crest, but this feature is not visible on *A. bucchichi*.

Hind limb: Contrary to the illustrations of Carroll and deBraga (1992) the only elements of the hind limbs of *Aigialosaurus bucchichi* that are preserved on the Vienna Museum slab are portions of the right femur, fibula, and pes, and the terminal phalanges of the left pes (both sets of phalanges appear to have been painted to increase visibility, but they are nonetheless made of bone). The distal end of the right femur and all of the right carpals have been poorly reconstructed using plaster. The remaining elements of the hind limbs are preserved as impressions.

The head of the right femur appears to be offset slightly from the main axis of the bone; this is also the case in *A. dalmaticus*. Both the proximal and distal tips of the right fibula are covered by plaster, meaning that the best look at the lower hind limb is found in the impressions of the left tibia and fibula. The tibia is considerably more robust than the fibula, which is long and slender, and the impression indicates that the proximal epiphysis of the tibia may not have been fused to the shaft of the bone. This situation is not seen in the hind limb of *A. dalmaticus*, but the forelimb does show signs of unfused epiphyses. As the bone is not preserved it is impossible to say if the impression is due to an unfused epiphysis or is a result of premortem, postmortem but preburial, or taphonomic stresses.

The impressions of the left tarsals are not detailed enough to be of any use, and any remnants of the right tarsals have been completely covered in plaster. The metatarsals of the right pes are elongate and almost identical to the metacarpals. The phalangeal count appears to be the same 2-3-4-5-3 that is seen in the manus. The hind limb of *A. bucchichi* appear almost identical in structure to that of *A. dalmaticus* and was no doubt used primarily for terrestrial locomotion and tucked to the body while the animal was swimming.

DISCUSSION

Several previous authors (Carroll and deBraga 1992, Caldwell et al. 1995, Caldwell 2000) have suggested that *Opetiosaurus bucchichi* and *A. dalmaticus* are congeneric if not conspecific, whereas Bell (1993, 1997) and Polcyn et al. (1999) support a continued generic differentiation. Carroll and deBraga (1992) utilized both taxa in their discussion of the generalized aigialosaurian body plan but no detailed comparison was performed. This study has corrected some oversights of the previous studies, and a detailed comparison is now possible between the two most-complete aigialosaur specimens.

Aigialosaurus and *Opetiosaurus* have historically been treated as distinct genera on the basis of several morphological characters. Bell (1997) differentiates *O. bucchichi* and *A. dalmaticus* on the basis of features of the jugal, tympanic ala, basipterygoid processes of the basisphenoid, the dentary medial parapet, and the scapulacoracoid complex. A detailed comparison of the two specimens has shown that all of these points are flawed, mostly on the basis that *A. dalmaticus* is too poorly preserved to see the anatomical details discussed. The jugal of *A. dalmaticus* is poorly preserved and it is impossible to determine the presence or absence of a posteroventral process. The same is true of the basipterygoid processes of the basisphenoid of *A. dalmaticus*, in addition to the fact that the basisphenoid of *A. bucchichi* was not visible for comparison at the time the characters were scored for Bell's (1997) analysis. The dentary medial parapet is poorly preserved in both of the specimens examined, although it can be scored on the basis of the right dentary of *A. bucchichi*. The character analyzing the ontogenetic timing of scapulacoracoid fusion is a poor character as there are no ontogenetic data for aigialosaurs. Besides this fact, there is not enough of the scapulacoracoid of *A. dalmaticus* preserved to determine whether or not the two elements are fused, as they are in extant varanids and *A. bucchichi*, or separate, as they are in mosasaurs.

The lone character used by Bell (1997) to differentiate *A. dalmaticus* and *A. bucchichi* that is upheld by this study is the shape of the tympanic ala of the quadrate. The curvature of the tympanic ala in the right quadrate of *A. dalmaticus* is much tighter than that seen on *A. bucchichi*. However, given the generally poor preservation of *A. dalmaticus* this difference could very well be a result of taphonomic stresses and thus is a dubious character upon which to differentiate genera; it is provisionally accepted here as a diagnostic character of the species.

Kornhuber (1901) originally differentiated *Opetiosaurus* from *Aigialosaurus* on the basis of the former's "special, outstanding dentition." The tooth morphology is different between the two species with *A. dalmaticus* showing no sign of the expanded tooth bases seen clearly in *A. bucchichi*. However, there are relatively few teeth preserved in *A. dalmaticus*, and those that are preserved are generally heavily weathered or damaged. The dentitions of the two species are difficult to compare, but the unique dental morphology of *A. bucchichi* is identified here as a diagnostic character for the species.

Other than the two questionable differences mentioned above, the portions of the body that are comparable in both specimens are almost identical. The cranial, vertebral, and appendicular characteristics, together with the close geographical proximity of their respective localities, give every indication that *A. dalmaticus* and *A. bucchichi* are extremely closely related. It is on the basis of these similarities that the author has determined that *Opetiosaurus* (Kornhuber 1901) is a junior generic synonym to *Aigialosaurus* (Kramberger 1892). Because the stratigraphic relationship of the two specimens is poorly defined and the poor preservation of *A. dalmaticus* makes comparison between the two specimens difficult, the author suggests maintaining a specific differentiation between the two specimens, and supports the nomenclature first suggested by Caldwell et al. (1995). *Aigialosaurus dalmaticus* remains the holotype for the family Aigialosauridae, and the genus *Aigialosaurus*. *Opetiosaurus bucchichi* is here placed within the genus *Aigialosaurus* and is renamed *A. bucchichi.*

Bell and Polcyn (in press) used the tree topologies retrieved in their recent systematic analysis to suggest that Aigialosauridae should be a monotypic family including only *A. dalmaticus*. Bell and Polcyn (in press) did allow that should *Aigialosaurus* and *Opetiosaurus* ever be convincingly synonymised, as they have been here, that both species should be included in the family. This synonymy indicates that there may be problems in character coding in the data matrix of Bell and Polcyn (in press) that cause *A. dalmaticus* and *A. bucchichi* to consistently appear as paraphyletic sister taxa in their results. With detailed redescriptions of both taxa available (see Dutchak and Caldwell [in press] for the revision of *A. dalmaticus*) the character scorings of Bell and Polcyn (in press) can be revised and their evolutionary hypotheses tested.

CONCLUSIONS

A detailed comparison of *Aigialosaurus bucchichi* and *A. dalmaticus* revealed numerous features of both specimens that had been misidentified in previous studies. The only study to quantify the differences between *A. bucchichi* and *A. dalmaticus* (Bell 1997) did so using characters which, with one exception, cannot be diagnosed or compared between the two specimens. By improving upon previous descriptions of *Opetiosaurus bucchichi* (Kornhuber 1901, Carroll and deBraga 1992) and using Dutchak and Caldwell's (in press) description of *A. dalmaticus*, it has been established that a generic differentiation between the two specimens is not merited. The two aigialosaur species from Hvar, Croatia are considered here to be congeneric and provisionally differentiated at the species level by several equivocal characters that may prove to be the results of taphonomic processes.

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FIGURE 3-1. The Vienna Museum specimen of *Aigialosaurus bucchichi* redrawn from Carroll and deBraga (1992). Grey outlines indicate elements visible only as impressions.

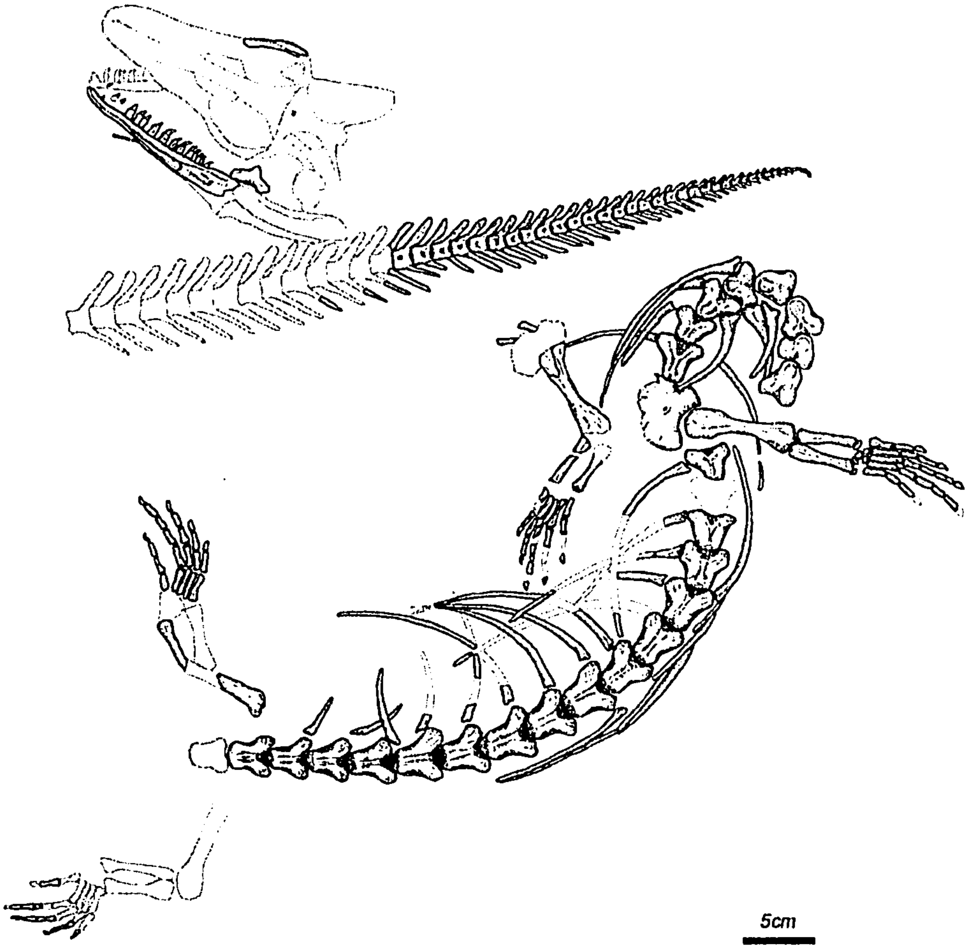
5cm

FIGURE 3-2. The ventral aspect of *Aigialosaurus bucchichi* from the Austrian Geological Survey slab. Abbreviations: at, atlas; art, articular; bo, basioccipital; bs, basisphenoid; d, dentary; ect, ectopterygoid; ept, epipterygoid; ex, exoccipital; m, maxilla; pa, palatine; pof, postorbitofrontal; pro, prootic; pt, pterygoid; q, quadrate; sq, squamosal; st, supratemporal; sta, stapes.

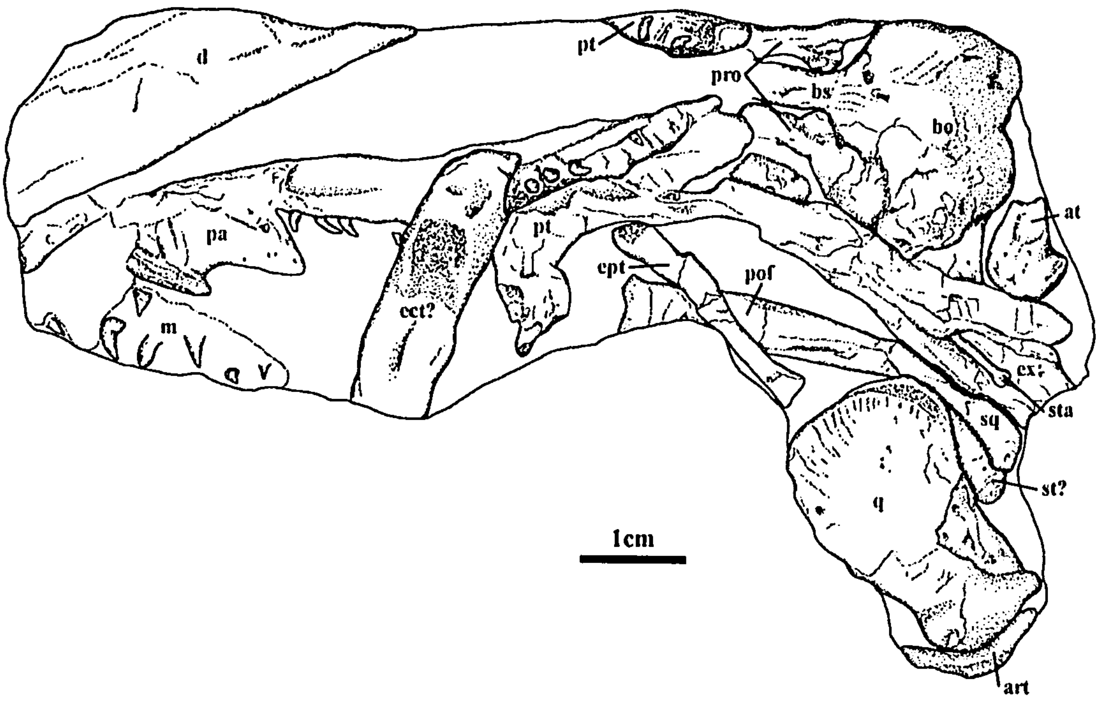
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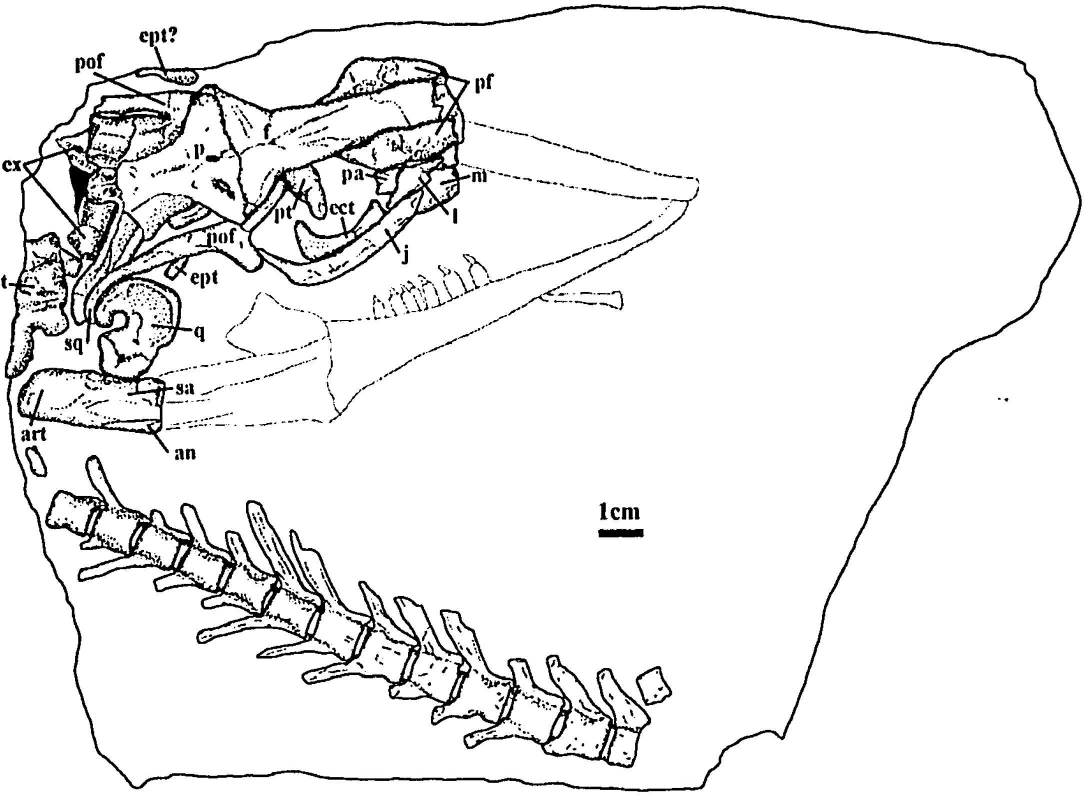
FIGURE 3-3. The dorsal aspect of *Aigialosaurus bucchichi* from the Austrian Geological Survey slab. Elements outlined in grey are preserved as impressions. Abbreviations: an, angular; art, articular; at, atlas; ect, ectopterygoid; ept, epipterygoid; ex, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; p, parietal; pa, palatine; pf, prefrontal; pof, postorbitofrontal; pt, pterygoid; q, quadrate; sa, surangular; sq, squamosal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CHAPTER FOUR

THE INTERRELATIONSHIPS OF THE ANGUIMORPHA WITH SPECIFIC REFERENCE TO *AIGIALOSAURUS*

INTRODUCTION

The most complete systematic analysis of relationships within Mosasauroidea was completed by Bell and Polcyn (in press) based almost entirely on the previous work of Bell (1993 and 1997). As a preliminary step to any systematic work, the author must determine a suitable outgroup with which to polarize characters and root the tree for the ingroup analysis. Bell (1993) determined his outgroup by inserting Mosasauroidea, as a single terminal taxon, into the data matrix of Estes et al. (1988), who analysed the interrelationships of squamates but excluded mosasauroids. This analysis revealed mosasauroids to be nested somewhere within Anguimorpha. Bell (1993) and all studies that have subsequently used modified versions of that matrix (Bell 1997, Christiansen and Bonde 2002, Bell and Polcyn in press, Polcyn and Bell in press) have used the identical outgroup without further testing the systematic relationships of mosasauroids within either Squamata or Anguimorpha.

Bell (1993) was not the first to investigate the relationship of mosasauroids within Squamata. Carroll and deBraga (1992) ran an abbreviated systematic analysis that included ten anguimorph taxa coded for 15 characters. Not surprisingly, with so many taxa and so few characters the resulting topologies were relatively unresolved. However, the results indicated that "Aigialosauridae" (aigialosaurs were assumed to represent a monophyletic group) were closely associated with varanoid lizards. DeBraga and Carroll (1993) produced a larger study that included ingroup mosasauroids (aigialosaurs were again assumed to be monophyletic) in addition to three recognised anguimorph clades (Necrosauridae, Helodermatidae, and Varanidae). The results of the analysis indicated "Aigialosauridae" and Varanidae are sequential sister taxa to Mosasauridae. The characters of deBraga and Carroll (1993) are relatively poorly diagnosed, leaving their conclusions open for debate. For this reason, subsequent workers have largely bypassed their study.

Nydam (2000) modified an anguimorph data matrix that had been developed through a series of studies (Pregill et al. 1986, Norell et al. 1992, Norell and Gao 1997, Gao and Norell 1998). This matrix includes numerous fossil taxa and represents an opportunity to further investigate the findings of Bell's (1993) outgroup analysis. The fact that the Nydam (2000) matrix has been used in numerous previous studies allows for streamlining of testing as the taxa that introduce the most instability into the analysis have already been identified. By testing the relationships of mosasauroids to other anguimorphs it will be possible to test the validity of the taxa used by Bell (1993) to root his mosasauroid ingroup analysis. Any new information that might lead to changes in coding might have a profound effect on the results of subsequent mosasauroid ingroup analyses.

MATERIALS AND METHODS

Aigialosaurus was added to the most recent incarnation (Nydam 2000) of a well-known anguimorph data matrix (30 taxa and 105 characters). The matrix was analysed using the Heuristic search option in PAUP version 4.0b10 (Swofford 2002). All multistate characters were treated as unordered and unweighted. Characters were mapped onto the tree using the DELTRAN character optimization setting. This identifies synapomorphies for more exclusive clades and terminal taxa as opposed to more inclusive clades near the base of the tree. A 1000 replicate bootstrap analysis was run in order to determine relative branch support for each clade retrieved in the Heuristic analysis. A decay analysis was also run in order to assess the amount of character uncertainty present in the analysis.

Characters

The characters and taxa used in this analysis are from Nydam's (2000) interpretation of Gao and Norell (1998). This matrix includes 90 osteological characters (of which 83 can be scored for fossil taxa [Nydam 2000]) and 15 soft-anatomy characters. The character definitions (from Gao and Norell 1998) can be found in Appendix I and the data matrix, as coded by Nydam (2000), is in Appendix II.

Outgroup

Scincomorpha, Gekkota, and Iguania were used to root the ingroup tree based on the systematic results of Estes et al. (1988).

Ingroup

The ingroup taxa are include both extant and fossil specimens. The taxic composition reflects the specific interests of Gao and Norell (1998) who focused on the relationships of fossil taxa from the Gobi Desert, but the analysis also includes New World and European taxa, and thus taxic composition is not considered a problem. *Aigialosaurus* was added to the ingroup composition suggested by Nydam (2000), who found that removal of *Palaeosaniwa*, *Eosaniwa*, *Restes*, *Exostinus*, *Parasaniwa*, and *Bainguis* from the matrix of Gao and Norell (1998) significantly reduced uncertainty within the analysis and did not significantly affect the overall topologies of the resulting trees.

RESULTS

When the matrix of 30 taxa and 105 characters was analysed using the Heuristic algorithm of PAUP, 45 shortest phylogenies of 271 steps were retrieved. The Consistency Index (C.I.) for these trees was 0.531, the Retention Index (R.I.) was 0.770, and the Homoplasy Index (H.I.) was 0.469. The Strict consensus tree (Fig. 4-1) shows *Aigialosaurus* nested within Varanoidea in a polytomy with *Paravaranus* and a clade of *Proplatynotia* and *Saniwides.* The taxa in this polytomy form the sister group to the clade of *Telmasaurus*, *Saniwa*, *Varanus*, *Lathanotus* and *Cherminotus.* The Highest Percentage-Rule consensus (Fig. 4-2) finds the clade of *Aigialosaurus* and *Paravaranus* to be the sister group to the clade of *Telmasaurus*, *Saniwa*, *Varanus*, *Lanthanotus* and *Cherminotus.* The 1000 replicate bootstrap analysis tree (Fig. 4-3) has the same topology as the Highest Percentage-Rule tree, and shows that the branch support throughout most of the tree is relatively poor.

DISCUSSION

The placement of *Aigialosaurus* within Anguimorpha in this study is difficult to compare with previous studies for a variety of reasons. Many of the previous global squamate analyses (Lee 1997 and 1998, Caldwell 1999, Lee and Caldwell 2000, Rieppel and Zaher 2000) were designed to deal with different questions and thus included considerably different taxa (most notably the ever-problematic Serpentes). To further complicate the problem, most previous analyses that had focused on aigialosaurs refer to either their close affinity (Carroll and deBraga 1992, deBraga and Carroll 1993) or relatively distant relation to (Caldwell et al. 1995) "varanoids". Unfortunately, the definition of the taxon Varanoidea (and hence "varanoid") remains difficult to determine. The taxonomy within Anguimorpha is problematic as various authors have attempted to introduce new taxonomic definitions based on systematic analyses that have produced widely disparate results. As a result, the term "Varanoidea" as defined by Lee (1997) is synonymous with the clade "Platynota" of Gao and Norell (1998), who define Varanoidea as including the last common ancestor of Varanidae and *Telmasaurus* and all its descendants. This definition places *Aigialosaurus* in a clade with *Paravaranus* as the sister group to Varanoidea within Platynota (here defined as the most recent common ancestor of the Monstersauria and Varanidae and all its descendants, after Gao and Norell [1998]).

Aigialosaurus shows numerous character states that Gao and Norell (1998) suggest as synapomorphies of Platynota, including possession of a well-developed intramandibular hinge, extensive medial exposure of the angular, and a blunt anterior process of the surangular. However, it should also be noted that *Aigialosaurus* cannot be scored for the four characters used by Gao and Norell (1998) to diagnose Varanoidea. This state of affairs means that the exclusion of *Aigialosaurus* from Varanoidea should be treated as tentative until further investigations have been conducted.

Lee's (1997) stem "platynotans" (*Proplatynotia* and *Paravaranus*) are found to be nested as members of consecutive sister groups to varanids in the current analysis. It is interesting to note that *Paravaranus* and "Aigialosauridae" were widely separated in the phylogeny of Lee (1997), whereas *Aigialosaurus* groups closely with *Paravaranus* in the current study. This difference in placement could be due to numerous factors including the types of characters used in the different studies (the most likely reason), the fact that *Paravaranus* is only a partial specimen and its lack of data makes it more mobile in different tree topologies, and that Lee (1997) may have been using descriptions to code "Aigialosauridae" that have been shown to be erroneous or lacking in various morphological details. These problems are compounded by differences in character coding that are pointed out by Gao and Norell (1998).

Paravaranus is represented by a single partial skull (Borsuk-Bialynicka 1984) from the Upper Cretaceous Nemegt Basin of China. *Aigialosaurus* and *Paravaranus* differ in only one of the 21 characters for which they can both be scored: the shape of the lateral borders of the frontal (character 7). This apparent similarity is misleading as the shapes and relative sizes of almost every comparable element in the two specimens differ significantly. The fact that both *Paravaranus* and *Aigialosaurus* have pterygoid teeth is hardly surprising as the lack of pterygoid teeth in *Varanus* represents the exception rather than the rule within Anguimorpha.

The results of this systematic analysis show much better resolution within Anguimorpha than the outgroup analysis conducted by Bell (1993), which was based on the matrix of Estes et al. (1988). The placement of *Aigialosaurus* within Gao and Norell's (1998) Platynota indicates that some of the taxa used by Bell (1993) to root his mosasauroid tree may be superfluous. Instead of using ten widely disparate squamate taxa to code the mosasauroid outgroup, it might be a useful exercise to limit the outgroup to taxa within Anguimorpha (thereby eliminating skinks, gekkos and iguanids). As the position of mosasauroids within Anguimorpha becomes clearer it should be possible to determine a more accurate set of character states for the ancestral mosasauroid which could help sort out ingroup mosasauroid relationships.

The exclusion of Serpentes from the matrix of Nydam (2000) does not allow the current analysis to test the validity of clade Pythonomorpha (Serpentes and mosasauroids), supported by numerous authors (Lee 1997 and 1998, Caldwell 2000, Pierce and Caldwell 2004). Following the logic of these studies, if snakes have a relatively close relationship to mosasauroids then the placement of *Aigialosaurus* deep within Anguimorpha indicates that snakes also arose within this group. The placement of snakes within Squamata continues to a contentious issue whose discussion lies beyond the scope of this study, but insertion of serpentiforms into this data matrix would be an interesting exercise for future researchers.

CONCLUSIONS

The lack of robust, universally accepted, definitions of Platynota and Varanoidea makes taxonomy within Anguimorpha extremely unstable. *Aigialosaurus* is tentatively placed as a platynotan anguimorph that, along with *Paravaranus*, forms the sister group to Varanoidea when using the taxonomic definitions suggested by Gao and Norell (1998). The topologies of the shortest trees found here appear to be extremely plastic due in part to the fragmentary nature of many of the fossil taxa included. The relative completeness of both *Aigialosaurus* specimens and many more derived mosasauroid taxa should encourage future researchers to include them in systematic analyses rather than continuing to overlook this large source of data.

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FIGURE 4-1. Strict consensus tree constructed from 45 shortest cladograms of 271 steps (29 taxa and 105 characters).

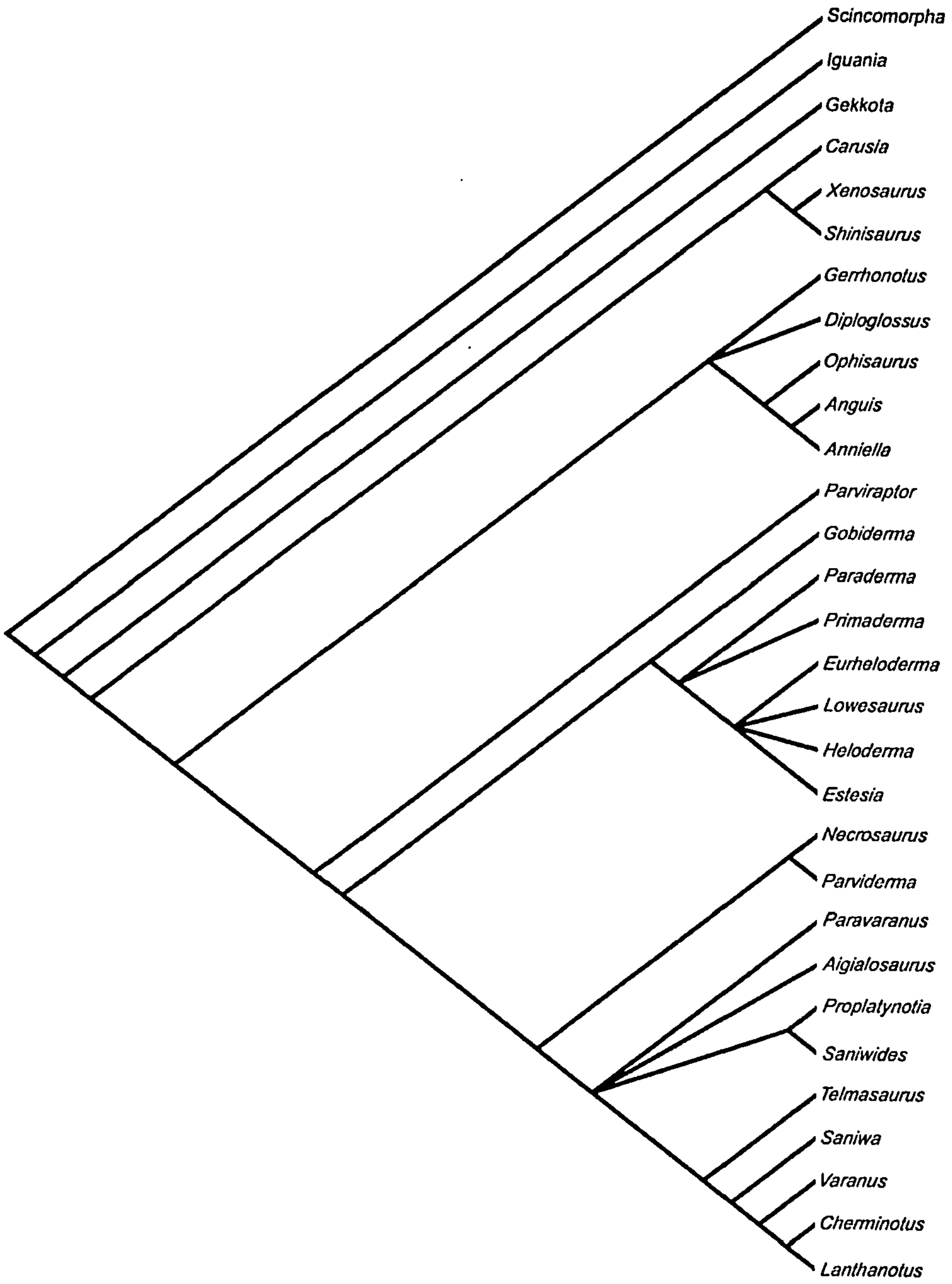

Scincomorpha
Iguania
Gekkota
Carusia
Xenosaurus
Shinisaurus
Gerrhonotus
Diploglossus
Ophisaurus
Anguis
Anniella
Parviraptor
Gobiderma
Paraderma
Primaderma
Eurheloderma
Lowesaurus
Heloderma
Estesia
Necrosaurus
Parviderma
Paravaranus
Aigialosaurus
Proplatynotia
Saniwides
Telmasaurus
Saniwa
Varanus
Cherminotus
Lanthanotus

FIGURE 4-2. The Highest Percentage-Rule consensus tree constructed from the 45 shortest cladograms (29 taxa and 105 characters). All branch supports are 100 unless otherwise indicated.

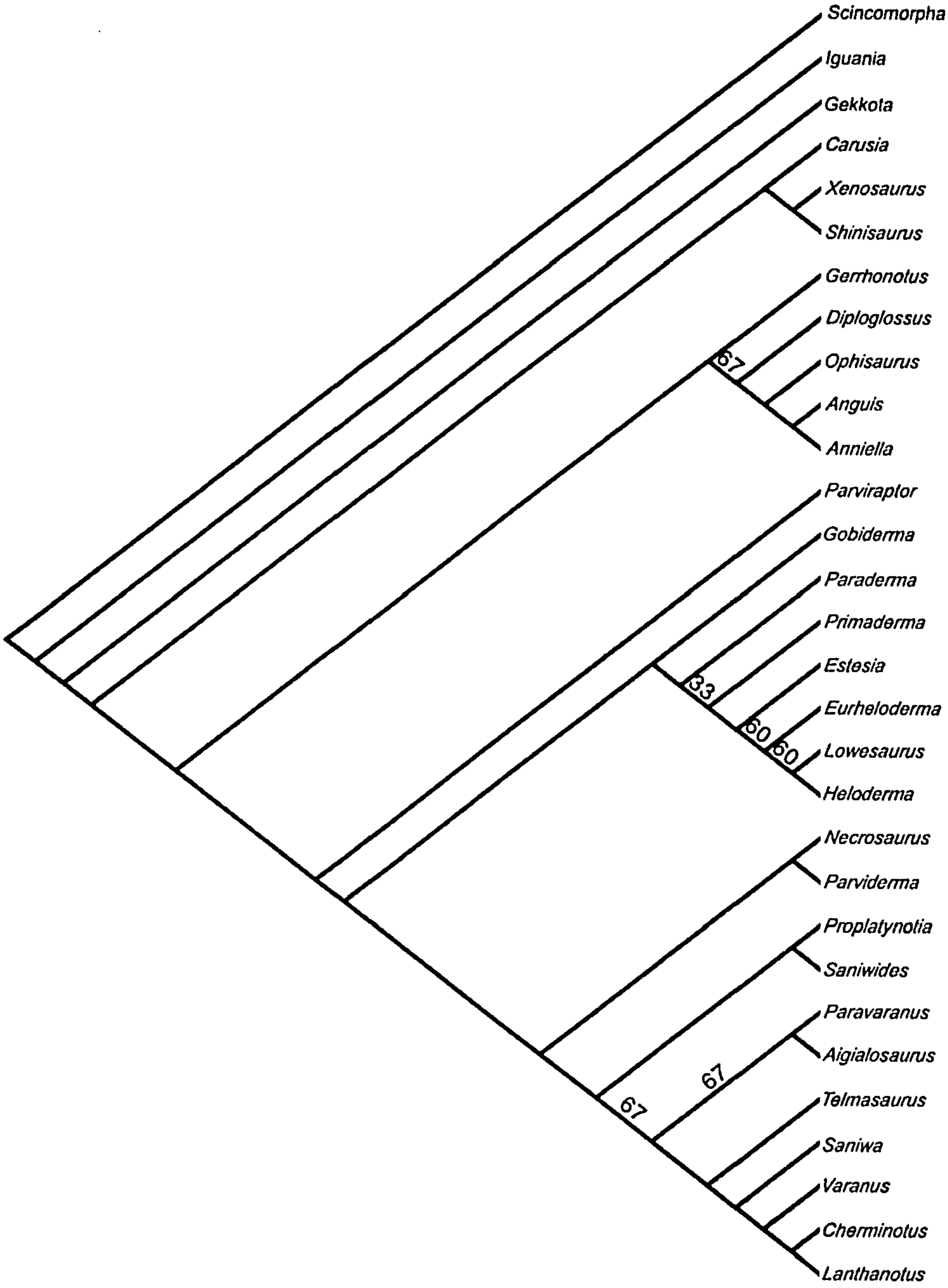
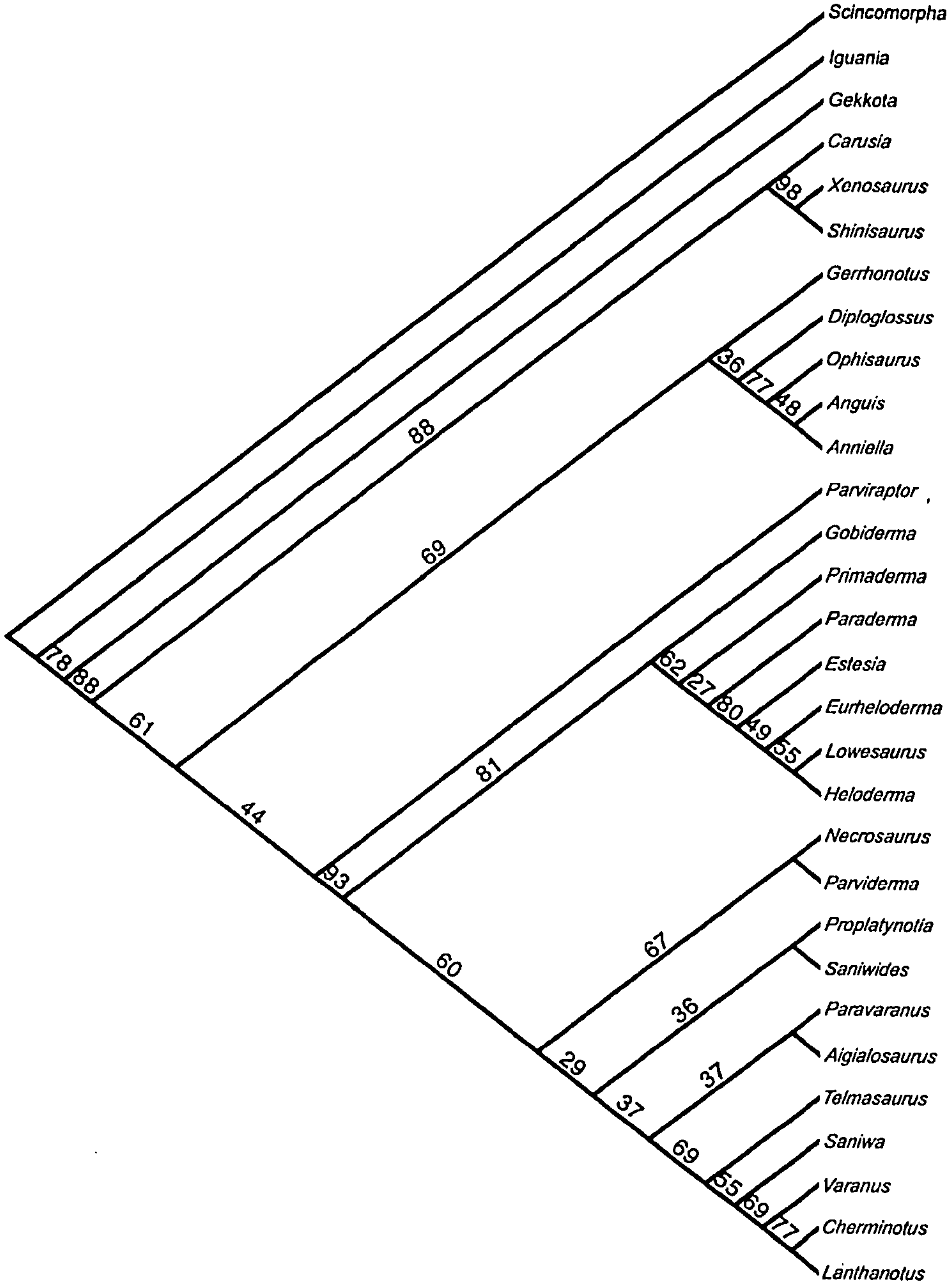

Scincomorpha
Iguania
Gekkota
Carusia
Xenosaurus
Shinisaurus
Gerrhonotus
Diploglossus
Ophisaurus
Anguis
Anniella
67
Parviraptor
Gobiderma
Paraderma
Primaderma
Estesia
Eurheloderma
Lowesaurus
Heloderma
33
60
60
Necrosaurus
Parviderma
Proplatynotia
Saniwides
Paravaranus
Aigialosaurus
67
67
Telmasaurus
Saniwa
Varanus
Cherminotus
Lanthanotus

FIGURE 4-3. Tree showing branch support values retrieved from a 1000 replicate bootstrap test.


Scincomorpha
Iguania
Gekkota
Carusia
Xenosaurus
Shinisaurus
Gerrhonotus
Diploglossus
Ophisaurus
Anguis
Anniella
Parviraptor
Gobiderma
Primaderma
Paraderma
Estesia
Eurheloderma
Lowesaurus
Heloderma
Necrosaurus
Parviderma
Proplatynotia
Saniwides
Paravaranus
Aigialosaurus
Telmasaurus
Saniwa
Varanus
Cherminotus
Lanthanotus
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APPENDIX I

Character List (from Gao and Norell 1998)

1. Premaxillary-maxillary aperture absent (0), or present (1). "Aperture" to mean structure that opens at the premaxillary-maxillary suture rather than within the premaxilla. In lizards such as *Varanus* both the aperture and premaxillary foramen are present on the palate.

2. Nasal bones paired and have extensive suture contact along midline (0), or paired with limited contact ½ or less length of the element (1), or fused (2).

3. Nasal and prefrontal bones in broad contact (0), or separated by contact of frontal with maxilla (1), or separated by gap (2).

4. Nasal and maxillary bones in broad contact (0), or entirely or largely separated by gap (1), or separated by prefrontal (2).

5. Nasal process of maxilla located at the anterior (0), or middle (1), or posterior part of maxilla (2).

6. Frontals are paired in adult stage (0), or fused (1).

7. Lateral border of frontals more or less parallel-sided (0), or constricted between orbits and hourglass-shaped (1), or trapezoidal (2).

8. Subolfactory processes of frontals poorly defined (0), or well developed as lateral wall of olfactory tract (1).

9. Subolfactory processes of frontals do not contact each other ventrally (0), extensive contact along midline (1), closely approach or contact anteromedially (2), or closely approach or contact posteromedially (3).

10. Prefrontal not entering external narial opening (0), entering the opening owing to strong anterior extension of prefrontal (1), or entering opening owing to strong retraction of nares (2).

11. Prefontal does not (0), or does contact postfrontal above orbit (1).

12. Jugal/squamosal contact on supratemporal arch absent (0), or present (1).

13. Jugal well developed and angulated (0), strongly reduced with little or no angulation (1).

14. Posteroventral process of jugal well developed (0), nearly or entirely lost (1).

15. Postorbital arch complete (0), or broken (1).

16. Dilation of postorbital branch of jugal absent (0), or present (1).

17. Dermal ornamentation of postorbital branch of jugal absent (0), or present (1).

18. Ectopterygoid laterally concealed by maxilla and jugal (0), or exposed on ventral edge of skull (1).

19. Both postfrontal and postorbital (0), or only postfrontal enter the orbit (1).

20. Postorbital/postfrontal fusion absent (0), or present (1).

21. Canthal crest on temporal arch absent (0), or present (1).

22. Parietal foramen present (0), or absent (1).

23. Descensus parietalis presents as a lateral flange of the parietal table (0), as ventral creast beneath the table (1), or as a strongly elongated ventral process extending to or just medial to the epepterygoid (2).

24. Supratemporal arch present (0), or absent (1).

25. Supratemporal fenestra wide open (0), narrowed and elongated (1), strongly reduced and nearly closed (2), or entirely lost (3).

26. Origin of temporal musculature on dorsolateral aspect (0), or on ventral aspect of parietal table (1).

27. Hypoglossal foramen not enlarged (0), or enlarged and confluent with vagal foramen (1).

28. Posterior opening of vidian canal located at prootic/basisphenoid suture (0), or penetrates basisphenoid only (1).

29. Facial foramen in recessus vena jugularis single (0), or double (1).

30. Entocarotid fossa within recessus vena jugularis well developed (0), strongly reduced (1), or essentially lost (2).

31. Basioccipital/basisphenoid suture obtusely angulate and laterally diagonal (0), or roughly a straight line suture in keeping with anterior shifting of spheno-occipital tubercle (1).

32. Distinct medial projection anteroventral to mesopterygoid fossa absent (0), of present to enhance basipterygoid process/pterygoid articulation (1).

33. Suprtemporal process of parietal in dorsal aspect flat (0), or narrow with sharp crest (1).

34. Anterior extension of supratemporal does not (0), or does reach level of apex of parietal notch (1).

35. Tympanic crest of quadrate large (0), or crest strongly reduced (1).

36. Pterygoid lappet of quadrate absent (0), or present (1). [Coding of *Gobiderma pulchrum* based on MAE 96-163.]

37. Muzzle tapered, narrowing anteriorly (0), or blunt and rounded (1).

38. Posterior lacrimal foramen single (0), or double (1).

39. Premaxillary teeth large (0), or abruptly smaller than maxillary teeth (1).

40. Plicidentine infolding of teeth absent (0), or present (1).

41. Marginal teeth are not (0), or are widely spaced with expanded tooth bases (1).

42. Replacement teeth developed entirely or partially in resorption pits (0), or developed posteriorly without presence of resorption pits (1).

43. Maxillary tooth row extends extensively suborbital (0), or slight suborbital with no more than three tooth positions (1), or entirely antorbital (2).

44. Maxillary teeth number more than 13 (0), 10-13 (1), or nine or less (2).

45. Venom groove on marginal teeth absent (0), or present (1).

46. Incisive process of premaxilla as a single spine (0), or bipartite (1).

47. Vomer short of slightly elongated (0), or strongly elongated to nearly twice the length of palatine, reaching level of posterior end of tooth row (1).

48. Aperture for Jacobson's organ confluent with internal narial opening (0), or separated from the narial opening by vomer-maxillary contact (1).

49. Posterior extension of choana ends far anterior (0), or ends close to or at posterior end of maxillary tooth row (1).

50. Palatal shelves of vomer wide (0), or narrow (1).

51. Palatine longer than wide (0), or equally wide as long (1).

52. Palatine teeth present (0), or absent (1).

53. Pterygoid teeth present (0), or absent (1).

54. Anterolateral process of pterygoid short and fits into a notch of ectopterygoid (0), or extended dorsally on ectopterygoid to contact jugal (1).

55. Ectopterygoid in palatal view does not contact palatine anteriorly (0), or does, excluding maxilla from suborbital fenestra (1).

56. Posterolateral end of dentary having no notch only (0), or presence of both a coronoid and a surangular notch (1), or notches strongly reduced or lost owing to development of intermandibular hinge (2).

57. Surangular in lateral view strongly tapered anteriorly (0), weakly tapered (1), or blunt in keeping with the development of intermandibular hinge (2).

58. Surangular does not extend anteriorly beyond (0), or slightly beyond (1), or well beyond coronoid eminence (2).

59. Anterior extension of splenial far beyond midpoint of tooth row (0), retracted to or posterior to midpoint of tooth row (1).

60. Posterior extension of splenial beyond coronoid eminence (0), or terminates anterior to or below the eminence (1).

61. Splenial-dentary suture firm (0), or loose, with much connective tissue between the two bones (1).

62. Intramandibular septum within Meckelian canal absent (0), or present as oblique or vertical septum (1).

63. Anterior process of coronoid is not (0), or is elongate and extensively exposed dorsally (1).

64. Subdental shelf normally developed (0), or lost in keeping with fusion of dentary tube (1), or strongly reduced as a slope (2).

65. Ventral border of subdental shelf does not (0), or does notch to form dorsal and anterior border of anterior inferior alveolar foramen (1).

66. Meckelian canal open medially for entire length (0), or open ventrally anterior to anterior inferior alveolar foramen (1), or completely closed as a dentary tube (2).

67. Strong reduction of mandibular fossa absent (0), or present (1).

68. Medial exposure of angular bone small (0), or extensive (1).

69. Retroarticular process not widened (0), or widened (1).

70. Retroarticular process not (0), or strongly twisted (1).

71. Retroarticular process posteriorly directed (0), or deflected medially (1).

72. Cephalic osteoderms absent (0), present as thin and platelike tesserae (1), or fragmented and thickened as subconical mounds (2).

73. Dermal rugosities absent (0), present with vermiculate sculpture (1), or present with conspicuously pitted surfaces (2).

74. Ossified palpebrals absent (0), or present (1).

75. Lacrimal duct single (0), or double (1).

Axial Characters

76. Number of cervical vertebrae eight of less (0), nine (1), tend or more (2).

77. Cervical intercentrum intervertebral or fixed under anterior part of following centrum (0), sutured to posterior part of preceding centrum (1), or fused to posterior part of preceding centrum (2).

78. Neural spines low and broad (0), or narrow and tall (1).

79. Precondylar constriction of vertebrae absent (0), or present (1).

80. Number of presacral vertebrae fewer than 26 (0), or 26 or more (1).

81. Autotomy on caudal vertebrae present (0), or absent (1).

82. Peduncles on cervical and caudal vertebrae absent (0), or present (1).

83. Caudal chevrons contact centrum condyle (0), suture to centrum only (1), or fuse to centrum (2).

Appendicular characters

84. Epicoracoid contacts suprascapula and mesoscapula (0), or not (1).

85. Posterior coracoid emargination absent (0), or present (1).

86. Interclavicle T-shaped or anchor-shaped without anterior process (0), or cruciform with prominent anterior process (1), vestigious or entirely lost in adults (2).

87. Mesosternum present (0), or absent (1).

88. Rib attachments on sternum more than three pairs (0), or three pairs (1), or two or fewer pairs (2).

89. Strong elongation of symphysial process of pubis absent (0), or present (1).

90. Body osteoderms absent (0), present dorsally (1), or present both dorsally and ventrally (2).

Soft anatomy characters

91. M. episterno-cleido-mastoideus inserts mainly on paroccipital process (0), or has extensive insertion on parietal (1).

92. M. constrictor colli does not (0), or does extensively cover first ceratobranchials (1).

93. Origin of 3b-layer of MAME profundus from supratemporal and parietal (0), or supratemporal only (1).

94. M. geniomyoideus absent (0), present but completely superficial to m. genioglossus medialis (1), or insertion at least partly invades deep to m. genioglossus medialis (2).

95. M. genioglossus lateralis single bundle and not inserted into hyobranchial skeleton (0), or subdivided into separate bundles and inserted into hyobranchials (1).

96. Insertion of m. levator pterygoidii extends posteriorly beyond columellar fossa of pterygoid (0), or restricted anteriorly (1).

97. Anterior head of m. pseudotemporalis profundus absent (0), or present but not expanded (1), present and expanded (2), or lost by fusion (3).

98. Bodenaponeurosis with broad base extending onto lateral edge of mandibular fossa (0), or narrow base attached only to caudomesial edge of coronoid (1).

99. Hemibacula (mineralized horns of hemipenis) absent (0), or present (1).

100. Foretongue not notched or cleft for less than 10% of length (0), cleft for 10-20% of length (1), or deeply cleft from 20% up to over 50% of length (2).

101. Carotid duct present (0), or absent (1).

102. Gland of Gabe absent (0), or present (1).

103. Cochlear duct not robust (0), or robust and broad, limbus elongate and heavy (1).

104. Ulnar nerve superficial (0), or deep in forearm (1).

105. Second epibranchial present (0), or absent (1).

APPENDIX II

Character Matrix

		1	2	3	4	5	6	7	8	9	10	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
1	Aigialosaurus	?	?	?	?	?	1	2	?	?	?	0	0	1	1	0
2	Paravaranus	?	2	2	1	2	1	0	0	0	2	0	?	1	1	0
3	Scincomorph	0 & 1	0	1	0	1	0 & 1	0	0	0	0	0	0 & 1	0	0	0
4	Iguania	0 & 1	0	0	0	0	1	1	0	0	0	0	1	0	0	0
[illegible]	Gekkota	0	0	0 & 1	0	1	0 & 1	0	1	1	0	0	0	1	1	1
[illegible]	Carusia	0	0	1	0	0	1	1	1	0	0	0	1	0	0	0
[illegible]	Exostinus	?	?	?	?	0	1	1	1	0	?	0	?	0	0	0
[illegible]	Restes	?	?	?	?	0	1	1	1	0	?	0	?	0	0	0
9	Necrosaurus	?	0	?	0	1	1	1	1	0	0	?	?	?	?	?
10	Bainguis	?	?	?	?	?	0	0	1	0	0	?	?	1	1	?
11	Proplaynotia	0	0	1	0	2	0	0	1	0	0	0	?	1	1	0
12	Parviderma	?	0	1	0	?	1	1	1	0	0	0	?	?	?	?
13	Gobiderma	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
14	Saniwides	0	0	1	?	2	0	0	1	0	0	0	0	1	1	0
15	Paraderma	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
16	Parasaniwa	?	?	?	?	1	1	1	1	0	?	?	?	?	?	?
17	Cherminotus	0	0	2	1	2	0	0	1	3	2	1	0	1	1	?
18	Eurheloderma	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
19	Lowesaurus	?	?	?	?	1	0	2	1	2	?	?	0	0	0	0
20	Heloderma	0	0	2	1	1	0	2	1	2	2	1	0	0	0	0
21	Saniwa	1	2	2	1	2	0	0	1	3	2	0	0	1	1	0
22	Telmasaurus	?	?	?	?	2	0	0	1	3	?	0	0	1	1	0
23	Varanus	1	2	2	1	2	0	0	1	3	2	0	0	1	1	1
24	Lanthanotus	0	2	2	1	2	0	2	1	3	2	1	0	1	1	0
25	Estesia	0	0	2	1	2	0	0	1	0	2	1	0	0	1	0
26	Xenosaurus	0	1	0	0	0	1	1	1	0	0	0	1	0	0	0
27	Shinisaurus	0	1	0	2	0	1	1	1	0	1	0	1	0	0	0
28	Gerrhonotus	0	0 & 1	0 & 1	0	1	1	1	1	0	0	0	0	0	0	0
29	Diploglossus	1	0 & 1	1	0	1	0	0	1	0	0	0	0	0	0	0
30	Ophisaurus	1	0	0	0	1	0	2	1	0	0	0 & 1	0	1	1	0
31	Anguis	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0
32	Anniella	0	0	0	0	1	0	0	1	1	0	1	0	1	1	1
33	Primaderma	?	?	?	0	1	?	?	?	?	0	?	?	?	?	?
34	Parviraptor	?	?	?	0	0	?	0	1	2	?	?	?	?	?	?

		16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
[illegible]	Aiglalosaurus	0	0	0	?	1	0	0	0	0	0	?	?	?	?	?
[illegible]	Paravaranus	0	0	0	0	?	0	0	0	0	0	0	0	?	?	0
[illegible]	Scincomorph	0	0	0	0	0&1	0	0	1	0	0	0&1	0	0&1	0	0
[illegible]	Iguania	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
[illegible]	Gekkota	0	0	0	9	0	9	1	0	1	3	1	0	0	0	0
[illegible]	Carusia	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0
[illegible]	Exostinus	1	1	?	?	?	?	0	0	?	?	1	?	?	?	?
[illegible]	Restes	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Necrosaurus	?	?	?	0	1	?	0	0	?	?	0	?	?	?	?
[illegible]	Bainguis	?	?	?	1	?	?	?	?	?	?	0	?	?	?	?
[illegible]	Proplaynotia	0	0	?	0	0	?	0	0	0	0	0	?	?	?	0
12	Parviderma	?	?	?	0	?	?	0	0	?	?	0	?	?	?	?
13	Gobiderma	0	0	0	0	0	0	0	0	0	1	1	0	0	?	0
14	Saniwides	0	0	0	0	1	0	0	0	0	0	0	0	?	?	0
15	Paraderma	?	?	?	?	?	?	0	0	?	?	1	?	?	?	?
16	Parasaniwa	?	?	?	?	?	?	0	0	?	?	0	?	?	?	?
17	Cherminotus	0	0	0	?	?	9	0	0	1	3	0	1	?	?	2
18	Eurheloderma	?	?	?	?	?	?	1	0	?	?	1	?	?	?	?
19	Lowesaurus	0	0	?	?	?	?	1	0	?	?	1	?	?	?	?
20	Heloderma	0	0	0	0	1	9	1	0	1	3	1	0	0	0	2
21	Saniwa	0	0	0	0	0	0	0	0	0	0	0	1	1	1	?
22	Telmasaurus	0	0	0	0	0&1	0	0&1	0	0	0	0	0	?	?	2
23	Varanus	0	0	1	0	1	0	0	0	0	0	0	1	1	1	2
24	Lanthanotus	0	0	1	0	1	9	1	2	1	3	0	1	1	1	2
25	Estesia	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0
26	Xenosaurus	1	1	1	0	1	1	0	0	0	0	1	0	0	0	1
27	Shinisaurus	1	1	1	0	1	1	0	0	0	0	0	0	0	0	1
28	Gerrhonotus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
29	Diploglossus	0	0	0	0&1	0&1	0	0	0	0	1	1	0	0	0	0
30	Ophisaurus	0	0	1	1	0	0	0	0	0	2	1	0	0	0	1
31	Anguis	0	0	0	1	0&1	0	0&1	0	0	2	1	0	0	0	1
32	Anniella	0	0	1	1	0	9	0	2	1	3	0	0	0	0	2
33	Primaderma	?	?	?	?	?	?	?	0	?	?	1	?	?	?	?
34	Parviraptor	?	?	?	?	?	?	0	?	?	?	1	?	?	?	?

	31	32	33	34	35	36	37	38	39	40	41	42	[illegible]	[illegible]	45
Aiglalosaurus	?	?	1	?	0	0	0	?	?	?	1	?	1	?	?
Paravaranus	0	1	1	?	?	?	0	0	?	?	1	1	1	?	0
Scincomorph	0&1	0	0	0	0	0&1	0	0	0	0	0	0	0	0	0
Iguania	0	0	0&1	0&1	0	0	0	0	0	0	0	0	0	0	0
Gekkota	0	0	0	0	0	0	0&1	0	0	0	0	0	0	0	0
Carusia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Exostinus	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0
Restes	?	?	?	?	?	?	?	?	?	0	0	0	0	0	0
Necrosaurus	?	?	1	?	?	?	0	?	?	1	1	1	?	0&1	0
Bainguis	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?
Proplaynotia	0	?	?	?	?	?	0	0	1	?	1	1	1	1	0
Parviderma	?	1	?	?	?	?	?	?	?	1	1	1	?	?	?
Gobiderma	0	1	0	1	0	1	0	0	1	1	1	1	1	1	?
Saniwides	0	1	1	?	1	0	0	0	1	1	1	1	1	1	0
Paraderma	?	?	?	?	?	?	1	?	1	1	1	1	?	1	0
Parasaniwa	?	?	?	?	?	?	?	?	?	1	1	1	?	1	0
Cherminotus	0	1	1	?	1	0	1	?	?	1	1	1	2	2	0
Eurheloderma	?	1	0	?	?	?	1	?	?	1	1	1	2	1	1
Lowesaurus	?	?	?	?	?	?	1	?	?	1	1	1	2	1	1
Heloderma	0	1	0	1	0	1	1	0	1	1	1	1	2	2	1
Saniwa	0	1	1	?	1	0	0	1	1	1	1	1	1	1	0
Telmasaurus	0	1	1	0	1	0	?	1	?	1	1	1	?	?	?
Varanus	1	1	1	1	1	0	0&1	1	1	1	1	1	2	1	0
Lanthanotus	1	1	1	1	1	0	1	1	1	1	1	1	2	1	0
Estesia	0	1	0	1	0	1	1	0	1	1	1	1	2	1	1
Xenosaurus	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Shinisaurus	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Gerrhonotus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Diploglossus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Ophisaurus	0	1	0	0	1	0	0	0	1	0	0	0	0	0&1	0
Anguis	0	1	0	0	1	0	0	0	1	0	0	0	1	2	0
Anniella	0	1	0	1	1	0	0	0	1	0	0	0	2	2	0
Primaderma	?	?	?	?	?	?	1	?	1	1	1	?	?	?	0
Parviraptor	?	?	1	0	?	?	0	?	?	0	0	0	0	0	0

	46	47	48	49	50	51	52	53	54	55	56	57	58	[illegible]	[illegible]
Aiglalosaurus	?	?	?	?	?	?	1	0	0	?	?	2	0	0	1
Paravaranus	?	1	?	2	1	1	?	0	?	?	?	?	?	0	1
Scincomorph	0	0	0	0	0	0	1	0&1	0	0	0	0	0&1	0	0
Iguania	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0&1
Gekkota	0	0&1	0	0&1	0	0	1	1	0	0&1	0	0	0	1	0
Carusia	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0
Exostinus	?	?	?	?	?	?	?	?	?	?	?	1	1	0	?
Restes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Necrosaurus	?	?	?	?	?	?	0	0	?	0	?	?	?	1	?
Bainguis	?	?	?	0	?	?	?	?	?	?	?	?	?	0	?
Proplaynotia	1	1	1	1	1	?	0	0	?	1	?	2	2	1	1
Parviderma	?	?	?	?	?	?	0	0	?	?	2	2	2	?	1
Gobiderma	1	1	1	2	1	1	0	0	1	1	2	2	2	1	1
Saniwides	1	1	?	1	1	1	0	0	?	1	2	2	2	1	1
Paraderma	1	?	?	?	?	?	?	?	?	?	2	2	?	1	?
Parasaniwa	?	?	?	?	?	?	?	0	?	?	2	2	2	1	?
Cherminotus	1	1	?	2	1	1	?	0	?	1	2	2	2	1	1
Eurheloderma	?	?	?	?	?	?	?	0	?	?	2	2	2	1	?
Lowesaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Heloderma	1	1	0	2	1	1	0	0&1	1	1	2	2	2	1	1
Saniwa	1	1	1	1	1	1	0	0	?	1	2	2	2	1	1
Telmasaurus	?	?	?	?	?	1	0	0	?	1	?	?	?	?	?
Varanus	1	1	1	2	1	1	1	1	0&1	1	2	2	2	1	1
Lanthanotus	1	1	1	2	0	1	0&1	0	0	1	2	2	2	1	1
Estesia	1	1	1	2	1	1	?	?	1	1	2	2	2	?	?
Xenosaurus	1	0	0	0	0	0	1	1	0	0	1	1	1	0	0
Shinisaurus	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0
Gerrhonotus	1	0	1	0	0	0	1	0&1	0	0	1	0	2	0	0
Diploglossus	1	0	1	0	0	0	1	1	0	0	1	0	2	0&1	0
Ophisaurus	1	0	1	0	0	0	0	0	1	0	1	0	2	0	0
Anguis	1	0	1	0	0	0	1	0&1	1	0	1	0	2	1	0
Anniella	0	1	1	1	0	0	1	1	1	1	1	0	2	1	0
Primaderma	?	?	1	?	?	?	?	?	?	?	?	?	?	1	?
Parviraptor	?	0	0	0	?	1	1	0	0	1	?	?	?	?	?

		61	62	63	64	65	66	67	68	69	70	71	72	73	74	75
1	Aigialosaurus	?	?	1	?	?	?	?	1	0	0	0	0	0	?	?
2	Paravaranus	?	?	?	2	?	?	1	?	?	?	?	?	?	?	?
3	Scincomorph	0	0	0&1	0	0	0	0	0	0	0	0	0&1	0&1	0&1	0
4	Iguania	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Gekkota	0	0	1	1	9	2	0	0	1	0	1	0	0	0	0
6	Carusia	0	1	0	0	0	1	1	0	0	0	0	2	1	1	0
7	Exostinus	?	1	0	0	0	1	?	?	?	?	?	2	1	?	?
8	Restes	?	?	?	?	?	?	?	?	?	?	?	2	1	?	?
9	Necrosaurus	?	1	?	2	0	1	?	?	?	?	?	1	0	1	?
10	Bainguis	?	?	?	2	?	?	?	?	?	?	?	1	0	1	?
11	Proplaynotia	1	?	1	2	0	1	1	1	0	0	?	1	0	?	?
12	Parviderma	1	?	1	2	0	1	1	1	?	?	?	1	1	1	?
13	Gobiderma	1	?	1	2	0	1	1	1	0	0	1	2	2	?	?
14	Saniwides	1	?	1	2	0	1	1	1	0	0	1	?	?	?	?
15	Paraderma	?	1	?	2	0	1	?	?	?	?	?	2	2	?	?
16	Parasaniwa	?	1	?	2	0	1	?	?	?	?	?	1	2	?	?
17	Cherminotus	1	?	1	2	?	1	1	1	0	0	?	?	?	?	?
18	Eurheloderma	?	1	?	2	0	1	?	?	?	?	?	2	2	?	?
19	Lowesaurus	?	1	?	?	?	?	?	?	?	?	?	2	2	?	?
20	Heloderma	1	1	1	2	0	1	1	1	0	0	1	2	2	0	1
21	Saniwa	1	?	1	2	?	1	1	1	0	0	1	?	?	1	?
22	Telmasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Varanus	1	1	1	2	0	1	1	1	0	0	1	1	2	1	1
24	Lanthanotus	1	1	1	2	0	1	1	1	0	0	1	1	2	0	1
25	Estesia	?	?	1	2	?	1	1	?	0	0	?	?	?	?	?
26	Xenosaurus	0	1	0	0	0	1	1	0	0	0	1	2	1	1	0
27	Shinisaurus	0	1	0	0	0	1	1	0	0	0	1	2	1	1	0
28	Gerrhonotus	0	1	0	2	1	1	1	0	1	1	1	1	0&1	1	0
29	Diploglossus	0	1	0	2	0	1	1	0	1	1	1	1	0	1	0
30	Ophisaurus	0	1	0	2	1	1	1	0	1	1	1	1	0	1	0
31	Anguis	0	1	0	2	1	1	1	0	1	1	1	1	0	1	0
32	Anniella	0	1	0	2	1	1	1	0	1	1	1	0	0	1	0
33	Primaderma	?	1	?	2	0	1	?	?	?	?	?	2	2	?	?
34	Parviraptor	?	1	?	2	?	1	?	?	?	?	?	?	?	?	?

		76	77	78	79	80	81	82	83	84	85	86	87	88	[illegible]	[illegible]
1	Aigialosaurus	?	?	?	1	1	1	?	2	?	?	?	?	?	?	?
2	Paravaranus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	Scincomorph	0	0	0	0	0	0	0	0&1	0	0	0&1	0	0	1	0&1
4	Iguania	0	0	0	0	0	0&1	0	0	0&1	0&1	0	0	0	0	0
5	Gekkota	0	0	0	0	0	0	0	0	0&1	0&1	1	0	0&1	0	0
6	Carusia	?	?	?	0	?	?	0	?	?	0	1	?	?	?	?
7	Exostinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8	Restes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9	Necrosaurus	?	1	0	0	?	?	1	1	?	?	?	?	?	?	?
10	Bainguis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2
11	Proplaynotia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	Parviderma	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Gobiderma	?	?	1	0	?	?	?	0	?	?	?	?	?	?	?
14	Saniwides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15	Paraderma	?	?	1	0	?	?	0	?	?	?	?	?	?	?	?
16	Parasaniwa	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?
17	Cherminotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Eurheloderma	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?
19	Lowesaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20	Heloderma	0	1	1	0	1	1	0	0	1	0	9	1	1	0	1
21	Saniwa	0	1	0	1	?	1	1	1	?	0	1	?	?	?	?
22	Telmasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Varanus	1	1	0	1	1	1	1	1	1	1	0&1	1	2	0	0&1
24	Lanthanotus	1	1	0	1	1	1	1	1	1	1	?	1	2	0	1
25	Estesia	?	?	1	0	?	?	0	?	?	?	?	?	?	?	?
26	Xenosaurus	0	2	0	0	1	1	0	0	0	0	0	0	0	0	1
27	Shinisaurus	0	2	0	0	0	0	0	0	0	0	1	?	0	0	1
28	Gerrhonotus	0	2	0	0	1	0	0	2	0	0	1	0	1	1	2
29	Diploglossus	0	2	0	0	1	0	0	2	0	0	1	0	1	1	2
30	Ophisaurus	0	2	0	0	1	0	0	2	0	0	0&2	0	1	1	2
31	Anguis	0	2	0	0	1	0	0	2	0	0	2	0	1	1	2
32	Anniella	2	2	0	0	1	0	0	2	9	9	2	1	9	1	2
33	Primaderma	?	1	?	0	?	?	?	?	?	?	?	?	?	?	?
34	Parviraptor	?	?	0	0	?	0	?	?	?	?	?	?	?	?	?

		91	92	93	94	95	96	97	98	99	100	101	102	103	104	105
1	Aigialosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
2	Paravaranus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
3	Scincomorph	?	0	0	0	0	0	1	0	0	0& 1	0	0	0	0& 1	0
4	Iguania	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	Gekkota	?	0& 1	0	0	0	0	0& 1	0	0	0	0	0	0	0	0
6	Carusia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
7	Exostinus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
8	Restes	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
9	Necrosaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
10	Bainguis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
11	Proplaynotia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	Parviderma	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
13	Gobiderma	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
14	Saniwides	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
15	Paraderma	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
16	Parasaniwa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
17	Cherminotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
18	Eurheloderma	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
19	Lowesaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
20	Heloderma	1	0	1	2	1	0& 1	1	1	0	2	1	1	1	1	0
21	Saniwa	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
22	Telmasaurus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
23	Varanus	1	1	1	2	1	1	2	0& 1	1	2	1	1	1	1	1
24	Lanthanotus	1	1	1	1	1	1	2	0	1	2	1	1	1	1	1
25	Estesia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
26	Xenosaurus	0	0	0	1	1	0	1	1	0	1	0	0	0	0	1
27	Shinisaurus	0	?	0	1	0	0	1	0	0	1	0	0	0	0	1
28	Gerrhonotus	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
29	Diploglossus	0	0	0	1	0	1	1	0	0	1	0	0	0	0	1
30	Ophisaurus	0	0	0	1	0	0	2	0	0	1	0	0	0	0	1
31	Anguis	0	0	0	1	0	0	2	0	0	1	0	0	0	0	1
32	Anniella	0	0	0	1	0	0	3	1	0	1	?	0	?	0	1
33	Primaderma	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
34	Parviraptor	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

CHAPTER FIVE

AN EXAMINATION OF MOSASAUROID INTERRELATIONSHIPS USING NEW INFORMATION FROM *AIGIALOSAURUS DALMATICUS* AND *AIGIALOSAURUS BUCCHICHI* (SQUAMATA: MOSASAUROIDEA)

INTRODUCTION

Bell and Polcyn (in press), the most recent examination of mosasauroid interrelationships, propose a new hypothesis of multiple evolutionary occurrences of paddle-like limbs throughout various mosasaurian lineages (Fig. 5-1). This new study supports previous suggestions (Bell 1993, 1997) that aigialosaur-grade taxa (specimens with mosasaurian cranial and/or caudal features but generalized terrestrial anguimorph limbs) represent a non-monophyletic assemblage. Several of these taxa, traditionally assumed to be basal mosasauroids, are hypothesized to be sister taxa to separate mosasaurian subfamilies. Additionally, *Aigialosaurus* (=*Opetiosaurus*) *bucchichi* and *A. dalmaticus* are consistently found to represent sequential sister taxa to all other mosasauroids.

Thorough reexamination of both *A. dalmaticus* (Dutchak and Caldwell submitted) and *A. bucchichi*, along with discovery and preparation of new anatomical data from *A. bucchichi*, have shown many of the character codings used for both of these taxa by Bell and Polcyn (in press) to be erroneous. By correcting these data and streamlining both the taxa and characters used in the matrix it is possible to test both the evolutionary hypothesis of multiple evolutionary occurences of paddle-like limbs of Bell and Polcyn (in press), and the monophyly of the aigialosaur-grade taxa.

MATERIALS AND METHODS

A character/taxon matrix composed of 31 taxa and 129 morphological characters was compiled. The matrix was analysed using the Heuristic algorithm of PAUP version

4.0b10 (Swofford 2002). A Bootstrap analysis was performed to determine relative support for inferred relationships. Several tests were performed by removing various taxa (taxonomic jacknifing) to determine which taxa introduced the most uncertainty into the analysis. All multistate characters were treated as unordered and all characters were left unweighted. The ACCTRAN (Accelerated Transformation) character optimization was used in order to identify synapomorphies for more inclusive clades as opposed to promoting convergence/homoplasy with the DELTRAN (Delayed Transformation) character optimization.

Characters

The characters used in this study were initially taken from a previous study of mosasauroid interrelationships (Bell and Polcyn in press). This matrix was initially composed of 41 taxa and 144 morphological characters. Ten taxa and 15 characters were either removed or combined, leaving 31 taxa and 129 characters. In addition to the removals and combinations, many character descriptions were modified in order to clarify the anatomical references. Numerous characters were recoded for *Aigialosaurus dalmaticus*, *A. bucchichi*, and the Trieste aigialosaur. A list of major changes made to the Bell and Polcyn (in press) matrix is visible in Appendix I and the character definitions are in Appendix II. The complete data matrix is found in Appendix III.

Outgroup

The hypothetical outgroup was taken from Bell (1997), and was in turn derived from Bell's (1993) outgroup. Bell (1993) constructed his outgroup by attempting to determine the interrelationships of mosasauroids within Squamata. Mosasauroids were coded as a single taxon and inserted into the data matrix of Estes et al. (1988). The resulting trees indicated that mosasauroids had their ancestry somewhere within Anguimorpha, although the entire group formed an unresolved polytomy. Bell (1993) then coded each terminal anguimorph taxon for each of the 151 characters to be used for the ingroup mosasauroid analysis (those 151 characters have been pared down to the 129 used in this study). These codings were done using extant anguimorph representatives as relatively complete specimens were required and the fossil taxa tend to be extremely fragmentary. The codings of the outgroup taxa were used to determine the polarity for the hypothetical outgroup used for the ingroup analysis. Where the outgroup taxa were polymorphic or could not be coded the characters were left unpolarized.

Ingroup

The purpose of this study is to examine the interrelationships of aigialosaurs within Mosasauroidea. To this end, only taxa that have been suggested to have mosasauroid affinities are included in the analysis. All of the character codings were drawn from Bell and Polcyn (in press), although numerous more derived taxa from that study were deemed to be superfluous and were combined with conspecific or congeneric taxa. Several taxa that have not been properly described in the literature (the "Trieste aigialosaur," "taxon novum," *Tylosaurus novum sp.*, *Ectenosaurus* "composite," *Clidastes novum sp.*) have been left in the matrix. Should any of these taxa ("taxon novum" especially) prove to be interesting with regards to basal mosasauroid interrelationships it is hoped that their descriptions in the literature will be expedited.

Specimen List

A list of specimens used to score the data matrix can be found in Bell (1993). Bell and Polcyn (in press) removed *Platecarpus somenensis* from their matrix as the material is not diagnostic. The specimens used to code taxa that have subsequently been added to the matrix by Bell and Polcyn (in press) are not identified in their analysis and thus are listed here: *Angolasaurus bocagei* (Lingham-Soliar 1994): SGMA 12-60, BMNH R11901-R11904; *Haasiasaurus gittelmani* (Polcyn et al. 1999): EJ693, EJ694, EJ696, EJ697, EJ698, EJ700, EJ701, EJ703, EJ704, EJ705; *Russellosaurus coheni* (Polcyn and Bell in press): SMU73056; *Tethysaurus nopcsai* (Bardet et al. 2003): MNHN GOU1, MNHN GOU2, MNHN GOU3; *Yaguarasaurus columbianus* (Páramo 1991): BRV 68.

Institutional Abbreviations

BMNH, British Muesum of Natural History, London, England; BRV, Colecciones paleontológicas del Departamento de Geociencias de la Universiad Nacional de Colombia, Bogota, Columbia; EJ, 'Ein Yabrud specimen, The Hebrew University, Jerusalem, Israel; MNHN, Muséum National d'Histoire Naturelle, Paris, France;

SGMA, Servicos de Geologia a Minas de Angola; SMU, Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas, USA.

RESULTS AND DISCUSSION

The following are the results of eleven taxonomic jackknife tests performed on the data matrix. Test one includes all taxa and characters. Test two excludes "taxon novum". Test three excludes *Aigialosaurus dalmaticus*. Test four excludes *A. bucchichi*. Test five excludes *Haasiasaurus gittelmani*. Test six excludes *Dallasaurus turneri*. Test seven excludes the "Trieste aigialosaur". Test eight excludes *Halisaurus*. Test nine excludes all undescribed specimens (the "Trieste aigialosaur", "taxon novum", *Tylosaurus novum sp.*, *Clidastes novum sp.*, and *Ectenosaurus* composite). Test ten excludes both *A. dalmaticus* and *A. bucchichi*. Test eleven assumes the monophyly of the genus *Aigialosaurus* and combines *A. dalmaticus* and *A. bucchichi* into a single taxon.

Test 1: All taxa included

Results- When the matrix of 31 taxa and 129 characters was run, PAUP retrieved 18 shortest cladograms of 354 steps with Consistency Indices (CI) of 0.463, Retention Indices (RI) of 0.734 and Homoplasy Indices (HI) of 0.537. The strict (Fig. 5-2) and Highest Percentage-rule (Fig. 5-3) consensus trees indicate that the taxonomic groupings are extremely robust across the 18 shortest trees with only three areas of uncertainty: the relationship of *Aigialosaurus dalmaticus* and *A. bucchichi* to each other, the relationship of *Clidastes moorevillensis* within clidastine mosasaurs, and the higher level relationships within russellosaurine mosasaurs.

The resolution at the base of the tree is much better than that achieved by Bell (1997) who found a basal polytomy involving a large number of taxa. The clade of (*Haasiasaurus gittelmani* (Trieste aigialosaur + *Halisaurus*)) is found to be the sister group to all other mosasauroids. *Aigialosaurus* and (*Dallasaurus turneri* + "taxon novum") are found to be sequential sister taxa to Natantia. Bell's (1997) Mosasaurinae remain intact with the aforementioned fluctuation within *Clidastes*. The internal relationships of the Russellosaurina are unstable, with *Ectenosaurus*, *Tylosaurus*, platecarpines and the clade of (*Tethysaurus* (*Yaguarasaurus* + *Russellosaurus*)) having uncertain affinities with one another.

A bootstrap test of 1000 replicates was run in order to estimate the confidence levels of the inferred relationships. The results of this test (Fig. 5-4) indicate that while several groupings (Mosasaurinae, tylosaurs, and Plotosaurini) are extremely robust, the relationships at the base of the tree are still relatively poorly supported.

Character Distribution Across the Preferred Tree

The following is a list of synapomorphies that support each of the clades found in the preferred shortest cladogram (Fig. 5-5). The numbers in brackets indicate the character number, the CI of the character, and the state change, respectively. Single arrows (→) indicate equivocal characters and double arrows (⇒) indicate unequivocal characters.

Mosasauroidea: all taxa in the analysis except the outgroup

Parietal epaxial muscle insertions both posterior and dorsal between suspensorial rami (18, 0.5, 0→1), parietal foramen ventral opening surrounded by a rounded, elongate ridge (21, 0.5, 0→1), jugal postero-ventral angle slightly obtuse, near 120 degrees (34, 0.667, 0⇒1), coronoid postero-medial process present (66, 0.2, 0→1), presence of zygosphenes and zygantra (83, 0.167, 0⇒1), absence of pisiforms (119, 0.5, 0→1).

Clade A: *Haasiasaurus gittelmani*, the Trieste aigialosaur, *Halisaurus*

Postero-dorsal process of maxilla present, but does not exclude the prefrontal from the narial opening (32, 0.167, 0→1), quadrate ventral condyle gently domed or convex (54, 0.25, 0→1), coronoid with expanded posterior wing (65, 0.333, 0⇒1), atlas neural arch with no notch in the anterior border (81, 0.333, 0→1), neural spines elongate behind middle of tail (95, 0.5, 0→1), head and trunk longer than tail (99, 0.5, 0→1), scapula about half the size of coracoid (100, 0.333, 0⇒1), scapula with distinct fan-shaped widening (101, 0.667, 0⇒1), scapula-coracoid not interdigitating (104, 0.5, 0→1), radiale small or absent (117, 0.5, 0⇒1), five or less carpals (118, 0.5, 0⇒1), pubic tubercle a thin semi-circular crest-like blade located close to the acetabulum (123, 0.5, 0→1), long ischiatic tubercle (124, 0.5, 0→1).

Clade B: the Trieste aigialosaur and *Halisaurus*

Quadrate suprastapedial process long, ending below the midpoint of the quadrate shaft (39, 0.4, 1⇒2), ridge on ventro-medial edge of suprastapedial process indistinct, straight and/or narrow (40, 0.25, 1⇒0), no projection of bone anterior to the first tooth on the dentary (61, 0.333, 1→0), dentary medial parapet strap-like, enclosing about half the height of the tooth attachment in a shallow channel (62, 0.667, 0→1), surangular-articular suture at midpoint of glenoid fossa on lateral edge (70, 0.333, 0→1), some synapophyses extend well below the ventral margin of the vertebral centrum (87, 0.333, 0→1), vertebral synapophysis dorsal ridge connecting synapophyses with prezygapophyses present on posterior trunk vertebrae (91, 0.333, 0→1), 30 or 31 presacral vertebrae (93, 0.667, 0→1), posterior emargination of scapula deeply concave (103, 0.5, 0→1), humerus about 1.5 to 2 times as long as wide at the distal tip (107, 0.6, 0→1), humerus delto-pectoral crest split into two separate insertion areas (110, 0.5, 0→1).

Clade C: *Aigialosaurus dalmaticus*, *A. bucchichi*, *Dallasaurus turneri*, "taxon novum", and Natantia.

Parietal posterior shelf absent (22, 0.333, 0→1), uniform curvature of quadrate ala, (47, 0.5, 0⇒1), long basioccipital tubera (57, 0.5, 0→1), 17-19 dentary teeth (60, 0.556, 0→1), strong and elevated tooth carinae (78, 0.5, 1→2), vertically oriented vertebral condyles (88, 0.333, 0⇒1), post-glenoid process of humerus distinctly enlarged (108, 0.5, 0→1).

Clade D (***Aigialosaurus***): *A. dalmaticus* and *A. bucchichi*

Postero-dorsal process of the maxilla absent (33, 0.5, 2→0), vertebral condyles essentially equidimensional (89, 0.5, 1→2).

Clade E: *Dallasaurus turneri*, "taxon novum", and Natantia

Very short premaxillary rostrum (1, 0.375, 0⇒1), frontal alae are rounded postero-laterally (11, 0.5, 0⇒1), parietal foramen close to, or barely touching fronto-parietal suture (20, 0.333, 0→1), tooth facets present (75, 0.333, 0⇒1), less than two sacral vertebrae (94, 0.5, 0⇒1), distal tip of radius broadly expanded (115, 0.667, 0→2), posterior thoracic vertebrae markedly longer than anterior thoracic vertebrae (129, 0.333, 0→1).

Clade F: *Dallasaurus turneri* and "taxon novum"

Internarial bar of premaxilla barely narrower than rostrum (2, 0.5, 0→1), premaxilla internarial bar dorsal keel present (4, 0.333, 0→1), entrance for the fifth cranial nerve removed posteriorly from rostrum (5, 0.333, 0→1), frontal with distinct narial embayment (9, 0.2, 0→1), all three ridges at fronto-parietal suture almost horizontal with one another (15, 0.5, 0→1), parietal epaxial musculature inserted posteriorly between suspensorial rami (18, 0.5, 1→0), presence of a distinct parietal shelf protruding posteriorly between suspensorial rami (22, 0.333, 1→0), vertebral synapophyses extend below ventral margin of vertebral centra (87, 0.333, 0⇒1), vertebral condyles laterally compressed (90, 0.333, 0→1).

Natantia: Mosasaurinae and Russellosaurina

Nasals absent (6, 0.333, 0⇒1), fronto-parietal suture with overlapping flanges (14, 1.0, 0⇒1), greatest width of parietal suspensorial rami is horizontal as opposed to vertical or oblique (23, 1.0, 0⇒1), forked distal tip of parietal sandwiches the tip of the supratemporal (24, 0.5, 0→1), 15-16 maxillary teeth (31, 0.5, 0→2), quadrate tympanic rim about 50-65% of height of quadrate shaft (50, 0.333, 0⇒1), distinct upward deflection of anterior edge of quadrate ventral condyle (55, 0.25, 0→1), dentary medial parapet equal in height to lateral wall of dentary (62, 0.667, 0⇒2), tooth replacement in "sub-dental crypts" (80, 0.333, 0→1), distinct fan-shaped widening of scapula (101, 0.667, 0⇒1), length and distal width of humerus virtually equal (107, 0.6, 0⇒2), humerus delto-pectoral crest split into two distinct insertion areas (110, 0.5, 0⇒1), humerus ectepicondyle present (113, 0.5, 0→1), humerus entepicondyle present (114, 0.5, 0⇒1), iliac crest elongate and cylindrical (122, 0.333, 0→1), appendicular epiphyses formed from thick unossified cartilage (126, 1.0, 0→1).

Mosasaurinae: *Clidastes liodontus*, *C. moorevillensis*, *C.* novum sp., *C. propython*, Plotosaurini, and Globidensini

Moderately protruding rostrum (1, 0.375, 1⇒2), supra-orbital crest of prefrontal present as a distinct overhanging wing (25, 1.0, 0⇒1), wide postorbitofrontal (28, 0.5, 0⇒1), maxillary-premaxillary suture terminates between the fourth and ninth maxillary tooth (32, 0.167, 0⇒1), jugal postero-ventral angle close to 90 degrees (34, 0.667, 1⇒2), pterygoid teeth arise from a thin pronounced vertical ridge (37, 1.0, 0⇒1), suprastapedial process of quadrate has a distinct dorsal constriction (40, 0.25, 1⇒0), coronoid with greatly expanded posterior wing (65, 0.333, 0⇒1), postero-medial process of coronoid present (66, 0.2, 1→0), high, thin surangular coronoid buttress rising rapidly posteriorly (69, 1.0, 0⇒1), vertebral condyles essentially equidimensional (89, 0.5, 1⇒2), vertebral synapophysis dorsal ridge connecting distal synapophysis with prezygapophysis on posterior trunk vertebrae (91, 0.333, 0⇒1), 32 or more presacral vertebrae (93, 0.667, 0⇒2), several dorsally elongate neural spines behind middle of tail (95, 0.5, 0⇒1), haemal arches about 1.5 times longer than neural arches (96, 1.0, 0⇒1), haemal arches fused to centra (97, 0.5, 0⇒1), head and trunk longer than tail (99, 0.5, 0→1), humerus ectepicondylar groove absent (112, 1.0, 0⇒1), ulna contacts centrale (116, 1.0, 0⇒1), pisiforms present (119, 0.5, 1→0), broadly expanded metacarpal I (120, 1.0, 0⇒1), astragalus lacks notch but has pedunculate fibular articulation (125, 1.0, 0→1), appendicular epiphyses missing or extremely thin (126, 1.0, 1→2).

Clade G: *Clidastes moorevillensis*, *C.* novum sp., *C. propython*, Plotosaurini, and Globidensini

Thick quadrate ala (45, 0.2, 0⇒1), slightly laterally compressed vertebral centra (90, 0.333, 0→1).

Clade H: *Clidastes moorevillensis* and *C.* novum sp.

Have 15-16 dentary teeth (60, 0.556, 1→2).

Clade I: *Clidastes propython*, Plotosaurini, and Globidensini

Frontal nearly triangular with relatively straight sides (7, 1.0, 0⇒1), coronoid medial wing contacts angular (67, 0.5, 0⇒1), presence of hyperphalangy (127, 0.5, 0→1).

Clade J: Plotosaurini and Globidensini

Maximum length to width ratio of frontal is less than or equal to 1.5:1 (8, 0.5, 2⇒0), frontal median flange is long (17, 0.333, 0→1), prefrontal contacts postorbitofrontal (26, 0.333, 0. ⇒1), squamosal ramus of postorbitofrontal reaches the end of the supratemporal fenestra (30, 0.333, 0⇒1), 17-19 maxillary teeth (31, 0.5, 2→1), coronoid posterior wing with distinct medial crescentic pit (68, 1.0, 0⇒1), no tooth facets (75, 0.333, 1→0), crowns of posterior marginal teeth are swollen near the tip or above the base (77, 0.333, 0→1), presence of tooth carinae serrations (79, 0.333, 0→1), coracoid neck gradually tapers to a relatively narrow base (105, 0.5, 0⇒1), anterior coracoid emargination present (106, 0.5, 0⇒1).

Clade K (Plotosaurini): *Mosasaurus* and *Plotosaurus*

Presence of premaxilla internarial bar dorsal keel (4, 0.333, 0⇒1), narrow postorbitofrontals (28, 0.5, 1⇒0), suprastapedial process of quadrate ends well above mid-height of quadrate shaft (39, 0.4, 1⇒0), thin quadrate ala (45, 0.2, 1⇒0), antero-dorsal rim of quadrate ala more tightly curved than the rest of the rim (47, 0.5, 1→0), presence of quadrate alar groove (49, 0.5, 0⇒1), quadrate central median ridge forms a broadly inflated dome around the stapedial pit (52, 1.0, 0⇒1), quadrate ventral median ridge diverges ventrally (53, 0.25, 0⇒1), quadrate ventral condyle is convex or domed (54, 0.25, 0⇒1), no upward deflection of the anterior edge of the quadrate ventral condyle (55, 0.25, 1⇒0), articular retroarcticular process inflection almost 90 degrees (71, 0.5, 0→1), presence of zygosphenes and zygantra (83, 0.167, 1→0), zygosphenes and zygantra present only on a few vertebrae (84, 0.333, 0→1), synapophyses of middle trunk vertebrae are distinctly laterally elongate (86, 0.5, 0→1), condyles of posterior trunk vertebrae are not higher than they are wide (90, 0.333, 1→0), length of cervical vertebrae equal to or greater than the longest trunk vertebra (92, 1.0, 0⇒1), extreme widening of the scapula (101, 0.667, 1→2), distal width of humerus slightly greater than the length of the shaft (107, 0.6, 2⇒3), glenoid condyle of humerus saddle-shaped, sub-triangular in proximal view, and depressed (109, 1.0, 0⇒1), phalanges are blocky and hourglass-shaped (121, 1.0, 0⇒1).

Clade L (Globidensini): *Globidens*, *Prognathodon overtoni*, *Plesiotylosaurus crassidens*, and *Prognathodon rapax*

Relatively inconspicuous midline dorsal keel of the frontal (10, 0.167, 0⇒1), prefrontal overlapped laterally by postorbitofrontal (27, 0.5, 0→1), presence of 13 maxillary teeth (31, 0.5, 1→4), quadrate suprastapedial process fused to an elaborated process from below (42, 0.333, 0⇒1), quadrate postero-ventral ascending rim is a high elongate crest (44, 0.5, 0⇒1), presence of 15-16 dentary teeth (60, 0.556, 1→2), tooth surfaces coarsely ornamented with bumps and ridges (74, 1.0, 0⇒1).

Clade M: *Prognathodon overtoni*, *Plesiotylosaurus crassidens*, and *Prognathodon rapax*

Premaxillary rostrum very short (1, 0.375, 2→1), anterior pterygoid teeth are large, approaching the size of the marginal teeth (38, 1.0, 0⇒1), strong, obtuse ridge present dorso-laterally on anterior face of quadrate ala (48, 1.0, 0⇒1), splenial-angular articulation is laterally compressed (63, 0.5, 2⇒1), glenoid condyle of humerus highly domed or protuberant (109, 1.0, 0⇒2).

Clade N: *Plesiotylosaurus crassidens* and *Prognathodon rapax*

Squamosal process of postorbitofrontal does not reach the end of the supratemporal fenestra (30, 0.333, 1⇒0), ventral condyle of quadrate gently domed (54, 0.25, 0⇒1).

Russellosaurina: *Tethysaurus nopscai*, *Yaguarasaurus columbianus*, *Russellosaurus coheni*, *Ectenosaurus sp.*, *Tylosaurus sp.*, *Platecarpus sp.*, *Angolasaurus bocagei*, and *Plioplatecarpus*

Frontal olfactory canal almost completely enclosed by descending process (12, 0.25, 0⇒1), presence of a tabular boss immediately anterior to the fronto-parietal suture (13, 0.5, 0⇒1), both lateral and medial flanges of frontal extended posteriorly at the fronto-parietal suture (16, 0.667, 1→2), parietal table is triangular with straight sides contacting in front of the suspensorial rami (19, 0.667, 0→1), parietal foramen well away from the fronto-parietal suture (20, 0.333, 1→0), ventral opening of parietal foramen is level with the main ventral surface (21, 0.5, 1→0), presence of transverse dorsal ridge on postorbitofrontal (29, 0.333, 0⇒1), squamosal ramus of postorbitofrontal reaches the end of the supratemporal fenestra (30, 0.333, 0⇒1), postero-dorsal process of maxilla does not prevent emargination of prefrontal on the narial opening (33, 0.5, 2⇒1), presence of postero-ventral process of jugal (35, 0.5, 0⇒1), stapedial pit of quadrate is extremely elongate with constricted middle (43, 0.4, 0→2), shallow alar concavity of quadrate conch (46, 0.333, 0⇒1), fan-shaped pterygoid process of basisphenoid (56, 1.0, 0⇒1), short basioccipital tubera (57, 0.5, 1→0), one to three large foramina present on the retroarticular process (72, 0.333, 0→1), teeth finely striate medially (73, 0.333, 1⇒0), extremely reduced atlas synapophysis (82, 0.5, 1→0), facets for rib articulation ovoid and shorter than the centrum height on posterior cervical and anterior trunk vertebrae (85, 0.5, 0→1), posterior portion of tail curved ventrally (98, 1.0, 0→1), humerus pectoral crest located medially (111, 1.0, 0→1), radiale small or absent (117, 0.5, 0→1), basilar artery exits basioccipital through two ventral foramina (128, 0.6, 0→1), posterior thoracic vertebrae not markedly longer than anterior thoracic vertebrae (129, 0.333, 1→0).

Clade O: *Tethysaurus nopscai*, *Yaguarasaurus columbianus*, and *Russellosaurus coheni*

Frontal ala tapers to a sharp point postero-laterally (11, 0.5, 1⇒0), triangular parietal table with posterior portion forming parasagittal crest (19, 0.667, 1→2), parietal suspensorial ramus overlaps supratemporal without interdigitation (24, 0.5, 1→0), ectopterygoid does not contact maxilla (36, 0.25, 0→1), no upward deflection of anterior edge of quadrate ventral condyle (55, 0.25, 1→0), canal for basilar artery enters basioccipital floor as a small pair (59, 0.75, 0⇒1), dentary does not have any projection of bone anterior to the first dentary tooth (61, 0.333, 1⇒0), dentary medial parapet is elevated and strap-like, enclosing about half the height of the tooth attachment in a shallow channel (62, 0.667, 2⇒1), splenial-angular articulation is laterally compressed (63, 0.5, 2⇒1), surangular articulates with articular in the middle of the glenoid on the lateral edge of the mandible (70, 0.333, 0⇒1), absence of tooth carinae (78, 0.5, 2→0), replacement teeth form in shallow excavations (80, 0.333, 1→0), synapophyses of middle trunk vertebrae are laterally elongate (86, 0.5, 0→1), some synapophyses extend below the ventral margin of the centrum on some cervical vertebrae (87, 0.333, 0→1), condyles of trunk vertebrae are inclined (88, 0.333, 1→0), condyles of anterior trunk vertebrae are extremely dorsoventrally depressed (89, 0.5, 1→0), scapula is about half the size of the coracoid (100, 0.333, 0→1), iliac crest is blade-like and points postero-dorsally (122, 0.333, 1→0).

Clade P: *Yaguarasaurus columbianus* and *Russellosaurus coheni*

Quadrate tympanic rim is almost as high as the quadrate shaft (50, 0.333, 1⇒0), presence of 15-16 dentary teeth (60, 0.556, 1→2), tooth carinae are present, but extremely weakly developed (78, 0.5, 0→1).

Clade Q: *Ectenosaurus sp., Tylosaurus sp., Platecarpus sp., Angolasaurus bocagei*, and *Plioplatecarpus*

Entrance of the fifth cranial nerve into the premaxilla removed posteriorly from rostrum (5, 0.333, 0→1), presence of 17-19 maxillary teeth (31, 0.5, 2→1), presence of 13 dentary teeth (60, 0.556, 1⇒4), dorsal margin of scapula very convex (102, 1.0, 1⇒0), posterior emargination of scapula deeply concave (103, 0.5, 0⇒1), scapula-coracoid suture lacks interdigitation (104, 0.5, 0⇒1), absence of ectepicondyle of humerus (113, 0.5, 1→0), pubic tubercle is a thin, semi-circular, crest-like blade located close to the acetabulum (123, 0.5, 0→1), basilar artery exits the basioccipital through two foramina on the antero-dorsal edge of the basisphenoid (128, 0.6, 1→3).

Clade R: *Ectenosaurus clidastoides* and "*E.* composite"

Presence of a distinct horizontal parietal shelf projecting posteriorly between the suspensorial rami (22, 0.333, 1→0), presence of a distinct dorsal constriction of the quadrate suprastapedial process (40, 0.25, 1⇒0), suprastapedial process of quadrate fused to an elaborated process below (42, 0.333, 0⇒1), postero-ventral ascending tympanic rim of quadrate present as a high or elongate crest (44, 0.5, 0⇒1), long and deep groove present in antero-lateral edge of quadrate ala (49, 0.5, 0→1), canal for basilar artery enters basioccipital floor as a single bilobate canal (59, 0.75, 0→3), splenial-angular articulation essentially smooth concavo-convex surfaces (63, 0.5, 2⇒0), posterior wing of coronoid greatly expanded (65, 0.333, 0⇒1), presence of tooth fluting (76, 0.5, 0⇒1), posterior thoracic vertebrae are markedly longer than the anterior thoracic vertebrae (129, 0.333, 0→1).

Clade S: *Tylosaurus sp.*, *Platecarpus sp.*, *Angolasaurus bacagei*, and *Plioplatecarpus*

Maximum length to width ratio of frontal less than or equal to 1.5:1 (8, 0.5, 2⇒0), presence of a distinct narial embayment on frontal (9, 0.2, 0⇒1), fairly low and inconspicuous midline dorsal keel of frontal (10, 0.167, 0→1), lateral flanges of frontal extended posteriorly (16, 0.667, 2→0), long frontal median ridge (17, 0.333, 0→1), presence of 13 maxillary teeth (31, 0.5, 1→4), ventral median ridge of quadrate diverges ventrally (53, 0.25, 0→1), zygosphenes and zygantra present on only a few vertebrae (84, 0.333, 0→1), facets for rib articulation are tall and narrow on posterior cervical and anterior trunk vertebrae (85, 0.5, 1→0), post-glenoid process of humerus absent or very small (108, 0.5, 1⇒0), five or fewer carpals (118, 0.5, 0⇒1).

Clade T: *Tylosaurus nepaeolicus*, *T. proriger*, and *T. novum sp.*

Large and inflated premaxillary rostrum (1, 0.375, 1⇒3), internarial bar of premaxilla barely narrower than rostrum (2, 0.5, 0⇒1), presence of dorsal keel on internarial bar of premaxilla (4, 0.333, 0⇒1), presence of nasals (6, 0.333, 1⇒0), frontal olfactory canal not embraced centrally by descending process (12, 0.25, 1⇒0), median flange of frontal extended posterior at fronto-parietal suture (16, 0.667, 0→1), parietal table generally rectangular to trapezoidal with sides converging but not meeting (19, 0.667, 1→0), parietal foramen close to or barely touching the fronto-parietal suture (20, 0.333, 0→1), prefrontal contacts postorbitofrontal (26, 0.333, 0⇒1), prefrontal overlapped laterally by postorbitofrontal (27, 0.5, 0→1), maxillary-premaxillary suture terminates between fourth and ninth maxillary teeth (32, 0.167, 0→1), ectopterygoid does not contact the maxilla (36, 0.25, 0→1), quadrate ala is thick (45, 0.2, 0→1), dentary has a bony anterior projection greater than or equal to the width of a single tooth space (61, 0.333, 1⇒2), presence of postero-medial process of coronoid (66, 0.2, 1→0), no large foramina on lateral face of retroarticular process (72, 0.333, 1→0), presence of 30 or 31 presacral vertebrae (93, 0.667, 0→1), scapula about half the size of the coracoid (100, 0.333, 0⇒1), no coracoid anterior emargination (106, 0.5, 0⇒1), humerus about 1.5 to 2.0 times longer than its' distal width (107, 0.6, 2⇒1), humerus entepicondyle absent (114, 0.5, 1⇒0), distal tip of radius slightly expanded (115, 0.667, 2⇒1), presence of hyperphalangy (127, 0.5, 0→1), absence of exit for basilar artery from basioccipital (128, 0.6, 3→0).

Clade U: *Tylosaurus nepaeolicus* and *T. proriger*

Base of premaxillary internarial bar is rectangular (3, 1.0, 0⇒1), oblique, median frontal, and parietal ridges almost horizontal at fronto-parietal suture (15, 0.5, 0⇒1), no transverse dorsal ridge on postorbitofrontal (29, 0.333, 1→0), single, thin, quadrate ventral median ridge (53, 0.25, 1→0), basioccipital tubera are antero-posteriorly elongate with rugose venro-lateral surfaces (58, 1.0, 0⇒1), presence of tooth carinae serrations (79, 0.333, 0⇒1), lack of zygosphenes and zygantra (83, 0.167, 1⇒0).

Clade V: *Platecarpus planifrons*, *P. tympaniticus* 600, *P. tympaniticus* 8769, *Angolasaurus bocagei*, and *Plioplatecarpus*

Entrance of the fifth cranial nerve into the premaxillary internarial bar close to the rostrum (5, 0.333, 1→0), presence of 12 maxillary teeth, (31, 0.5, 4→5), posterodorsal process of maxilla excludes the prefrontal from the dorsolateral rim of the narial opening (33, 0.5, 1⇒2), suprastapedial process of quadrate is long, ending distinctly below the mid-height of the quadrate shaft (39, 0.4, 1⇒2), stapedial pit of quadrate has a relatively narrow oval-shape (43, 0.4, 2⇒1), quadrate conch forms a deep bowl (46, 0.333, 1⇒0), quadrate tympanic rim is almost as high as quadrate shaft (50, 0.333, 1⇒0), quadrate ventral median ridge diverges ventrally (54, 0.25, 0⇒1), canal for basilar artery enters the basioccipital floor as a large pair (59, 0.75, 0⇒2), presence of 12 dentary teeth (60, 0.556, 4⇒5), atlas neural arch has no notch on the anterior border (81, 0.333, 0⇒1), presence of a short ischiatic tubercle (124, 0.5, 0→1).

Clade W: *Angolasaurus bocagei, Platecarpus tympaniticus* 600, *P. tympaniticus* 8769, and *Plioplatecarpus*

Postero-ventral ascending tympanic rim of quadrate is a high elongate crest (44, 0.5, 0⇒1), no bony projection of the dentary anterior to the first tooth (61, 0.333, 1⇒0), presence of distinct tongues and grooves on splenial-angular articular surfaces (64, 1.0, 0→1).

Clade X: *Platecarpus tympaniticus* 600, *P. tympaniticus* 8769, and *Plioplatecarpus*

Prefrontal contacts postorbitofrontal (26, 0.333, 0⇒1), suprastapedial ridge of quadrate is wide, broadly rounded, and curving downward, especially above the stapedial pit (41, 1.0, 0⇒1), dorsal median ridge of quadrate is a low, broadly inflated dome (51, 1.0, 0⇒1), canal for basilar artery enters the basioccipital floor as a single bilobate canal (59, 0.75, 2⇒3).

Clade Y: *Platecarpus tympaniticus* 8769, and *Plioplatecarpus*

Absence of a bony rostrum (1, 0.375, 1→0), parietal foramen close to or barely touching fronto-parietal suture (20, 0.333, 0→1), absence of zygosphenes and zygantra (83, 0.167, 1⇒0).

Discussion- This study was designed to test the interrelationships of basal mosasauroids. The results offer no support for a monophyletic grouping of aigialosaur-grade taxa, but the systematic positions of all taxa outside of Bell's (1993)

Natantia (defined as the most common ancestor of the Mosasaurinae and Russellosaurinae [here changed to Russellosaurina as per Polcyn and Bell {in press}] and all its descendents) are incredibly plastic. Bootstrap support for all branches outside of Natantia is below 50, with all branches except the Trieste aigialosaur/*Halisaurus* having bootstrap support values below 25. The inconclusive results are likely due to the poor and extremely partial preservation of most of the basal taxa and may be blamed as much on lack of data as homoplasy.

Aigialosaurus dalmaticus and *A. bucchichi* share only two equivocal characteristics that remove them from the (Natantia (*Dallasaurus turneri* + "taxon novum")) clade. Neither *A. dalmaticus* nor *A. bucchichi* can be scored for the shape of their vertebral condyles, and the presence of absence of a postero-dorsal process on the maxilla is difficult to determine in both species. The lack of autapomorphic characters within *Aigialosaurus* is likely responsible for the low bootstrap score of the monophyletic genus. This should not be seen as evidence that *A. dalmaticus* and *A. bucchichi* should retain a generic differentiation but instead as homoplasy caused by conservative morphology.

The *D. turneri*/"taxon novum" clade is also very poorly supported. While these two species have numerous equivocal characters indicating a possible close evolutionary relationship, both species are represented by extremely fragmentary specimens. Many of the equivocal characters uniting these two taxa are not present in one or the other. The placement of *D. turneri* outside of Natantia contradicts the placement of the taxon within the subfamily Mosasaurinae by Bell and Polcyn (in press); a taxonomic grouping that is not supported by any tests in this analysis.

The shift of *Halisaurus* to the base of the cladogram is a significant change from the tree suggested by Bell and Polcyn (in press) who consider the *Halisaurus*/Trieste aigialosaur clade to be nested as the sister group to the Russellosaurina. While the Trieste aigialosaur is still the sister taxon to *Halisaurus* in the current analysis, as suggested by Bell and Polcyn (in press), both taxa, along with *Haasiasaurus gittelmani*, are found to be the sister group to all other mosasauroids. This shift has once again nested all of the plesiopodal (terrestrial-limbed) taxa at the base of the tree, similar to the topology suggested by Bell (1997). The placement of *Halisaurus* at the base of the tree reduces the number of putative developments of paddle-like limbs from three, suggested by the preferred topology of Bell and Polcyn (in press) to two, once in *Halisaurus* and once within Natantia.

The topology of the preferred tree supports the validity of the clades Mosasauroidea, Natantia, Mosasaurinae (Bell 1997), and Russellosaurina (Polcyn and Bell in press). The family Mosasauridae, diagnosed by Bell (1993) to include the earliest common ancestor of *Halisaurus* and Natantia and all its descendants, becomes synonymous with the term Mosasauroidea due to placement of *Halisaurus* at the base of the tree.

Test 2: "taxon novum" excluded

Results- A heuristic search of 30 taxa and 129 characters retrieved 137 shortest trees with a length of 342 steps. The consistency index (CI) was 0.48, the retention index (RI) was 0.741 and the homoplasy index (HI) was 0.52. The strict consensus tree

(Fig. 5-6a) includes a basal polytomy of all remaining plesiopedal taxa and *Halisaurus*. The Highest Percentage Rule consensus tree (Fig. 5-6b) has the same general topology as the tree from test one, except *Aigialosaurus* has moved to the sister-taxon position with Natantia.

Discussion- The interrelationships of *Dallasaurus*, *Aigialosaurus dalmaticus*, and *A. bucchichi* remain unresolved. The inclusion of "taxon novum" appears to lend some stability to the tree (18 shortest trees when included, 137 when excluded) but the interrelationships of the basal taxa remain highly plastic regardless of the presence or absence of this taxon. "Taxon novum" was introduced into the original Bell (1993) data matrix and has been used in subsequent analyses (Bell 1997, Christiansen and Bonde 2002, Bell and Polcyn in press, Polcyn and Bell in press) despite the lack of a taxonomic diagnosis. The apparent position of this specimen near the base of the mosasauroid tree should encourage subsequent workers to study it in more detail.

Test 3: *Aigialosaurus dalmaticus* excluded

Results- A heuristic search of 30 taxa and 129 characters retrieved 30 shortest trees with a length of 352 steps. The consistency index (CI) was 0.463, the retention index (RI) was 0.729 and the homoplasy index (HI) was 0.537. The strict consensus (Fig. 5-7a) of the 30 shortest trees maintains the basal polytomy of plesiopodal taxa and *Halisaurus*. The Highest Percentage Rule consensus tree groups (Fig. 5-7b) *Aigialosaurus bucchichi* as the most basal mosasauroid, *Haasiasaurus* and

Dallasaurus as sequential sister taxa to the Trieste aigialosaur/*Halisaurus* clade, and "taxon novum" as the sister taxon to Natantia.

Discussion- This test indicates that the six characters for which *A. dalmaticus* can be scored but *A. bucchichi* cannot (characters 33, 58, 87, 88, 89, and 122) are instrumental in moving *Aigialosaurus* from the previously hypothesised basal position (Bell 1993, 1997, Bell and Polcyn in press) to the more derived position seen in this study. Three of these characters describe details of the vertebral column that are difficult to discern in *A. dalmaticus* and their systematic value should be treated with caution.

Test 4: *Aigialosaurus bucchichi* excluded

Results- A heuristic search of 30 taxa and 129 characters retrieved 21 shortest trees with lengths of 353 steps. The consistency index (CI) was 0.465, the retention index (RI) was 0.728 and the homoplasy index (HI) was 0.535. The strict consensus (Fig. 5-8a) maintains the basal polytomy seen in the other tests while the Highest Percentage Rule consensus tree (Fig. 5-8b) finds *Aigialosaurus dalmaticus*/*Dallasaurus* and *Haasiasaurus* to be the most basal sister groups to all other mosasauroids. The Trieste aigialosaur and *Halisaurus* continue to group together and "taxon novum" remains as the sister taxon to Natantia.

Discussion- The plesiopodal taxa and *Halisaurus* continue to have very plastic interrelationships near the base of the tree. The lack of significant change in tree statistics indicates that the presence or absence of *A. bucchichi* does not cause enormous amounts of instability among other taxa and thus that it should not be considered a keystone taxon in the analysis.

Test 5: *Haasiasaurus gittelmani* excluded

Results- A heuristic search of 30 taxa and 129 characters retrieved 15 shortest trees with lengths of 348 steps. The consistency index (CI) was 0.471, the retention index (RI) was 0.733 and the homoplasy index (HI) was 0.529. The strict consensus tree (Fig. 5-9a) shows "taxon novum" to be the sister taxon to all other mosasauroids, followed by the Trieste aigialosaur/*Halisaurus* clade and an *Aigialosaurs dalmaticus*, *A. bucchichi*, and *Dallasaurus* polytomy. The Highest Percentage Rule consensus tree (Fig. 5-9b) retrieves a paraphyletic *Aigialosaurus*, with *A. dalmaticus* being the sister group to Natantia.

Discussion- Removal of *Haasiasaurus* has a moderate effect on the interrelationships of the basal taxa in the analysis. This is the only test that resulted in *Aigialosaurus dalmaticus* and *A. bucchichi* representing sequential sister taxa to Natantia. The plasticity amongst the basal taxa is again in evidence as "taxon novum" jumps from the sister taxon to Natantia when all taxa are included, to the most basal mosasauroid when *Haasiasaurus* is removed.

Test 6: *Dallasaurus turneri* excluded

Results- A heuristic search of 30 taxa and 129 characters retrieved 61 shortest trees with lengths of 350 steps. The consistency index (CI) was 0.469, the retention index (RI) was 0.734 and the homoplasy index (HI) was 0.531. The strict consensus tree (Fig. 5-10a) shows no resolution among the basal taxa. The Highest Percentage Rule consensus (Fig. 5-10b) shows *Aigialosaurus dalmaticus/A. bucchichi* to be the sister group to all other mosasauroids and (*Haasiasaurus* (Trieste aigialosaur/*Halisaurus*)) and "taxon novum" to be sequential sister taxa to Natantia.

Discussion- Once again there is fluctuation among the basal taxa with the exception of the Trieste aigialosaur/*Halisaurus* clade. The absence of *Dallasaurus* has little effect on the stability of the tree, likely due to the specimen being so fragmentary (70.5% of data is coded as missing in the matrix).

Test 7: The Trieste aigialosaur excluded

Results- A heuristic search of 30 taxa and 129 characters retrieved 255 shortest trees with lengths of 352 steps. The consistency index (CI) was 0.466, the retention index (RI) was 0.732 and the homoplasy index (HI) was 0.534. The strict consensus tree (Fig. 5-11a) shows that the basal polytomy has been reduced to *Aigialosaurus dalmaticus*, *A. bucchichi*, and *Dallasaurus*. *Haasiasaurus* is found to be the sister taxon to Natantia and both *Halisaurus* and "taxon novum" are nested within Natantia. The Highest Percentage Rule consensus tree (Fig. 5-11b) has essentially the same topology as the strict consensus, but resolves a poorly supported non-monophyletic grouping of the genus *Aigialosaurus*.

Discussion- This is the only test that resulted in trees that even remotely resemble the preferred topology of Bell and Polcyn (in press) although, contrary to the findings presented here, in that study *Halisaurus* was found to be more closely related to russellosaurines than to mosasaurines. It appears that only its apparently close affiliation with the Trieste specimen keeps *Halisaurus* out of Natantia in other tests.

The Trieste specimen cannot be scored for 76% of the characters in the matrix and thus is very poorly diagnosed. Its position within the tree should be viewed with skepticism; however, the apparently close relationship with Halisaurus has drastic implications on limb evolution and origins scenarios and thus the taxon should be considered extremely important for future work in mosasauroid systematics. A detailed analysis and description of the Trieste aigialosaur is underway (A. Palci pers. comm.) that may allow for a better understanding of where the Trieste aigialosaur fits within Mosasauroidea.

Test 8: *Halisaurus* excluded

Results- A heuristic search of 30 taxa and 129 characters retrieved 27 shortest trees with lengths of 330 steps. The consistency index (CI) was 0.497, the retention index (RI) was 0.754 and the homoplasy index (HI) was 0.503. The strict consensus tree (Fig. 5-12a) shows *Haasiasaurus* nested with russellosaurs and *Dallasaurus* as the sister taxon to the Mosasaurinae. All other plesiopedal taxa form a basal polytomy with the Mosasaurinae + *Dallasaurus* and the Russellosaurina. The Highest Percentage Rule consensus tree (Fig. 5-12b) indicates that without *Halisaurus* there is no ambiguity as to where *Haasiasaurus* and *Dallasaurus* appear in the tree and that the Trieste aigialosaur is the sister taxon to all other mosasauroids.

Discussion- The presence of *Dallasaurus* and *Haasiasaurus* as the sister taxa to Mosasaurinae and *Tethysaurus*/*Yaguarasaurus*/*Russellosaurus* respectively would indicate three separate evolutionary occurrences of paddle-like limbs within Mosasauridae. Because the basal specimens lack so much data (an average of almost 60%) their plasticity allows them to group with any number of taxa, making the inclusion of *Dallasaurus* and *Haasiasaurus* in Natantia extremely unlikely. The Homoplasy Index is considerably lower than in any of the previous tests as *Halisaurus* is a relatively well known genus that possesses many classic mosasaurian features (not the least of which is paddle-like limbs); thus removal of *Halisaurus* eliminates numerous character reversals from the tree.

Test 9: All undescribed taxa ("the Trieste aigialosaur", "taxon novum", *Clidastes novum sp.*, *Tylosaurus novum sp.*, and *Ectenosaurus* composite) excluded

Results- A heuristic search of 26 taxa and 129 characters retrieved 48 shortest trees with lengths of 325 steps. The consistency index (CI) was 0.505, the retention index (RI) was 0.730 and the homoplasy index (HI) was 0.495. The strict consensus tree (Fig. 5-13a) indicates a basal polytomy of all plesiopedal taxa with *Halisaurus* being the sister taxon to all other hydropedal taxa. The clade of *Yaguarasaurus*, *Russellosaurus* and *Tethysaurus* falls out of the russellosaurs. The Highest Percentage Rule consensus (Fig. 5-13b) resolves a monophyletic *Aigialosaurus* as the sister group to all other mosasauroids.

Discussion- Numerous taxa were included in Bell's (1993) original matrix and have persisted throughout various subsequent analyses (Bell 1997, Christiansen and Bonde 2002, Bell and Polcyn in press). This test was designed to determine the extent of the effect of these unnamed taxa on the outcome of the analysis. The removal of the unnamed specimens did reduce the Homoplasy Index, but the resolution at the base of the tree remains extremely poor.

The topologies of the consensus trees of this test are the only results through this entire analysis that support Bell's (1993) taxonomic definition of Mosasauridae as a group of all hydropedal taxa to the exclusion of all plesiopedal taxa. All other results see hydropedal (*Halisaurus*) and plesiopedal taxa mixed amongst one another at the base of the mosasauroid tree. The position of *Halisaurus* as the sister taxon to Natania supports the findings of Bell (1997) and similarly contradicts the findings of Bell and Polcyn (in press) who placed *Halisaurus* as the sister taxon to Russellosaurina. Also of note is the movement of the *Yaguarasaurus*/*Russellosaurus*/*Tethysaurus* clade to the sister group position to Natantia. This change indicates the newly designated Russellosaurina (Polcyn and Bell in press) may not be robust.

The results of this test highlight the importance of having taxa described in the literature, making them available for common usage. With so few basal mosasauroid specimens available it is essential to the understanding of mosasauroid systematics that specimens such as the Trieste aigialosaur and "taxon novum" be as well understood as possible.

Test 10: *Aigialosaurus dalmaticus* and *A. bucchichi* excluded

Results- A heuristic search of 29 taxa and 129 characters retrieved 19 shortest trees with lengths of 348 steps. The consistency index (CI) was 0.468, the retention index (RI) was 0.727 and the homoplasy index (HI) was 0.532. The strict consensus tree (Fig. 5-14a) indicates a basal polytomy with "taxon novum" and a clade of all other plesiopedal taxa + *Halisaurus*. The Highest Percentage Rule consensus (Fig. 5-14b) resolves "taxon novum" as the most basal mosasauroid and a clade of *Haasiasaurus*/*Dallasaurus*/Trieste aigialosaur/*Halisaurus* as the sister group to Natantia.

Discussion- Removal of both *Aigialosaurus* specimens was designed to test whether these two specimens were causing a lack of resolution in the trees. It turns out that resolution is marginally increased at the base of the tree thanks to the removal of two taxa that have relatively conservative morphologies. The results of this test are as close as any of the tests come to recovering a monophyletic grouping of aigialosaur-grade taxa, but the close affinity of the Trieste aigialosaur and *Halisaurus* negates any possibility of retrieving a monophyletic plesiopodal grouping.

Test 11: Combination of *Aigialosaurus dalmaticus* and *A. bucchichi* into a single taxon

Results- A heuristic search of 30 taxa and 129 characters retrieved 6 shortest trees with lengths of 354 steps. The consistency index (CI) was 0.463, the retention index (RI) was 0.728 and the homoplasy index (HI) was 0.537. The strict consensus tree (Fig. 5-15a) has the same topology as the preferred tree from the first test with *Aigialosaurus* as the sister group to *Dallasaurus*/ "taxon novum" + Natantia. The Highest Percentage Rule consensus tree (Fig. 5-15b) shows the only variation in the tree is within *Clidastes* and the russellosaurs.

Discussion- Combining the two *Aigialosaurus* specimens tested whether the five characters that differentiate *A. dalmaticus* from *A. bucchichi* were resulting in any instability in the output trees. The resulting tree topology is exactly the same as that from the first test, indicating that the two *Aigialosaurus* specimens are not causing any instability.

CONCLUSIONS

The tree topologies resulting from this analysis indicate that it is possible that paddle-like limbs evolved twice in mosasaurs: once among halisaurs and once within Natantia. This contradicts the evolutionary scenario suggested by Bell and Polcyn (in press). The preferred tree topology supports many clades (Mosasauroidea, Natantia, and Mosasaurinae) delineated by Bell (1993, 1997), but also indicates the family Mosasauridae, as currently diagnosed, is a nonn-monophyletic taxon.

The results of the systematics tests show no support for a monophyletic assemblage of aigialosaurian taxa. Instead, plesiopedal taxa in various combinations appear to form consecutive sister taxa to Natantia. The exception to this rule is *Halisaurus* which is found to be the sister taxon to the Trieste aigialosaur. The suggestion of Bell and Polcyn (in press) to rediagnose the family Aigialosauridae to include only members of the genus *Aigialosaurus* is the only way to make 'aigialosaurs' a monophyletic group. Obviously this diagnosis would be of little use when attempting to discuss the larger picture of mosasauroid interrelationships, so it is suggested here that the terms 'plesiopodal' and 'hydropodal', as introduced by Polcyn and Bell (in press) should be used in place of 'aigialosaur-grade' and 'mosasaur-grade' in future discussions on this topic.

The Trieste aigialosaur is found to be the basal taxon that introduces the most instability into the analysis due to its apparent close relationship with *Halisaurus*. This relationship has great implications for scenarios of limb evolution and mosasauroid origins and represents an excellent starting point for future researchers.

Contrary to Bell and Polcyn (in press) *Dallasaurus turneri* is not a basal taxon within Russellosaurina, but is instead found to be a basal mosasauroid whose relationship outside of Natantia remains unresolved. The interrelationships of all basal taxa remain problematic as there is a large amount of missing data for these specimens. Because of this lack of data any suggestions regarding the relationships of the basal taxa in this analysis should be treated as tentative until further investigations are conducted.

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Estes, R., De Quieroz, K. and Gauthier, J., 1988. Phylogenetic relationships within Squamata. In: Estes, R. and Pregill, G. (eds.): Phylogenetic Relationships of the Lizard Families. Stanford University Press (Stanford):119-281.

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FIGURE 5-1. The preferred tree topology of Bell and Polcyn (in press) retrieved from a Heuristic search of 41 taxa and 144 characters. Tree length = 412 steps, C.I.= 0.4296, R.I.= 0.7572, and H.I.= 0.5704.

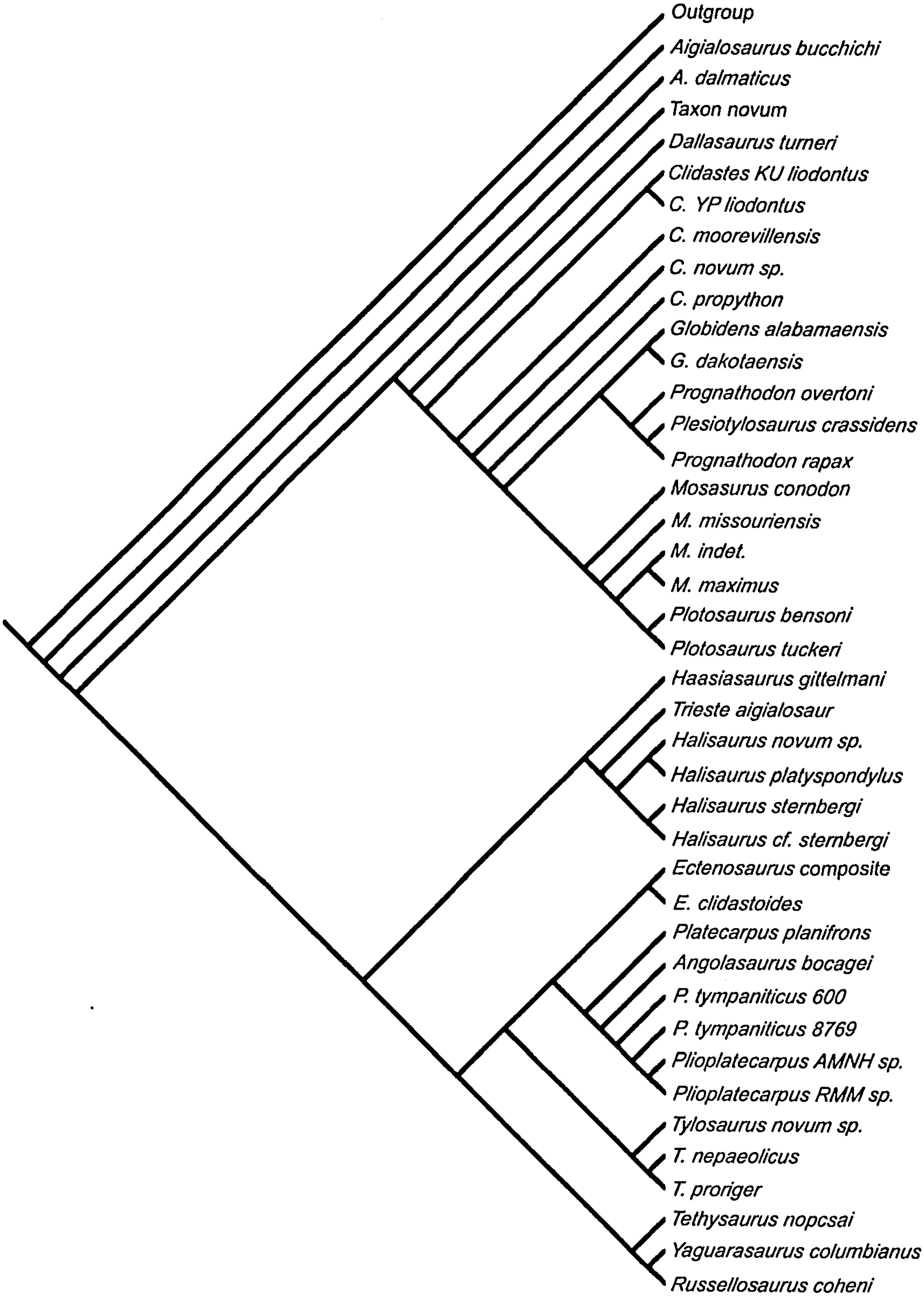

Outgroup
Aigialosaurus bucchichi
A. dalmaticus
Taxon novum
Dallasaurus turneri
Clidastes KU liodontus
C. YP liodontus
C. moorevillensis
C. novum sp.
C. propython
Globidens alabamaensis
G. dakotaensis
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Mosasaurus conodon
M. missouriensis
M. indet.
M. maximus
Plotosaurus bensoni
Plotosaurus tuckeri
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus novum sp.
Halisaurus platyspondylus
Halisaurus sternbergi
Halisaurus cf. sternbergi
Ectenosaurus composite
E. clidastoides
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus AMNH sp.
Plioplatecarpus RMM sp.
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni

FIGURE 5-2. Test 1. The strict consensus tree constructed from the 18 shortest cladograms of 354 steps (31 taxa and 129 characters).

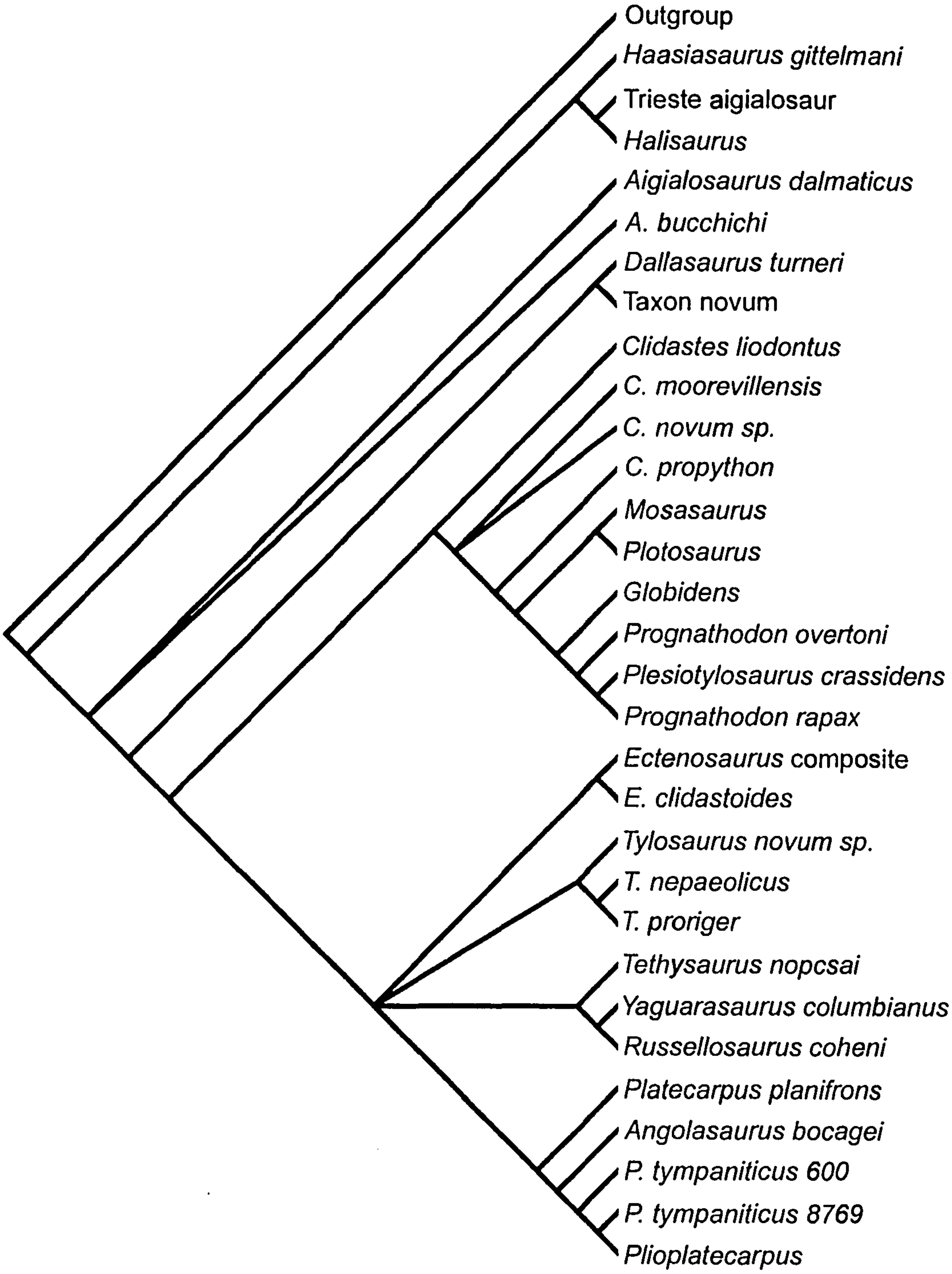

Outgroup
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-3. Test 1. The Highest Percentage Rule consensus tree constructed from the 18 shortest cladograms of 354 steps (31 taxa and 129 characters). Unless otherwise indicated, branch support for each node is 100.

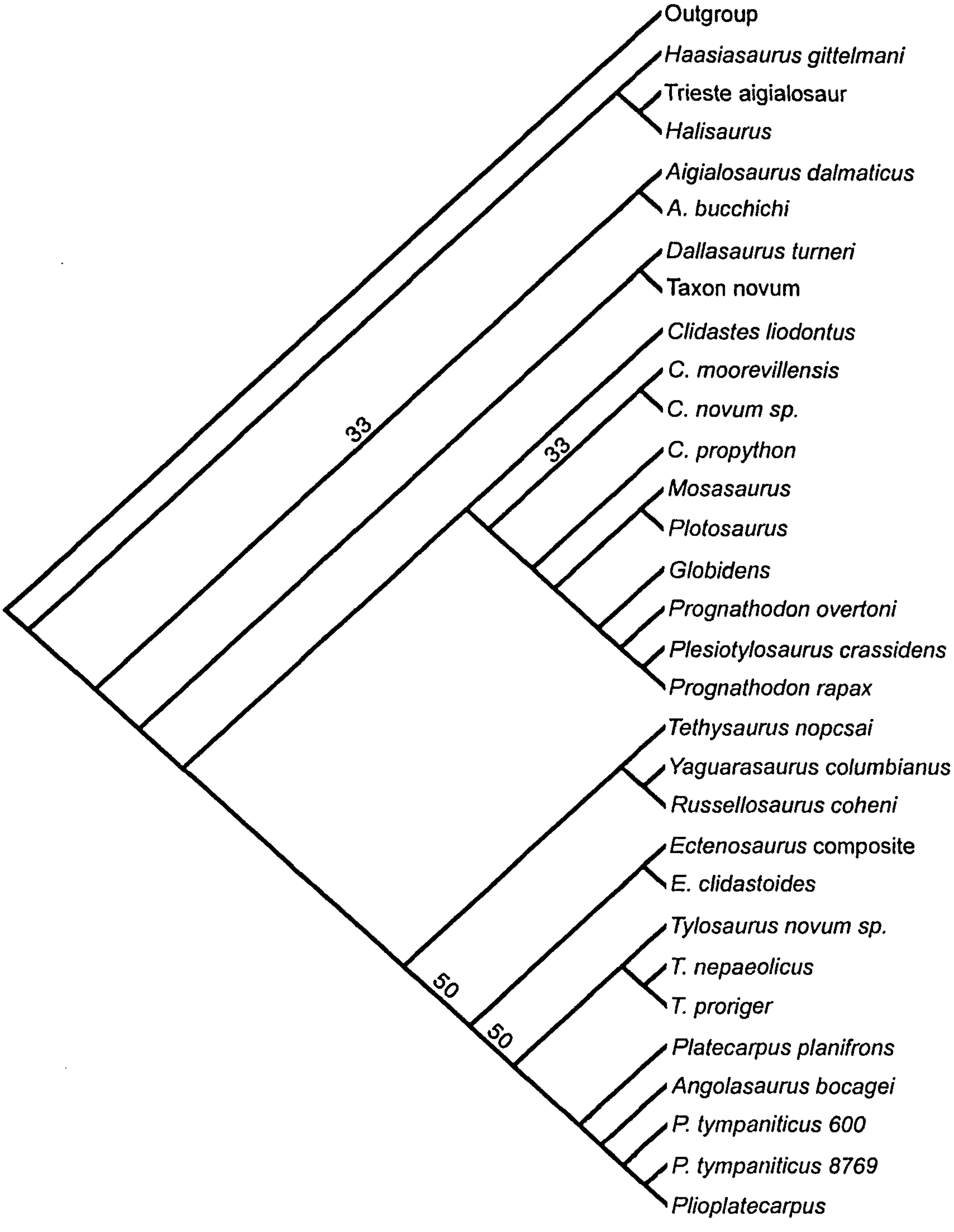

Outgroup
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
33
33
50
50

FIGURE 5-4. Test 1. Tree showing support values retrieved from a 1000 replicate bootstrap test.

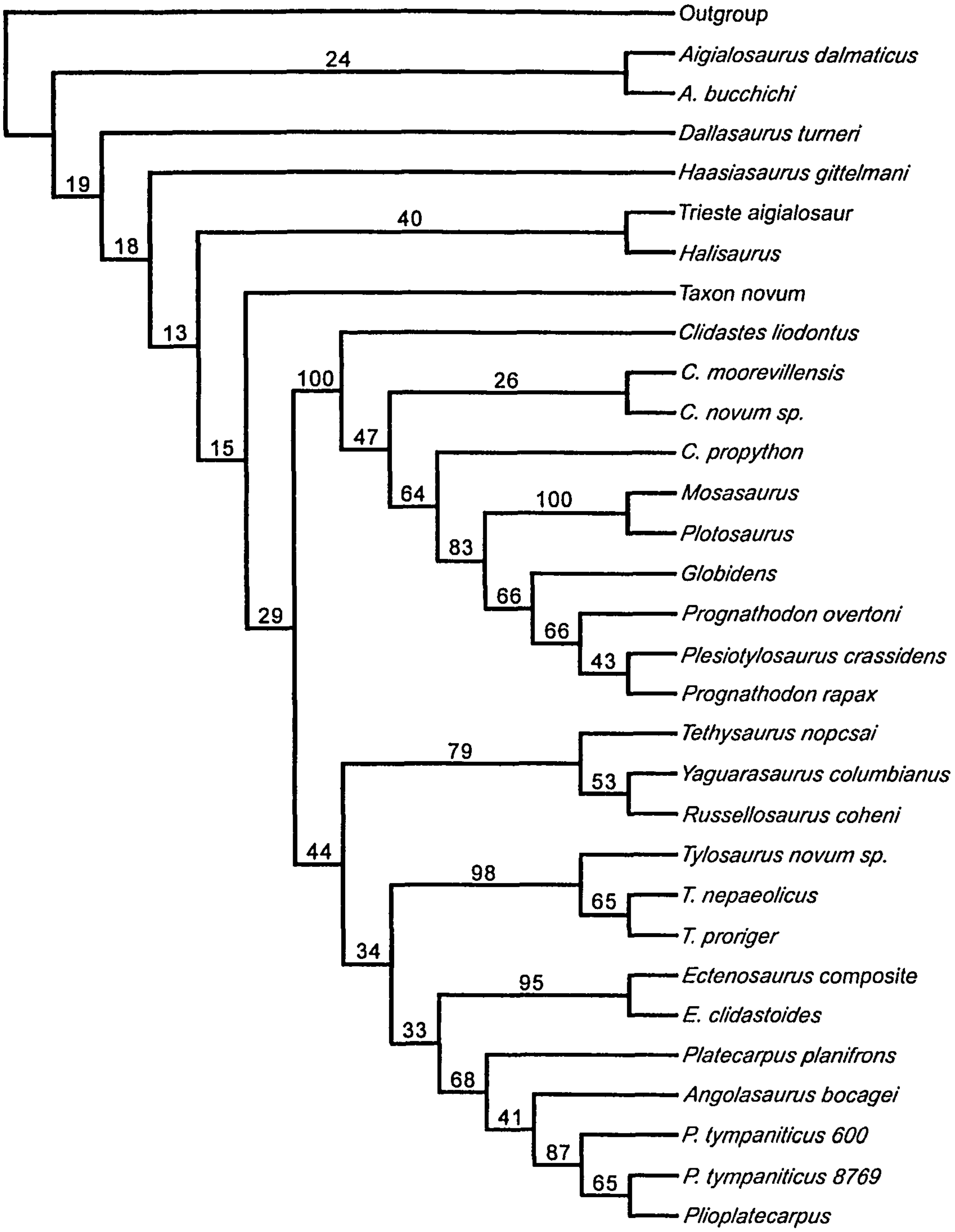

Outgroup
24
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
19
Haasiasaurus gittelmani
18
40
Trieste aigialosaur
Halisaurus
13
Taxon novum
Clidastes liodontus
100
26
C. moorevillensis
C. novum sp.
15
47
C. propython
64
100
Mosasaurus
Plotosaurus
83
Globidens
66
Prognathodon overtoni
66
43
Plesiotylosaurus crassidens
29
Prognathodon rapax
79
Tethysaurus nopcsai
53
Yaguarasaurus columbianus
Russellosaurus coheni
44
98
Tylosaurus novum sp.
65
T. nepaeolicus
T. proriger
34
95
Ectenosaurus composite
E. clidastoides
33
Platecarpus planifrons
68
Angolasaurus bocagei
41
P. tympaniticus 600
87
65
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-5. Test 1. Preferred shortest tree topology (354 steps, C.I.= 0.463, R.I.= 0.734, H.I.= 0.537) from heuristic search of 31 taxa and 129 characters. Character state changes for each labeled node are listed in text.

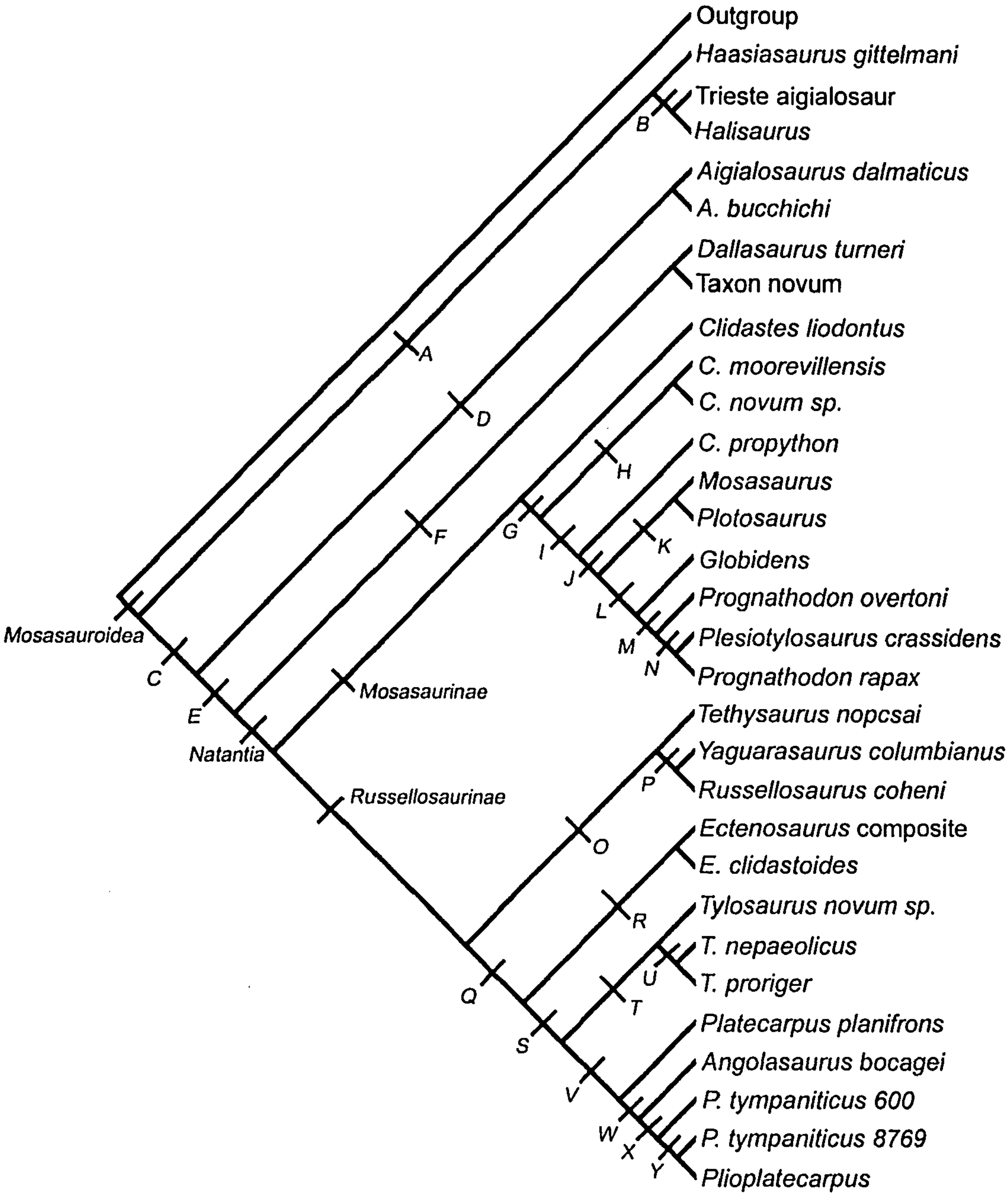
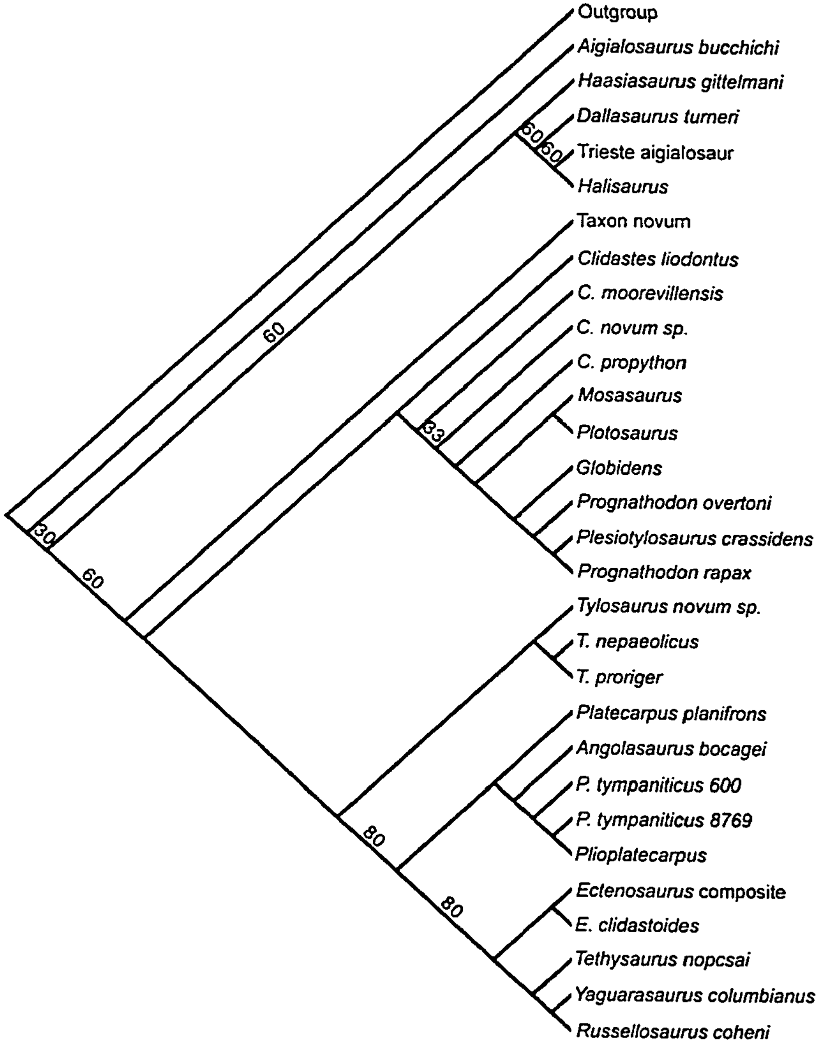

Outgroup
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Mosasauroidea
Natantia
Mosasaurinae
Russellosaurinae
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y

FIGURE 5-6. Test 2. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 137 shortest cladograms (length= 342 steps, C.I.= 0.480, R.I.= 0.741, H.I.= 0.520) retrieved from a Heuristic search of 30 taxa and 129 characters from which "taxon novum" was excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Dallasaurus turneri
Aigialosaurus dalmaticus
A. bucchichi
Clidastes liodontus
C. moorevillensis
C. taxon novum
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus composite
E. clidastoides
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
80
86
26
34
80
34
93
54
54


Outgroup
Aigialosaurus dalmaticus
A. bucchichi
Trieste aigialosaur
Dallasaurus turneri
Haasiasaurus gittelmani
Halisaurus
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-7. Test 3. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 30 shortest cladograms (length= 352 steps, C.I.= 0.463, R.I.= 0.729, H.I.= 0.537) retrieved from a Heuristic search of 30 taxa and 129 characters from which *Aigialosaurus dalmaticus* was excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Aigialosaurus bucchichi
Haasiasaurus gittelmani
Dallasaurus turneri
Trieste aigialosaur
Halisaurus
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus composite
E. clidastoides
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
60
30
60
60
60
33
80
80

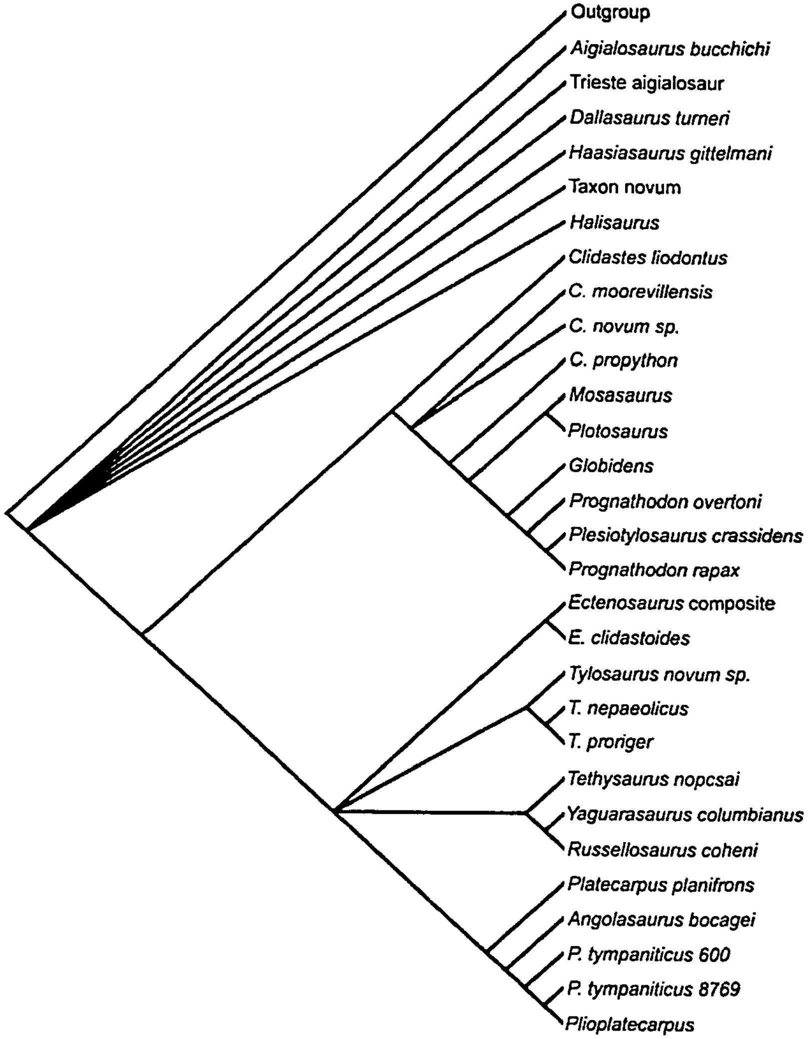
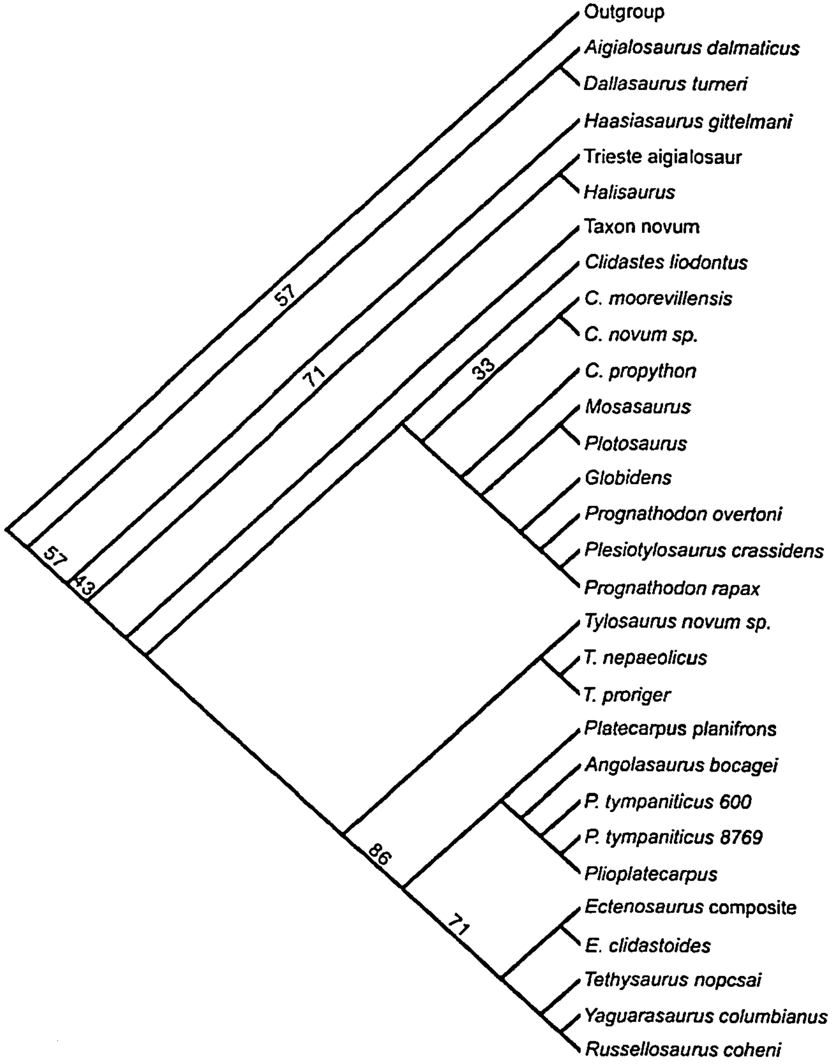
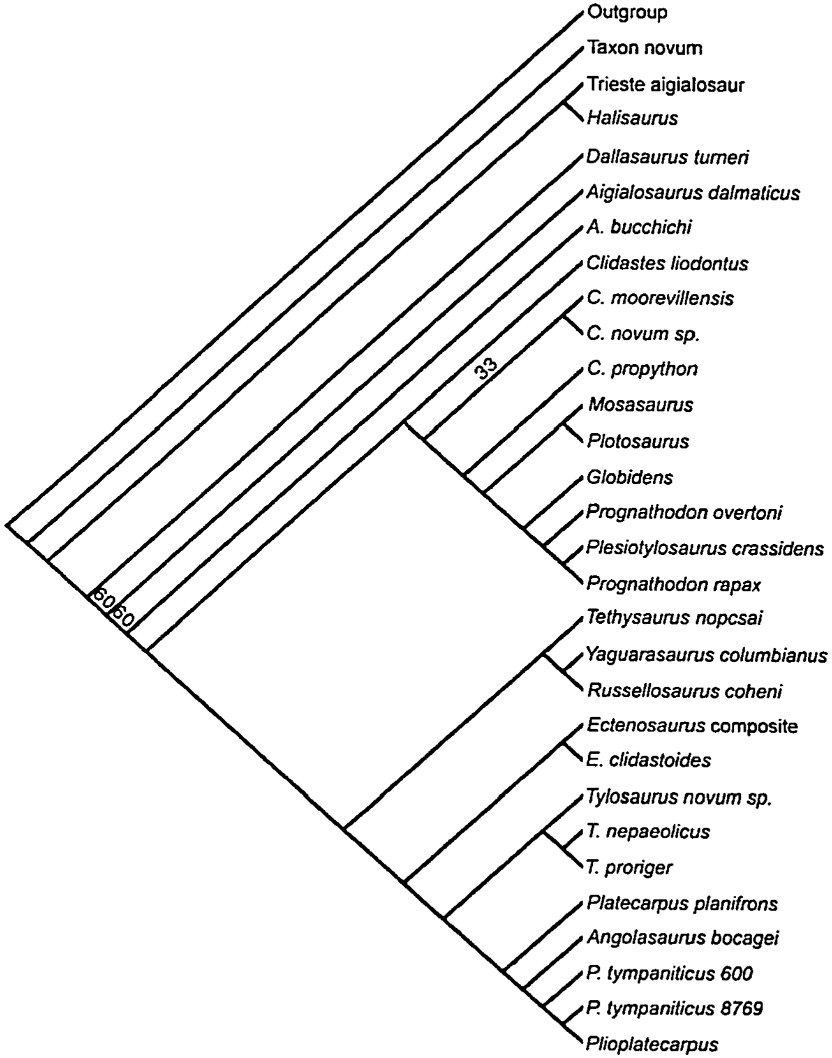

Outgroup
Aigialosaurus bucchichi
Trieste aigialosaur
Dallasaurus turneri
Haasiasaurus gittelmani
Taxon novum
Halisaurus
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-8. Test 4. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 21 shortest cladograms (length= 353 steps, C.I.= 0.465, R.I.= 0.728, H.I.= 0.535) retrieved from a Heuristic search of 30 taxa and 129 characters from which *Aigialosaurus bucchichi* was excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Aigialosaurus dalmaticus
Dallasaurus turneri
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus composite
E. clidastoides
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
57
71
33
57
43
86
71

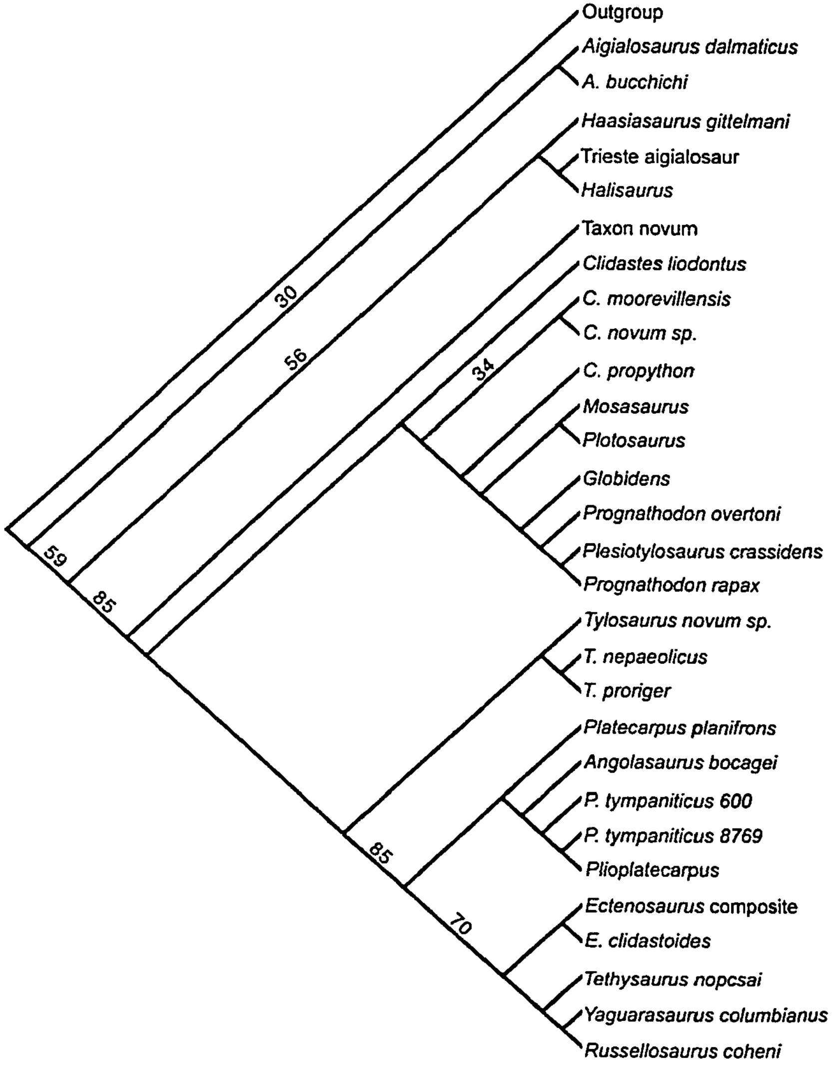

Outgroup
Aigialosaurus dalmaticus
Trieste aigialosaur
Dallasaurus turneri
Haasiasaurus gittelmani
Halisaurus
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-9. Test 5. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 15 shortest cladograms (length= 348 steps, C.I.= 0.471, R.I.= 0.733, H.I.= 0.529) retrieved from a Heuristic search of 30 taxa and 129 characters from which *Haasiasaurus gittelmani* was excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Taxon novum
Trieste aigialosaur
Halisaurus
Dallasaurus turneri
Aigialosaurus dalmaticus
A. bucchichi
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
33
60
60


Outgroup
Taxon novum
Trieste aigialosaur
Halisaurus
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-10. Test 6. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 61 shortest cladograms (length= 350 steps, C.I.= 0.469, R.I.= 0.734, H.I.= 0.531) retrieved from a Heuristic search of 30 taxa and 129 characters from which *Dallasaurus turneri* was excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Aigialosaurus dalmaticus
A. bucchichi
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus composite
E. clidastoides
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
30
56
34
59
85
85
70


Outgroup
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
Taxon novum
Trieste aigialosaur
Halisaurus
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-11. Test 7. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 255 shortest cladograms (length= 352 steps, C.I.= 0.466, R.I.= 0.732, H.I.= 0.534) retrieved from a Heuristic search of 30 taxa and 129 characters from which “the Trieste aigialosaur” was excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Aigialosaurus bucchichi
A. dalmaticus
Dallasaurus turneri
Haasiasaurus gittelmani
Halisaurus
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Taxon novum
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Ectenosaurus composite
E. clidastoides
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
60
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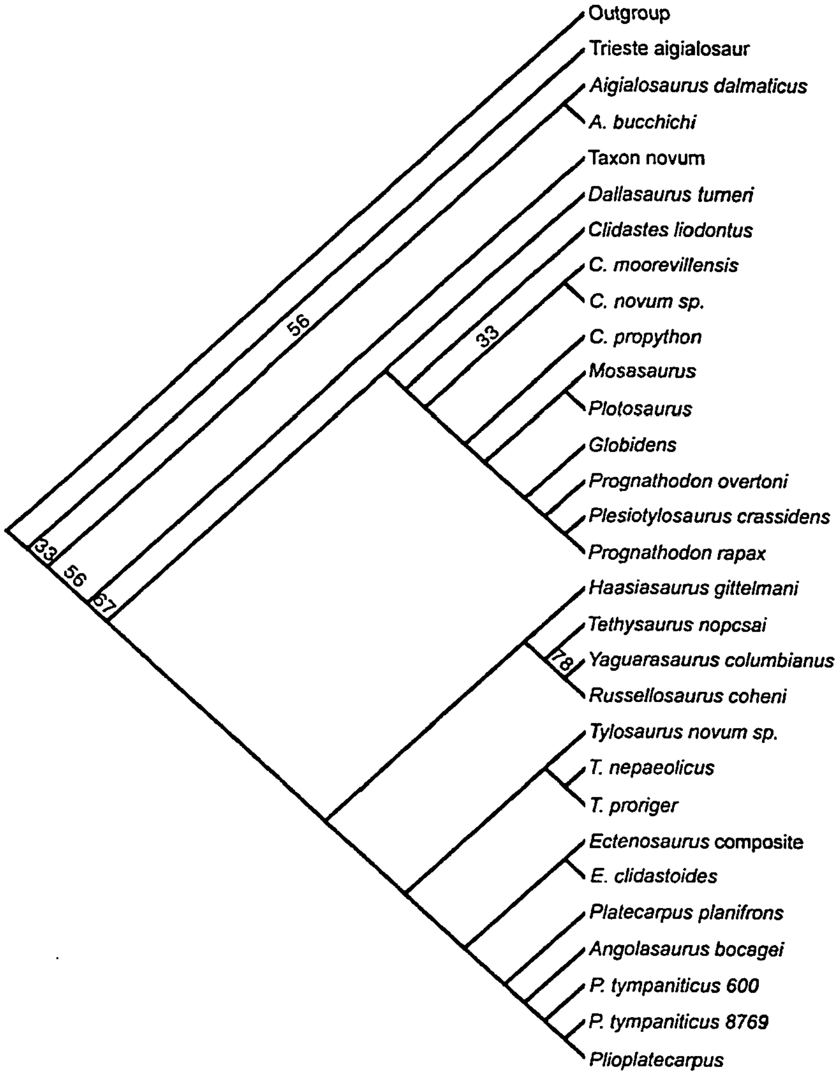
82


Outgroup
Aigialosaurus bucchichi
A. dalmaticus
Dallasaurus turneri
Haasiasaurus gittelmani
Taxon novum
Halisaurus
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Ectenosaurus composite
E. clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopcsai
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-12. Test 8. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 27 shortest cladograms (length= 330 steps, C.I.= 0.497, R.I.= 0.754, H.I.= 0.503) retrieved from a Heuristic search of 30 taxa and 129 characters from which *Halisaurus* was excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Trieste aigialosaur
Aigialosaurus dalmaticus
A. bucchichi
Taxon novum
Dallasaurus turneri
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Haasiasaurus gittelmani
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Ectenosaurus composite
E. clidastoides
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
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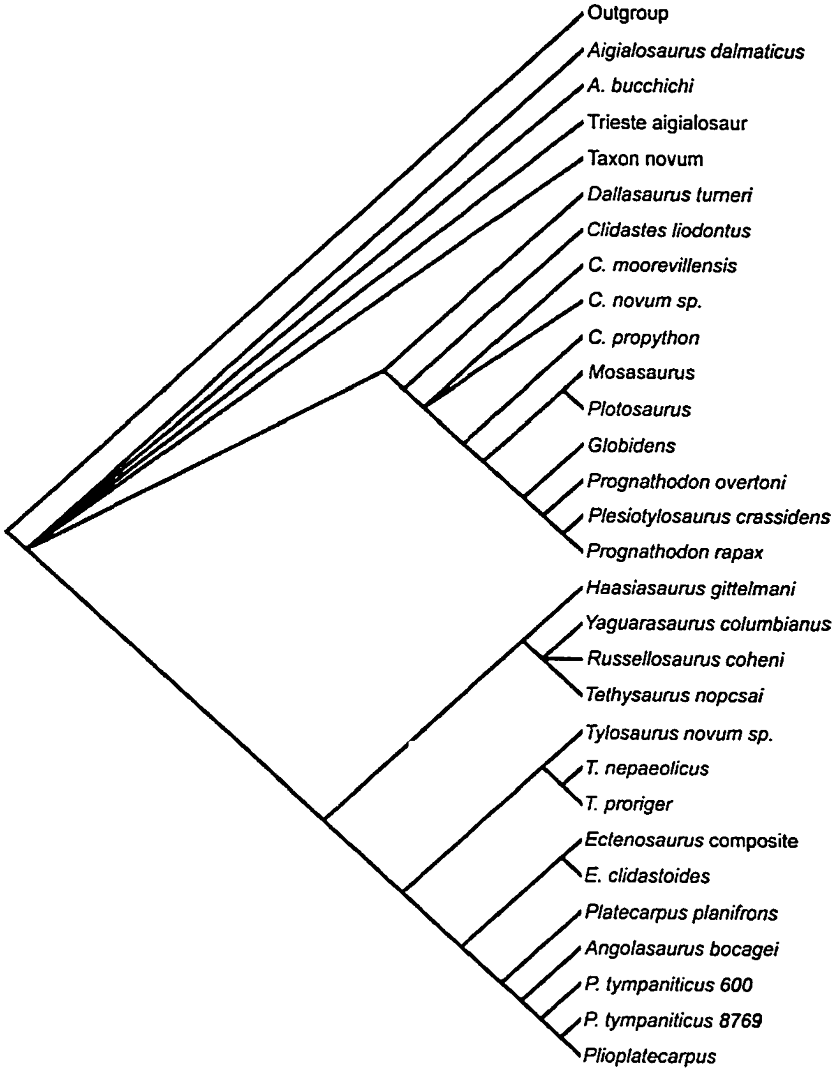

Outgroup
Aigialosaurus dalmaticus
A. bucchichi
Trieste aigialosaur
Taxon novum
Dallasaurus turneri
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Haasiasaurus gittelmani
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopcsai
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Ectenosaurus composite
E. clidastoides
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

FIGURE 5-13. Test 9. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 48 shortest cladograms (length= 325 steps, C.I.= 0.505, R.I.= 0.730, H.I.= 0.495) retrieved from a Heuristic search of 26 taxa and 129 characters from which “taxon novum”, *Clidastes* novum sp., *Tylosaurus* novum sp., *Ectenosaurus* composite, and “the Trieste aigialosaur” were excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
Haasiasaurus gittelmani
Halisaurus
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopcsai
Tylosaurus nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus clidastoides
Clidastes liodontus
C. moorevillensis
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
25
38
62
33
50
50

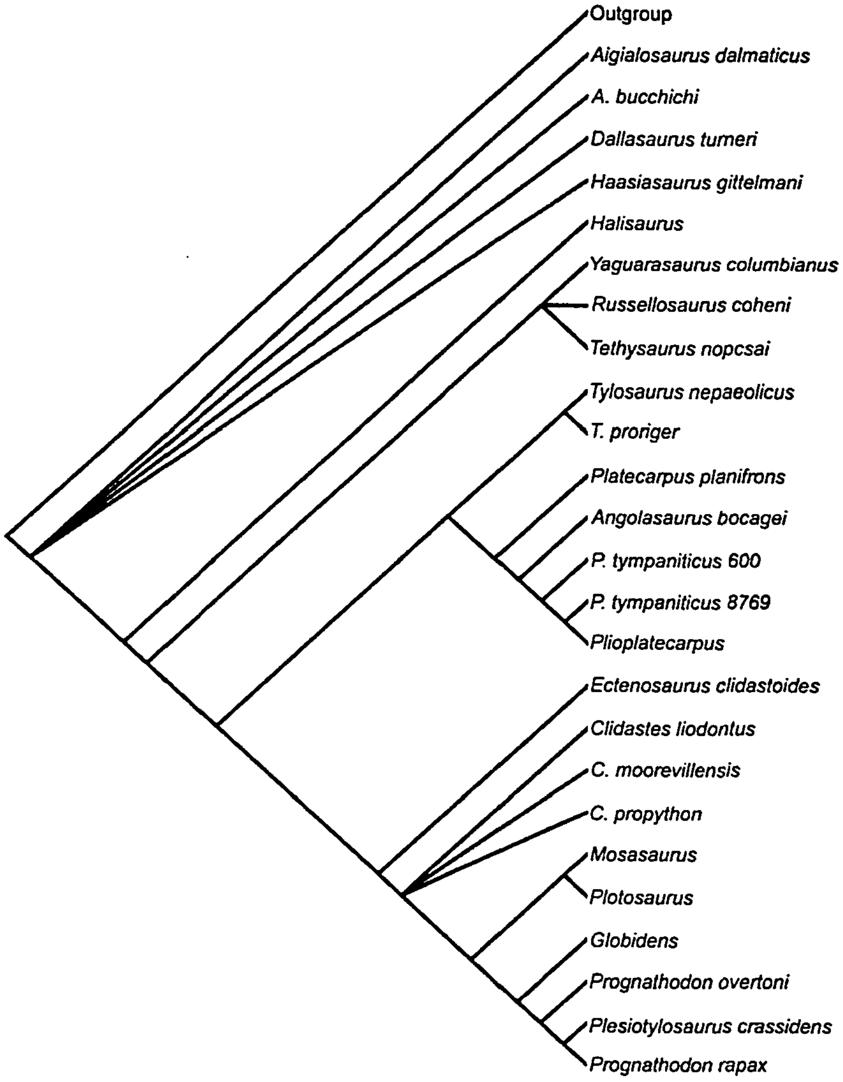
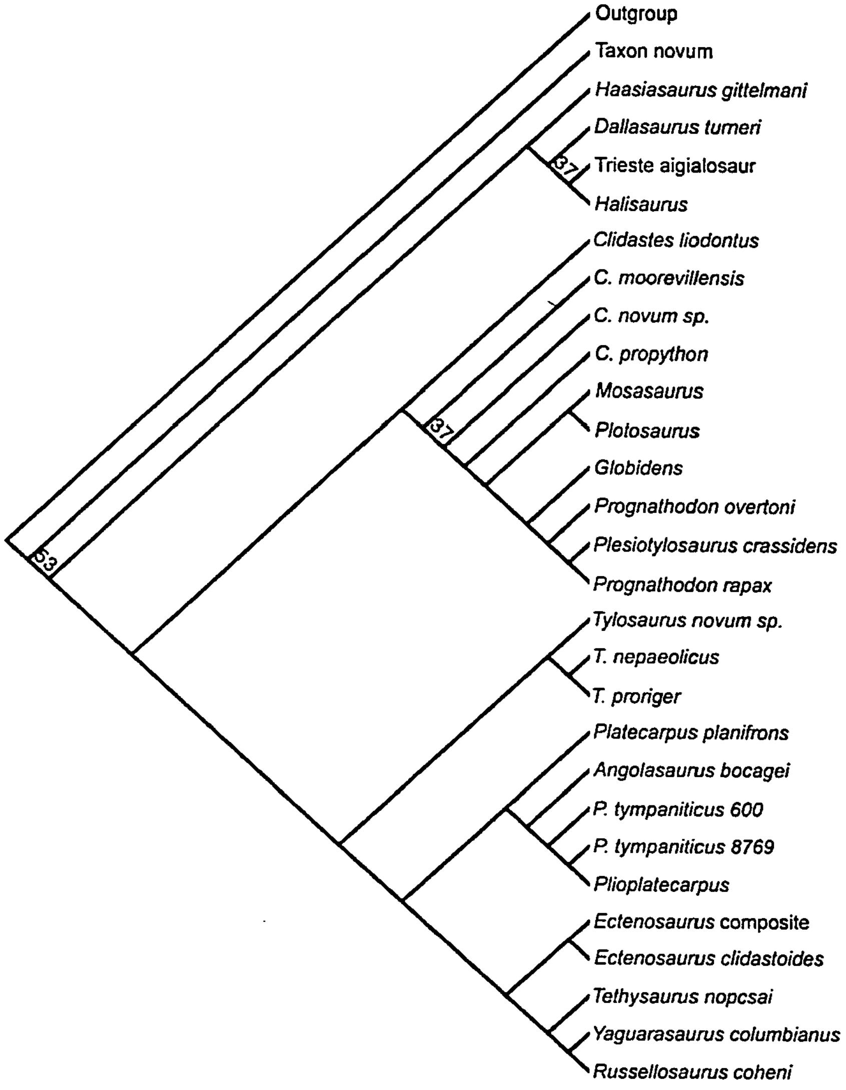

Outgroup
Aigialosaurus dalmaticus
A. bucchichi
Dallasaurus turneri
Haasiasaurus gittelmani
Halisaurus
Yaguarasaurus columbianus
Russellosaurus coheni
Tethysaurus nopcsai
Tylosaurus nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus clidastoides
Clidastes liodontus
C. moorevillensis
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax

FIGURE 5-14. Test 10. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 19 shortest cladograms (length= 348 steps, C.I.= 0.468, R.I.= 0.727, H.I.= 0.532) retrieved from a Heuristic search of 29 taxa and 129 characters from which *Aigialosaurus dalmaticus* and *A. bucchichi* were excluded. All branch supports are 100 except where otherwise indicated.


Outgroup
Taxon novum
Haasiasaurus gittelmani
Dallasaurus turneri
Trieste aigialosaur
Halisaurus
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus composite
Ectenosaurus clidastoides
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
53
37
37

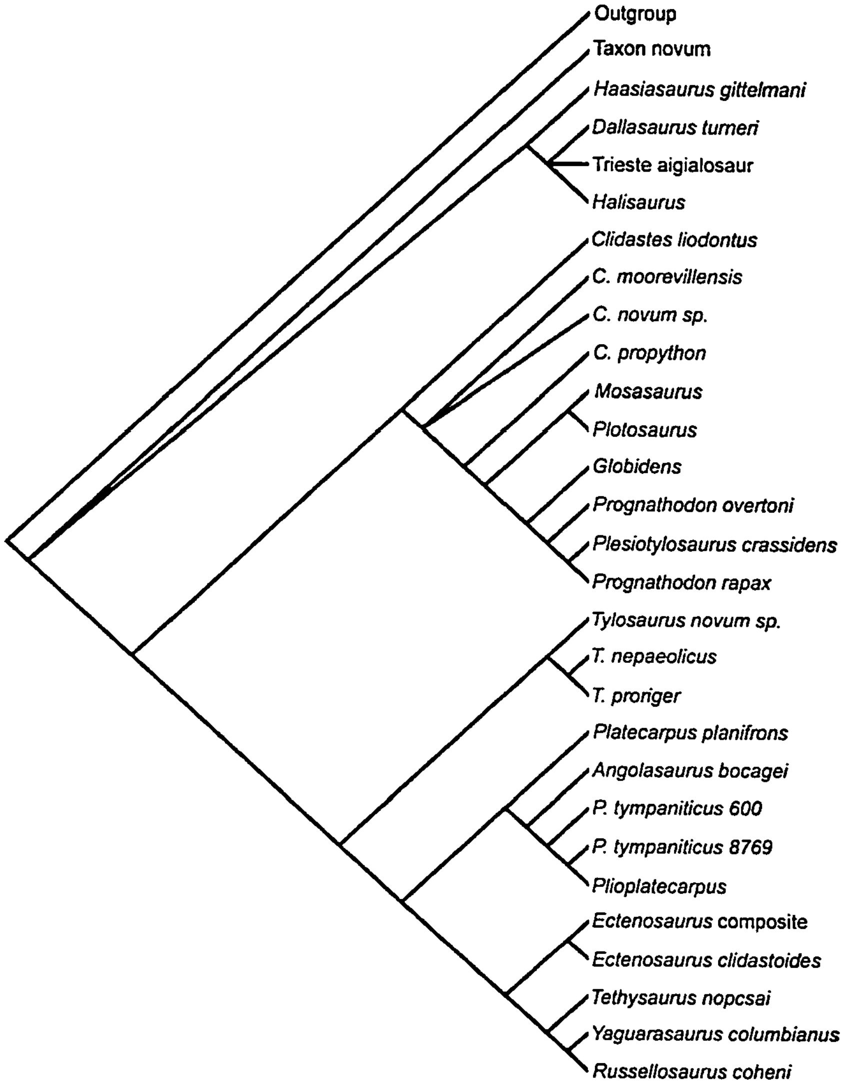
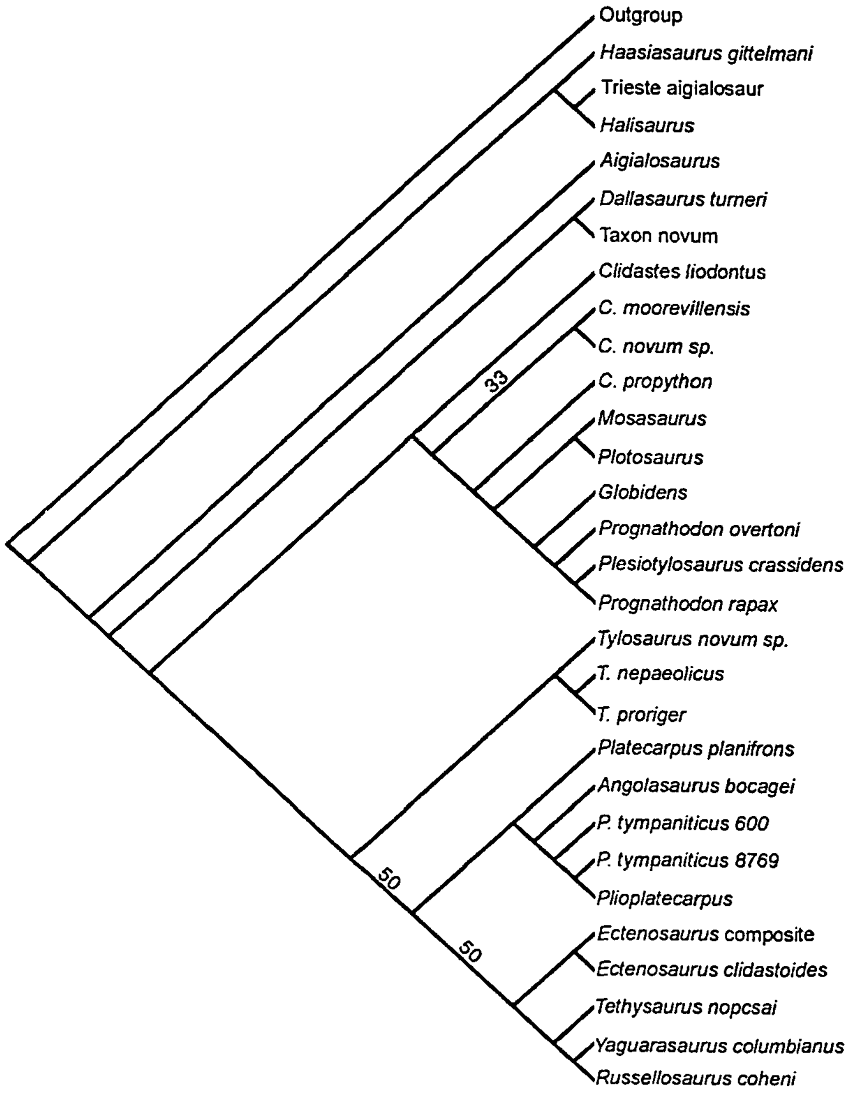

Outgroup
Taxon novum
Haasiasaurus gittelmani
Dallasaurus turneri
Trieste aigialosaur
Halisaurus
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus composite
Ectenosaurus clidastoides
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni

FIGURE 5-15. Test 11. The strict consensus (A) and Highest Percentage-rule consensus (B) trees constructed from 6 shortest cladograms (length= 354 steps, C.I.= 0.463, R.I.= 0.728, H.I.= 0.537) retrieved from a Heuristic search of 30 taxa and 129 characters in which *Aigialosaurus dalmaticus* and *A. bucchichi* were combined to form a single *Aigialosaurus* taxon. All branch supports are 100 except where otherwise indicated.


Outgroup
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Aigialosaurus
Dallasaurus turneri
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus
Ectenosaurus composite
Ectenosaurus clidastoides
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
33
50
50


Outgroup
Haasiasaurus gittelmani
Trieste aigialosaur
Halisaurus
Aigialosaurus
Dallasaurus turneri
Taxon novum
Clidastes liodontus
C. moorevillensis
C. novum sp.
C. propython
Mosasaurus
Plotosaurus
Globidens
Prognathodon overtoni
Plesiotylosaurus crassidens
Prognathodon rapax
Ectenosaurus composite
Ectenosaurus clidastoides
Tylosaurus novum sp.
T. nepaeolicus
T. proriger
Tethysaurus nopcsai
Yaguarasaurus columbianus
Russellosaurus coheni
Platecarpus planifrons
Angolasaurus bocagei
P. tympaniticus 600
P. tympaniticus 8769
Plioplatecarpus

APPENDIX I:

Changes to the taxon/character matrix of Bell and Polcyn (in press)

1. *Halisaurus novum sp.*, *H. platyspondylus*, *H. sternbergi*, and *H. cf. sternbergi* were all compiled into the single terminal taxon *Halisaurus.*

2. *Globidens alabamaensis* and *G. dakotaensis* were combined into the terminal taxon *Globidens.*

3. *Plotosaurus bensoni* and *P. tuckeri* were combined into the terminal taxon *Plotosaurus.*

4. *Plioplatecarpus AMNH sp.* and *Plioplatecarpus RMM sp.* were combined into the terminal taxon *Plioplatecarpus.*

5. *Clidastes KU liodontus* and *C. YP liodontus* were combined into the terminal taxon *Clidastes liodontus.*

6. Characters 3, 15, 54, 62, 80, 95, 99, 117, and 137 were removed from the matrix as they ceased to be informative following the reduction in the number of taxa.

7. Characters one and two, 37 and 38, 69 and 70, and 105 and 106 were combined to form multistate characters.

8. Character 23 was removed because the character diagnosis failed to accurately differentiate the relative size of various parietal foramina independent of placement in the parietal table and the size and shape of the stapedial pit of the quadrate.

9. Character 49 was removed because (as stated in the character definition) the various forms of the "infrastapedial process" are likely not homologous and thus should not be treated as such in a binomial character.

10. Characters were recoded to reflect new anatomical information or interpretations for *Aigialosaurus dalmaticus* (32 character scoring changes), *A. bucchichi* (38 scoring changes) and the "Trieste aigialosaurs" (4 scoring changes).

11. The terminology of many of the character definitions was modified to enhance comprehension.

APPENDIX II:

Character Definitions

Skull Characters

1. Premaxilla rostrum: total lack of a bony rostrum (0), rostrum very short (1), rostrum protrudes moderately (2), rostrum extremely large and inflated (3). This character is a combination of characters one and two from Bell and Polcyn (in press). *Yaguarasaurus columbianus* was characterized as having no rostrum in the first character (Bell and Polcyn in press) and then as having a short rostrum in the second character; thus, uncertainty dictates that the specimen be coded for both states in this matrix.

2. Premaxilla internarial bar width: narrow, distinctly less than half of the maximum width of the rostrum in dorsal view (0), or wide, being barely narrower than the rostrum (1).

3. Premaxilla internarial bar base shape: triangular (0), or rectangular (1). A vertical cross section through the junction of the internarial bar and the rostrum produces an inverted triangle in most taxa. In the derived state, this cross section is transversely rectangular because the broad ventral surface of the bar is planar.

4. Premaxilla internarial bar dorsal keel: absent (0), or present (1). In the derived condition a ridge rises above the level of a normally smoothly continuous transverse arch formed by the bones of anterior muzzle.

5. Premaxilla internarial bar venter: with entrance for the fifth cranial (facial) nerve close to rostrum (0), or nerve entrance removed posteriorly from rostrum (1). The conduit that marks the path of the fifth cranial nerve from the maxilla into the premaxilla is expressed as a ventro-lateral foramen within the premaxillary-maxillary sutural surface at the junction of the internarial bar and the rostrum. The derived condition includes a long shallow groove on the ventral surface of the internarial bar. Anteriorly the groove becomes a tunnel entering the bones at an extremely shallow angle, but disappearing below the surface at least 1 cm behind the rostrum.

6. Nasals: present (0), or absent (1). In most mosasauroids, nasals are not present even in well-preserved skulls and must be either always lost as a result of taphonomic processes, fused to the frontal or premaxilla, or lost evolutionarily.

7. Frontal shape: sides sinusoidal (0), or bone nearly triangular and sides relatively straight (1). In the derived condition, the area above the orbits is expanded and an isosceles triangle is formed by the rectilinear sides. In certain taxa a slight concavity is seen above the orbits, but the anterior and posterior to this there is no indication of a sinusoidal or recurved edge.

8. Frontal length to width ratio: maximum length to width ratio less than or equal to 1.5:1 (0), maximum length to width ratio between 1.5:1 and 2:1 (1), and maximum length to width ratio greater than 2:1 (2).

9. Frontal narial emargination: frontal not invaded by posterior end of nares (0), or distinct narial embayment present (1). In some mosasauroids the posterior ends of the nares are concomitant with the anterior terminus of the frontal prefrontal suture and, therefore, there is no marginal invasion of the frontal by the narial opening. However, in other mosasauroids this suture begins anterior and lateral to the posterior ends of the nares, causing a short emargination into the frontal.

10. Frontal midline dorsal keel: absent (0), or low, fairly inconspicuous (1), or high and well developed (2).

11. Frontal ala shape: tapers to a sharp point postero-laterally (0), or more broadly rounded postero-laterally (1). In state 0, the antero-lateral edge of the ala is smoothly concave, thus helping to form sharply pointed and laterally oriented posterior corners. In some Natantia, the antero-lateral edge of the ala may be concave, but the tip is not sharp and directed laterally.

12. Frontal olfactory canal embrasure: canal not embraced centrally by descending process (0), or canal almost or completely enclosed below (1). In state 1, short descending processes from the sides of the olfactory canal surround and almost, or totally, enclose the olfactory nerve.

13. Frontal postero-ventral midline: tabular boss immediately anterior to the frontal-parietal suture absent (0), or present (1). A triangular boss with a flattened ventral surface at the posterior end of the olfactory canal is the derived condition.

14. Frontal-parietal suture: apposing surfaces with low interlocking ridges (0), or with overlapping flanges (1). Plesiomorphically, an oblique ridge on the anterior sutural surface of the parietal intercalates between a single median posterior and a single lateral posterior ridge from the frontal. In the derived condition, these ridges are protracted into strongly overlapping flanges. The dorsal trace of the suture can be quite complex with a portion of the parietal embraced by the posterior extension of these frontal flanges.

15. Frontal-parietal suture overlap orientation: suture with oblique median frontal and parietal ridges contributing to overlap (0), or with all three ridges almost horizontal (1). In state 0, the median ridge from the frontal and the single parietal ridge are oriented at a distinct angle to the upper skull surface while the outer, or lateral, frontal ridge appears to be nearly horizontal. In *Tylosaurus nepaeolicus* and *T. proriger* (state 1), the obliquity of the intercalating ridges is reclined almost the horizontal, greatly expanding the amount of lateral overlap.

16. Frontal invasion of parietal: lateral flanges of frontal extended posteriorly (0), or median frontal flange extended posteriorly (1), or both extended posteriorly (2).

17. Frontal median flange length: median sutural flange short (0), or long (1). The median oblique sutural ridge discussed in character 15 is either short, not reaching back to the parietal foramen (state 0), or tightly embraces the foramen while extending backward to a position even with or beyond its posterior edge (state 1).

18. Parietal epaxial muscle insertions: dorsal surface relatively short with epaxial musculature insertion posterior between suspensorial rami only (0), or dorsal surface elongate with epaxial musculature insertion dorsal as well as posterior (1).

19. Parietal table shape: generally rectangular to trapezoidal with sides converging but not meeting (0), triangular with straight sides contacting in front of suspensorial rami (1), or triangular table with posterior portion forming parasagittal crest (2).

20. Parietal foramen position: foramen generally nearer to center of parietal table, well away from frontal-parietal suture (0), or close to or barely touching suture (1), or foramen straddling suture and deeply invading frontal (2). Generally in state 1, the distance from the foramen to the suture is about equal to or less than one foramen length.

21. Parietal foramen ventral opening: opening is level with main ventral surface (0), or opening surrounded by a rounded, elongate ridge (1).

22. Parietal posterior shelf: presence of a distinct horizontal shelf projecting posteriorly from between the suspensorial rami (0), or shelf absent (1). In some mosasauroids, a crescent-shaped shelf (in dorsal view) lies at the posterior end of the parietal medial to and below the origination of the suspensorial rami.

23. Parietal suspensorial ramus compression: greatest width vertical or oblique (0), or greatest width horizontal (1).

24. Parietal union with supratemporal: parietal suspensorial ramus overlaps supratemporal without interdigitation (0), or forked distal ramus of parietal sandwiches the tip of the supratemporal (1).

25. Prefrontal supra-orbital process: process absent or present as a small rounded knob (0), or process present as a distinct triangular, or rounded, overhanging wing (1). Note: This character should be characterized as either presence/absence or as absence/small process/large process. The absence of the process and the presence of a small process should not be treated as the same state. Unfortunately not enough information is present in the matrix to allow subdivision of the absence/small process character state. This should be a priority for future researchers.

26. Prefrontal contact with postorbitofrontal: elements do not contact each other (0), or elements in contact (1). State 1 is usually described as the frontal being emarginated over the orbits. Often this character can be evaluated by examining the ventral surface of the frontal where a depression outlines the limits of the suture for the two ventral elements.

27. Prefrontal-postorbitofrontal overlap: prefrontal overlapped ventrally by portorbitofrontal (0), or prefrontal overlapped laterally (1).

28. Postorbitofrontal shape: narrow (0), or wide (1). In *Clidastes* and Globidensini, the lateral extent of the element is almost equal to half the width of the frontal and the outline of the bone is basically squared. In all other ingroup and outgroup taxa it has a fairly narrow hourglass shape.

29. Postorbitofrontal transverse dorsal ridge: absent (0), or present (1). In state 1 an inconspicuous, low, and narrowly rounded ridge traces from the antero-lateral corner of the parietal suture across the top of the element to disappear behind the origin of the jugal process.

30. Postorbitofrontal squamosal ramus: does not (0), or does (1) reach end of supratemporal fenestra.

31. Maxillary tooth number: 20-24 (0), or 17-19 (1), or 14 (3), or 13 (4) or 12 (5).

32. Maxillary-premaxillary suture posterior terminus: suture ends above a point that is anterior to or even with the midline of the fourth maxillary tooth (0), or between the fourth and ninth teeth (1), or even with or posterior to the ninth tooth (2). These somewhat arbitrary divisions of the character states are designed to describe in more concrete terms those sutures that terminate far anteriorly, those that terminate less anteriorly, and those that terminate near the mid-length of the maxilla, respectively.

33. Maxilla posterodorsal process: process absent (0), the process does not prevent emargination of prefrontal on the dorsolateral edge of narial opening (1), or the process excludes the prefrontal from the rim of the narial opening (2). This character is a combination of characters 37 and 38 from Bell and Polcyn (in press). In that study *Halisaurus* is scored as lacking a postero-dorsal process of the maxilla that overlaps the anterior portion of the prefrontal (character 37). In the next character (38) *Halisaurus* is scored as having a portion of the maxilla extend postero-dorsally to exclude the prefrontal from the rim of the narial opening. As these two character states appear to be conflicting, *Halisaurus* was coded as both (0) and (2) in this matrix.

34. Jugal postero-ventral angle: angle very obtuse or curvilinear (0), or slightly obtuse, near 120 degrees (1), or 90 degrees (2).

35. Jugal postero-ventral process: absent (0), or present (1).

36. Ectopterygoid contact with maxilla: present (0), or absent (1).

37. Pterygoid tooth row elevation: teeth arise from robust, transversely flattened, main shaft of pterygoid (0), or teeth arise from thin pronounced vertical ridge (1). Plesiomorphically, the teeth emanate from the relatively planar surface of the thick, slightly dorso-ventrally compressed main shaft of the pterygoid. In the derived state a tall, thin dentigerous ridge emanates ventrally from a horizontal flange that forms the base of the quadratic ramus and the ectopterygoid process, causing the main pterygoid body to be trough-shaped.

38. Pterygoid teeth size: anterior teeth significantly smaller than marginal teeth (0), or anterior teeth large, approaching size of marginal teeth (1).

39. Quadrate suprastapedial process length: process short, ends at a level well above mid-height of the quadrate shaft (0), or process is of moderate length, ending very near the mid-height of the quadrate shaft (1), or process is long, ending distinctly below the mid-height of the quadrate shaft (2).

40. Quadrate suprastapedial process constriction: distinct dorsal constriction (0), or virtually no dorsal constriction (1).

41. Quadrate suprastapedial ridge: ridge on ventro-medial edge of suprastapedial process indistinct, straight and/or narrow (0), or ridge wide, broadly rounded, and curving downward, especially above stapedial pit (1).

42. Quadrate suprastapedial process fusion: no fusion present (0), or process fused to elaborated process from below (1).

43. Quadrate stapedial pit shape: pit broadly oval to almost circular (0), or relatively narrowly oval (1), or extremely elongate with a constricted middle (2). In state 0, the length to width ratio is less than 1.8:1; in state 1, it ranges from 1.8:1 to 2.4:1; and in state 2, it is greater than 2.4:1.

44. Quadrate postero-ventral ascending tympanic rim condition: small, low ridge present (0), or a high, elongate crest (1), or crest extremely produced laterally (2). In state 1, the extended rim causes a fairly deep sulcus in the ventral portion of the intratympanic cavity. In *Plioplatecarpus*, the entire lower tympanic rim and ala are expanded into a large conch (state 2) which tremendously increases the depth of the intratympanic cavity.

45. Quadrate ala thickness: ala thin (0), or thick (1). In state 0, the bone in the central area of the ala is only about 1 cm thick in medium-sized mosasaur specimens and that area is usually crushed or completely destroyed. Alternatively, the ala extends from the main shaft with only minor thinning, providing a great deal of strength to the entire bone (state 1).

46. Quadrate conch: ala and main shaft encompassing a deeply bowled area (0), or alar concavity shallow (1). A relatively deeper sulcus in the anterior part of the intratympanic cavity and more definition between the ala and the main shaft are feature of the plesiomorphic state.

47. Quadrate ala shape: antero-dorsal segment of tympanic rim more tightly curved than rest of rim (0), or rim with a uniformly circular curve throughout (1). A slight expansion of the antero-dorsal segment of the alar wing produces a lateral profile that very much resembles an ear or question mark in the plesiomorphic condition.

48. Quadrate ala ridge: no vertical ridge present dorso-laterally on anterior face of ala (0), or strong obtuse ridge present in that position (1).

49. Quadrate alar groove: absent (0), or long distinct, and deep groove present in anterolateral edge of ala (1).

50. Quadrate tympanic rim size: large, almost as high as quadrate (0), or smaller, about 50-65% of the height (1). In the derived state, a large portion of the dorsal articular surface and the ventral end of the main shaft is exposed in lateral view.

51. Quadrate dorsal median ridge: ridge is a relatively thin and high crest (0), or low, broadly inflated dome present (1). In state 1, the dorsal median ridge barely rises above the rest of the bone surface.

52. Quadrate central median ridge: relatively thin and distinct (0), or in form of smooth broadly inflated dome around stapedial pit (1). In state 1, the sharp median ridge loses definition in the area of the stapedial pit.

53. Quadrate ventral median ridge: a single thin ridge present (0), or thin ridge diverging ventrally (1). In the derived state, the anterior ridge continues to the ventro-medial corner of the bone, while the posterior ridge gradually curves posteriorly and merges into the postero-medial face of the bone near the infrastapedial process.

54. Quadrate ventral condyle: condyle saddle-shaped, concave in anteroposterior view (0), or gently domed, convex in any view (1).

55. Quadrate ventral condyle modification: no upward deflection of anterior edge of condyle (0), or presence of a distinct deflection (1).

56. Basisphenoid pterygoid process shape: process relatively narrow with articular surface facing mostly antero-laterally (0), or somewhat thinner, more fan-shaped with a posterior extension of the articular surface causing a more lateral orientation (1).

57. Basioccipital tubera size: short (0), or long (1). Long tubera are typically parallel-sided in posterior profile and protrude ventro-laterally at exactly 45 degrees from horizontal. Short tubera have relatively large bases that taper distally, and emanate more horizontally.

58. Basioccipital tubera shape: tubera not antero-posteriorly elongate (0), or antero-posteriorly elongate with rugose ventrolateral surfaces (1).

59. Basioccipital canal: canal for basilar artery enters basioccipital floor: as no canal (0), as a small pair (1), as a large pair (2), or as a single bilobate canal (3).

60. Dentary tooth number I: 20-24 (0), or 17-19 (1), or 15-16 (2), or 14 (3), or 13 (4), or 12 (5), or <12 (6).

61. Dentary anterior projection: no projection of bone anterior to first tooth (0), projection is less than the width of a complete tooth space (1), or projection is equal to or greater than the width of a single tooth space (2)..

62. Dentary medial parapet: parapet positioned at base of tooth roots (0), or elevated and strap-like, enclosing about half of the height of the tooth attachment in a shallow channel (1), or strap equal in height to lateral wall of dentary (2).

63. Splenial-angular articulation shape: splenial articulation in posterior view almost circular (0), or laterally compressed (1), or intermediate (2).

64. Splenial-angular articular surface: essentially smooth concavo-convex surfaces (0), or distinct horizontal tongues and grooves present (1).

65. Coronoid shape: coronoid with slight dorsal curvature, posterior wing not widely fan-shaped (0), or very concave above, posterior wing greatly expanded (1).

66. Coronoid postero-medial process: present (0), or absent (1).

67. Coronoid medial wing: does not reach angular (0), or contacts angular (1).

68. Coronoid posterior wing: without medial crescentic pit (0), or with distinct excavation (1). In state 1 there is a posteriorly open C-shaped excavation in the medial side of the posterior wing of the coronoid.

69. Surangular coronoid buttress: low, thick, about parallel to lower edge of mandible (0), or high, thin, rapidly rising posteriorly (1). A rounded dorsal edge of the surangular remains almost parallel to the ventral edge as it approaches the posterior end of the coronoid, meeting the latter element near its posteroventral edge in state 0. In the derived condition, the dorsal edge rises and thins anteriorly until meeting the posterior edge of the coronoid near its apex, making the posterior portion of the mandible appear triangular in lateral aspect.

70. Surangular-articular suture position: behind condyle in lateral view (0), or at middle of glenoid on lateral edge (1). In the derived condition there is usually an interdigitation in the dorsal part of the suture.

71. Articular retroarticular process inflection: moderate inflection, less than 60 degrees (0), or extreme inflection, almost 90 degrees (1).

72. Articular retroarticular process foramina: no large foramina on lateral face of retroarticular process (0), or one to three large foramina present (1).

73. Tooth surface I: teeth finely striate medially (0), or not medially striate (1).

74. Tooth surface II: teeth not coarsely textured (0), or very coarsely ornamented with bumps and ridges (1).

75. Tooth facets: absent (0), or present (1).

76. Tooth fluting: absent (0), or present (1).

77. Tooth inflation: crowns of posterior marginal teeth conical, tapering throughout (0), or crowns of posterior marginal teeth swollen near the tip or above the base (1).

78. Tooth carinae: absent (0), or present but extremely weak (1), or strong and elevated (2).

79. Tooth carinae serration: absent (0), or present (1).

80. Tooth replacement mode: replacement teeth form in shallow excavations (0), or in sub-dental crypts (1).

Postcranial Axial Skeleton

81. Atlas neural arch: notch in anterior border (0), or no notch in anterior border (1).

82. Atlas synapophysis: extremely reduced (0), or large and elongate (1). In state 1, a robust synapophysis extends well postero-ventral to the medial articular surface for the atlas centrum, and it may be pedunculate (*Clidastes*) or with a ventral "skirt" that gives it a triangular shape (*Mosasaurus*). A very small triangular synapophysis barely extends posterior to the medial articular edge in state 0.

83. Zygosphenes and zygantra: absent (0), or present (1).

84. Number of zygosphenes and zygantra: present on many vertebrae (0), present only on a few (1).

85. Synapophysis height: facets for rib articulations tall and narrow on posterior cervical and anterior trunk vertebrae (0), or facets ovoid, shorter than the centrum height on those vertebrae (1).

86. Synapophysis length: synapophysis of middle trunk vertebrae not laterally elongate (0), or distinctly laterally elongate (1). The lateral extension of the synapophysis from the middle of the trunk is as much as 70-80% of the length of the same vertebra in the derived state.

87. Synapophysis ventral extension: synapophysis extend barely or not at all below ventral margin of cervical centrum (0), or some extend far below ventral margin of centrum (1). In the derived state, two or more anterior cervical vertebrae have rib articulations that dip well below the centrum, causing a very deeply concave ventral margin in anterior profile.

88. Vertebral body inclination: condyles of trunk vertebrae inclined (0), or condyles vertical (1).

89. Vertebral condyle shape I: condyles of anterior trunk vertebrae extremely dorsoventrally depressed (0), or slightly depressed (1), or essentially equidimensional (2). In state 0, height to width ratio of anterior trunk vertebrae is close to 1:2. In state 1, the ratio is closer to 3:4. State 2 has a height to width ratio is essentially 1:1.

90. Vertebral condyle shape II: condyles of posterior trunk vertebrae not higher than wide (0), or slightly laterally compressed (1).

91. Vertebral synapophysis dorsal ridge: sharp ridge absent on posterior trunk synapophysis (0), or with a sharp-edged and anteriorly precipitous ridge connecting distal synapophysis with prezygapophysis (1). In the plesiomorphic condition the ridge may be incomplete or it may be rounded across the crest with the anterior and posterior sides about equally sloping.

92. Vertebral length proportions: cervical vertebrae distinctly shorter than longest vertebrae (0), or cervical length equal to or greater than the longest trunk vertebra (1).

93. Number of presacral vertebrae: 28 or 29 (0), 30 or 31 (1), or 32 or more (2). Presacral vertebrae are considered to be all those anterior the first vertebra bearing elongate transverse processes.

94. Sacral vertebrae number: two (0), or less than two (1). Numerous well-preserved specimens of derived mosasauroids have failed to show any direct contact of the pelvic girdle with vertebrae in the sacral region. Certainly, no transverse processes bear any type of concave facet for the ilium, and so it is generally assumed that a ligamentous contact was established with only one transverse process (Camp 1942). Depending on one's perspective, it could be said that derived mosasauroids have either no or one sacral vertebra. Conversely, it can be assumed that aigialosaurs retain the condition of having two sacral vertebrae that is seen in extant anguimorph lizards. This assumption is based on the need for aigialosaurs to counteract gravity when active on land.

95. Caudal dorsal expansion: neural spines of tail all uniformly shortened posteriorly (0), or several spines dorsally elongated behind middle of tail (1).

96. Haemal arch length: haemal arches about equal in length to neural arch of the same vertebra (0), or length about 1.5 times greater than neural arch length (1). This ratio may be as great as 1.2:1 in state 0. Comparison is most accurate in the middle of the tail and is consistent on those vertebrae in which the neural spines are also elongated.

97. Haemal arch articulation: arches articulating with the vertebral centra (0); or arches fused to centra (1). Haemal arches tend to fuse to the centra in elderly specimens of the outgroups, but these are still considered to exhibit state 0. All mosasaurines have fused haemals and all "russellosaurines" have articulating haemals.

98. Tail curvature: no structural downturn of the tail (0), or tail with decurved posterior portion (1).

99. Body proportions: head and trunk shorter than or about equal to tail length (0), or head and trunk longer than tail (1).

Appendicular skeleton

100. Scapula/coracoid size: both bones are approximately the same size (0), or scapula about half the size of coracoid (1).

101. Scapula width: no antero-posterior widening (0), or distinct fan-shaped widening (1), or extreme widening (2).

102. Scapula dorsal convexity: if scapula widened, dorsal margin very convex (0), or broadly convex (1). In state 0, the antero-posterior dimension is almost the same as the proximo-distal dimension. In state 1, the anter-oposterior dimension is much larger.

103. Scapula posterior emargination: posterior border of bone gently concave (0), or deeply concave (1). In the derived condition, there is a deeply arcuate emargination on the posterior scapular border just dorsal to the glenoid. It is immediately bounded dorsally by a corner which begins a straight-edged segment that continues to the dorsal margin.

104. Scapula-coracoid suture: Unfused scapula-coracoid contact has interdigitate suture anteriorly (0), or apposing surfaces without interdigitation (1). Although all outgroup taxa fuse this suture ontogenetically, an interdigitate suture is present early in life; therefore, the interdigitate suture is assigned as the plesiomorphic state.

105. Coracoid neck elongation: neck rapidly tapering from medial corners to a relatively broad base (0), or neck gradually tapering to a relatively narrow base (1). The derived state of this character gives an outline of the bone which fan-shaped and almost symetrical.

106. Coracoid anterior emargination: present (0), or absent (1).

107. Humerus length: humerus distinctly elongate, about three or more times longer than distal width (0), or shortened, about 1.5 to 2 times longer than distal width (1), or length and distal width virtually equal (2), or distal width slightly greater than length (3).

108. Humerus post-glenoid process: absent or very small (0), or distinctly enlarged (1).

109. Humerus glenoid condyle: if present, condyle gently domed and elongate oval in proximal view (0), or condyle saddle-shaped, sub-triangular in proximal view, and depressed (1), or condyle highly domed or protuberant and short ovoid to almost round in proximal view. In some taxa, the condylar surfaces of the limbs were finished in thick cartilage and there was no bony surface of the condyle to be preserved. This condition is scored as not represented. In some taxa, the glenoid condyle extends more proximally than does the post-glenoid process (state 2) and it is not ovoid as in the plesiomorphic state.

110. Humerus delto-pectoral crest: crest undivided (0), or split into two separate insertion areas (1). In the derived state, the deltoid crest occupies an antero-lateral or anterior position confluent with the glenoid condyle, while the pectoral crest occupies a medial or antero-medial area that may or may not be confluent with the glenoid condyle. The deltoid crest is often quite short, broad, and indistinct, being easily erased by taphonomic processes.

111. Humerus pectoral crest: located anteriorly (0), or medially (1). In the derived condition, the pectoral crest is located on the medial side of the humerus near the proximal tip.

112. Humerus ectepicondylar groove: groove or foramen present on disto-lateral edge (0), or absent (1).

113. Humerus ectepicondyle: absent (0), or present (1).

114. Humerus entepicondyle: absent (0), or present (1).

115. Radius shape: distal tip of radius not expanded (0), or distal tip slightly expanded (1), or distal tip broadly expanded (2).

116. Ulna contact with centrale: broad ulnare prevents contact of the two elements (0), or ulna contacts centrale (1).

117. Radiale size: large and broad (0), or small to absent (1).

118. Carpal reduction: carpals number six or more (0), or five or less (1).

119. Pisiform: present (0), or absent (1).

120. Metacarpal I expansion: spindle-shaped, elongate (0), or broadly expanded (1).

121. Phalanx shape: phalanges elongate, spindle-shaped (0), or blocky, hourglass-shaped (1).

122. Iliac crest: crest blade-like, points postero-dorsally (0), or elongate, cylindrical (1).

123. Pubic tubercle condition: tubercle an elongate protuberance located closer to mid-length of the shaft of the pubis (0), or a thin semicircular crest-like blade located close to acetabulum (1).

124. Ischiatic tubercle size: elongate (0), or short (1). In the ancestral condition the tubercle is as long as the shaft of the ischium is wide, but it is only a short narrow spur in the derived state.

125. Astragalus: notched emargination for crural foramen, without pedunculate fibular articulation (0), or without notch, pedunculate fibular articulation present (1). For state 0, the tibia and fibula are of equal length about the crural foramen and the astragalus contacts both to about the same degree. The form of the latter element is symmetrical and subcircular with a sharp proximal notch. In state 1, the outline of the element is basically reniform and the tibial articulation is on the same line as the crural emargination. The fibula is also shortened and its' contact with astragalus is narrow.

126. Appendicular epiphyses: formed from ossified cartilage (0), or from thick unossified cartilage (1), or epiphyses missing or extremely thin (2).

127. Hyperphalangy: absent (0), or present (1).

128. Exit for basilar artery from basioccipital: absent (0), through two ventral foramina (1), through a single ventral foramen (2), or through two foramina on antero-dorsal edge of basisphenoid (3).

129. Posterior thoracic vertebrae: not markedly longer than anterior thoracic vertebrae (0), markedly longer (1).

APPENDIX III

Data Matrix

		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Outgroup	0	0	0	0	0	0	0	?	0	0	?	?	0	0
[illegible]	A. dalmaticus	?	?	?	?	?	?	0	?	?	0	0	?	?	0
[illegible]	A. buccichi	0	?	?	?	?	?	0	?	?	0	0	?	?	0
[illegible]	Trieste Aglaiosaur	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Dallasaurus turneri	?	?	?	?	?	?	0	?	?	0	?	?	?	?
[illegible]	Haasiasaurus gittlemani	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Taxon novum	1	1	?	1	1	0	0	2	1	0	1	0	?	0
[illegible]	Halisaurus	0 / 1	0	0	0 / 1	0	0	0	2	0 / 1	0 / 1	0	0	0	0
[illegible]	C. liodontus	2	0	0	0	?	1	0	2	0	0	1	0	?	1
[illegible]	C. mooreville	2	0	0	0	0	1	0	2	0	0	1	0	0	1
[illegible]	C. novum sp.	2	0	0	0	0	1	0	2	0	0	1	0	?	1
[illegible]	C. propython	2	0	0	0	?	?	1	2	0	0	1	0	0	1
[illegible]	P. planifrons	1	0	0	0	0	1	0	0	1	0	1	1	?	1
[illegible]	P. tympaniticus 8769	0	0	0	0	0	?	0	0	1	1	1	1	1	1
[illegible]	P. tympaniticus 600	1	0	?	0	?	1	0	0	1	1	1	?	?	1
[illegible]	Plesio. crassidens	2	0	?	0	?	1	1	1	0	1	1	?	?	1
[illegible]	Progn. overtoni	1	0	0	0	?	?	1	0	0	1	1	0	0	1
[illegible]	Progn. rapax	1	0	0	0	?	?	1	0	0	0	1	0	0	1
[illegible]	T. nepaeolicus	3	1	1	1	?	0	0	0	1	0	1	0	1	1
[illegible]	T. novum sp.	3	1	0	1	1	0	0	0	1	1	1	0	1	1
[illegible]	T. proriger	3	1	1	1	1	0	0	0	1	1	1	?	1	1
[illegible]	Y. columbianus	0 / 1	0	?	0	?	1	0	2	0	0	0	?	?	?
[illegible]	Russellosaurus coheni	1	?	?	0	0	?	0	2	0	0	0	1	1	1
[illegible]	Angolasaurus bocagei	1	?	?	0	?	?	0	1	?	1	1	?	?	?
[illegible]	E. composite YP	1	0	0	0	1	?	0	2	?	0	?	1	1	1
[illegible]	E. clidastoid	2	0	?	0	?	1	0	2	0	0	1	?	?	1
[illegible]	Tethysaurus nopscai	1	0	?	0	?	1	0	2	1	1	0	?	?	1
[illegible]	Mosasaurus	2	0	0	1	?	1	0 / 1	0 / 1	0	0 / 1	1	?	?	1
[illegible]	Plotosaurus	1	0	0	1	?	0	1	0	1	0	1	?	?	1
[illegible]	Plioplatecarpus	?	?	?	?	?	?	0	0	1	1	1	0	0	1
[illegible]	Globidens	2	0	?	0	?	1	1	0	1	1	1	1	0	1

	115	116	117	118	119	120	121	122	123	124	125	126	127	128
Outgroup	?	?	?	0	0	0	0	?	?	0	0	0	?	0
A. dalmaticus	?	?	?	1	0	0	?	1	0	?	0	0	?	0
A. buccichi	?	?	?	1	0	0	?	1	0	?	0	0	?	0
Trieste Aigialosaur	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dallasaurus turneri	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Haasiasaurus gittlemani	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Taxon novum	1	?	?	0	0	1	?	0	0	0	0	0	?	0
Halisaurus	0	?	?	0 / 1	0	0 / 1	1	0	0	0	0	0	?	?
C. liodontus	0	1	0	1	0	1	1	1	1	?	1	0	?	1
C. mooreville	0	1	0	1	0	1	1	1	1	?	1	0	?	1
C. novum sp.	0	1	0	1	0	1	1	1	1	1	1	0	?	1
C. propython	0	1	0	1	0	1	1	1	?	?	1	0	?	1
P. planifrons	0	0	?	1	1	0	?	1	1	?	0	0	?	?
P. tympaniticus 8769	0	0	?	1	1	1	0	1	1	?	0	1	0	0
P. tympaniticus 600	0	0	?	1	1	0	?	?	1	?	0	1	0	0
Plesio. crassidens	0	1	1	1	0	1	?	1	1	?	1	1	1	1
Progn. overtoni	0	1	1	1	0	1	?	1	1	1	1	1	?	1
Progn. rapax	0	1	1	1	0	1	1	1	1	?	1	1	?	1
T. nepaeolicus	1	?	?	1	0	0	?	1	1	1	0	1	?	0
T. novum sp.	0	1	1	1	0	1	?	1	1	?	0	1	?	0
T. proriger	1	?	?	1	0	1	?	1	1	1	0	1	1	0
Y. columbianus	0	2	0	1	2	0	?	1	1	0	0	0	?	0
Russellosaurus coheni	0	2	0	1	2	0	0	1	1	0	0	0	?	0
Angolasaurus bocagei	0	?	?	1	1	0	?	1	?	?	0	0	?	0
E. composite YP	0	2	0	1	1	0	0	?	1	?	?	?	?	0
E. clidastoid	0	2	0	1	1	0	?	0	1	?	0	0	?	0
Tethysaurus nopscai	0	2	0	1	2	0	?	1	1	0	0	0	?	0
Mosasaurus	0	1	1	1	0	1 / 2	1	1	1	?	1	1	0	0
Plotosaurus	0	1	1	1	0	1	?	1	1	1	1	1	?	0
Plioplatecarpus	0	0	?	1	1	3	0	1	1	?	0	1	0	0
Globidens	0	1	0	1	0	1	?	1	1	?	1	0 / 1	?	1

		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Outgroup	0	0	?	0	2	0	?	0	0	0	?	?	?	0
[illegible]	A. dalmaticus	0	0	?	?	0	1	0	?	?	?	?	?	?	0
[illegible]	A. buccichi	0	0	?	?	?	1	0	?	0	0	1	?	?	0
[illegible]	Trieste Aigialosaur	?	?	?	?	?	?	?	?	?	?	2	0	?	0
[illegible]	Dallasaurus turneri	?	?	?	?	?	?	?	?	0	?	?	?	?	?
[illegible]	Haasiasaurus gittlemani	?	?	?	?	?	?	?	?	?	?	1	1	?	0
[illegible]	Taxon novum	?	0	0	0	2	?	?	?	0	0	1	1	?	0
[illegible]	Halisaurus	?	?	0	1 / 2	0 / 2	1	?	?	0 / 1	0	2	0	0	1
[illegible]	C. liodontus	0	0	2	1	2	2	?	?	1	0	1	0	?	0
[illegible]	C. mooreville	0	0	2	1	2	2	0	?	1	0	1	0	?	0
[illegible]	C. novum sp.	0	?	2	1	2	2	0	0	1	0	1	0	?	0
[illegible]	C. propython	0	0	2	1	2	?	?	?	1	0	1	0	?	0
[illegible]	P. planifrons	1	1	5	0	2	?	1	0	0	0	2	1	0	0
[illegible]	P. tympaniticus 8769	1	?	5	0	2	1	1	?	0	0	2	1	1	0
[illegible]	P. tympaniticus 600	1	1	5	?	2	1	1	?	0	0	2	1	1	0
[illegible]	Plesio. crassidens	0	0	4	1	1 / 2	?	?	?	1	1	1	0	?	1
[illegible]	Progn. overtoni	0	1	5	0	1 / 2	2	0	?	1	1	1	0	?	1
[illegible]	Progn. rapax	?	0	4	1	2	2	0	?	1	1	1	0	?	1
[illegible]	T. nepaeolicus	0	1	4	0	?	?	1	1	0	0	1	1	?	0
[illegible]	T. novum sp.	1	1	4	1	1	2	1	1	0	0	1	1	?	0
[illegible]	T. proriger	?	1	4	1	1	1	1	0	0	0	0	0	?	0
[illegible]	Y. columbianus	?	1	3	0	1	1	1	1	?	?	1	1	0	0
[illegible]	Russellosaurus coheni	1	1	2	0	1	1	1	1	0	0	1	1	0	0
[illegible]	Angolasaurus bocagei	?	?	5	0	?	?	?	1	?	?	2	1	0	0
[illegible]	E. composite YP	?	1	?	0	?	1	1	0	0	0	1	0	0	1
[illegible]	E. clidastoid	1	1	1	1	1	1	1	?	0	0	1	0	0	1
[illegible]	Tethysaurus nopscai	?	1	0	0	?	1	1	?	?	0	0	1	0	0
[illegible]	Mosasaurus	0	1	3	1	2	2	1	?	1	0	0	0	?	0
[illegible]	Plotosaurus	0	1	1	1	1	2	0	0	1	0	0	0	?	0
[illegible]	Plioplatecarpus	0	1	?	0	?	1	1	0	0	0	2	1	1	0
[illegible]	Globidens	0	1	4	1	2	2	0	?	1	0	1	0	?	1

		43	44	45	46	47	48	49	50	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Outgroup	?	?	0	0	0	0	0	0	0	0	0	0	0	?
[illegible]	A. dalmaticus	?	?	0	?	?	?	0	0	?	?	?	?	?	?
[illegible]	A. buccichi	?	?	0	0	1	0	0	0	?	?	?	?	?	?
[illegible]	Trieste Aigialosaur	?	0	0	0	0	0	0	0	?	?	?	?	?	?
[illegible]	Dallasaurus turneri	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Haasiasaurus gittlemani	2	?	0	0	0	?	?	?	?	?	0	?	?	?
[illegible]	Taxon novum	?	0	0	0	?	?	?	0	0	0	0	0	0	0
[illegible]	Halisaurus	0	0	0	0	0	0	0	0 / 1	0	0	0	1	0	?
[illegible]	C. liodontus	0	0	0	0	1	0	0	1	0	0	0	0	1	0
[illegible]	C. mooreville	0	0	1	0	1	0	0	1	0	0	0	0	1	0
[illegible]	C. novum sp.	0	0	1	0	1	0	0	1	0	0	0	0	1	?
[illegible]	C. propython	0	0	1	0	1	0	0	1	0	0	0	0	1	0
[illegible]	P. planifrons	1	0	0	0	1	0	0	0	0	0	1	1	1	?
14	P. tympaniticus 8769	1	1	0	0	1	0	0	0	1	0	1	1	1	?
[illegible]	P. tympaniticus 600	1	1	0	0	1	0	0	0	1	0	1	1	1	1
16	Plesio. crassidens	0	1	1	0	1	?	0	1	?	?	?	1	1	?
17	Progn. overtoni	0	1	1	0	?	1	?	1	0	0	0	0	1	?
[illegible]	Progn. rapax	0	1	1	0	1	1	0	1	0	0	0	1	1	0
19	T. nepaeolicus	2	0	1	1	1	0	0	1	0	0	0	0	1	1
20	T. novum sp.	2	0	1	1	1	0	0	1	0	0	1	0	1	1
21	T. proriger	2	0	0	0	1	0	0	1	0	0	0	0	1	1
22	Y. columbianus	2	0	0	1	1	0	0	0	0	0	0	0	0	1
23	Russellosaurus coheni	2	0	0	1	1	0	0	0	0	0	0	0	0	1
[illegible]	Angolasaurus bocagei	0	1	0	0	1	0	0	0	0	0	0	1	0	1
25	E. composite YP	2	1	0	1	1	0	?	1	0	0	0	?	?	1
26	E. clidastoid	?	1	0	1	1	?	1	1	0	0	0	?	?	1
27	Tethysaurus nopscai	2	0	1	1	1	0	?	1	0	0	0	0	0	1
28	Mosasaurus	0	0	0	0 / 1	0 / 1	0	1	0 / 1	0 / 1	1	1	1	0	0
[illegible]	Plotosaurus	0	0	0	0	0	0	1	1	0	1	1	1	0	0
30	Plioplatecarpus	0	2	0	0	1	0	0	0	1	0	0 / 1	1	1	?
31	Globidens	0 / 1	1	1	0	1	0	0	1	0	0	0 / 1	0	1	?

		57	58	59	60	61	62	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Outgroup	0	0	0	?	1	0	?	?	0	0	0	0	0	0
[illegible]	A. dalmaticus	?	0	?	?	?	?	?	?	0	?	?	?	?	?
[illegible]	A. buccichi	?	?	?	?	?	0	?	?	0	1	0	?	0	?
[illegible]	Trieste Aigialosaur	?	?	?	?	?	?	?	?	?	?	?	?	0	?
[illegible]	Dallasaurus turneri	?	?	?	?	1	0	2	0	?	?	0	?	0	?
[illegible]	Haasiasaurus gittlemani	?	?	?	0	1	0	1	0	1	0	0	0	0	0
[illegible]	Taxon novum	1	0	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Halisaurus	0	0	0	0	0	1	2	0	1	1	0	0	0	1
[illegible]	C. liodontus	1	0	0	1 / 2	1	2	2	?	1	0	0	0	1	0
[illegible]	C. mooreville	1	0	0	2	1	2	2	0	1	0	0	0	1	0
[illegible]	C. novum sp.	1	0	?	2	1	2	2	0	1	0	0	0	1	0
[illegible]	C. propython	1	0	0	1	1	2	2	0	1	?	1	0	1	0
[illegible]	P. planifrons	0	0	2	5	1	2	2	0	0	1	0	0	0	0
[illegible]	P. tympaniticus 8769	0	0	3	5	0	2	2	1	0	1	0	0	0	0
[illegible]	P. tympaniticus 600	0	0	3	5	0	2	2	1	0	1	0	0	0	0
[illegible]	Plesio. crassidens	?	?	?	2	1	2	?	?	1	0	1	?	1	0
[illegible]	Progn. overtoni	1	0	0	3	1	2	1	0	1	0	1	1	1	0
[illegible]	Progn. rapax	1	0	0	?	0	2	1	0	1	0	?	?	?	0
[illegible]	T. nepaeolicus	0	1	?	4	2	2	2	0	0	0	0	0	0	0
[illegible]	T. novum sp.	0	0	0	4	2	2	2	0	0	0	0	0	0	0
[illegible]	T. proriger	0	1	0	4	2	2	2	0	0	0	1	0	0	0
[illegible]	Y. columbianus	0	0	1	3	0	?	?	?	?	?	?	?	?	?
[illegible]	Russellosaurus coheni	0	0	1	2	0	1	1	0	0	1	0	0	0	1
[illegible]	Angolasaurus bocagei	0	0	2	5	0	2	2	?	0	1	0	0	0	1
[illegible]	E. composite YP	?	?	3	4	1	2	0	0	1	?	?	0	0	0
[illegible]	E. clidastoid	0	0	?	3	?	2	0	?	1	?	0	0	0	0
[illegible]	Tethysaurus nopscai	0	0	1	1	0	1	1	0	0	1	0	0	0	1
[illegible]	Mosasaurus	1	0	0	1 / 3	1	2	2	0	1	0	1	1	1	0
[illegible]	Plotosaurus	1	0	?	1	2	2	2	?	1	1	1	?	1	0
[illegible]	Plioplatecarpus	0	0	3	5	0	2	2	1	0	1	0	0	0	0
[illegible]	Globidens	1	0	0	?	?	?	2	0	1	0	?	1	1	0

		[illegible]	72	73	74	75	76	77	78	79	80	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Outgroup	?	0	?	0	0	0	0	?	0	0	0	?	0	0
[illegible]	A. dalmaticus	0	?	?	?	0	0	0	?	?	?	?	?	1	0
[illegible]	A. buccichi	0	?	?	?	0	0	0	?	?	?	?	?	1	0
[illegible]	Trieste Aigialosaur	0	?	?	?	?	?	?	?	?	?	1	1	1	?
[illegible]	Dallasaurus turneri	?	?	1	?	?	?	?	?	?	0	0	1	1	?
[illegible]	Haasiasaurus gittlemani	0	0	0	0	0	0	0	1	?	0	?	?	1	0
[illegible]	Taxon novum	?	?	1	0	1	0	0	2	0	0	0	0	0	?
[illegible]	Halisaurus	0	0	1	0	0	0	0	1	0	0 / 1	?	1	0	?
[illegible]	C. liodontus	0	?	1	0	1	0	0	2	0	1	0	1	1	0
[illegible]	C. mooreville	0	0	1	0	1	0	0	2	0	1	0	1	1	0
[illegible]	C. novum sp.	0	0	1	0	1	0	0	2	0	1	0	1	1	0
[illegible]	C. propython	0	0	1	0	1	0	0	2	0	1	0	1	1	0
[illegible]	P. planifrons	0	1	0	0	1	1	0	2	0	1	1	0	1	0
[illegible]	P. tympaniticus 8769	?	1	0	0	1	0	0	2	0	1	1	0	0	?
[illegible]	P. tympaniticus 600	0	?	0	0	1	0	0	2	0	1	1	0	1	1
[illegible]	Plesio. crassidens	?	?	1	?	0	0	0	2	?	1	?	?	?	?
[illegible]	Progn. overtoni	1	0	1	1	0	0	1	2	1	1	?	?	?	?
[illegible]	Progn. rapax	0	0	1	1	0	0	1	2	1	1	0	1	1	0
19	T. nepaeolicus	0	0	0	0	1	0	0	2	1	1	0	0	0	1
20	T. novum sp.	0	0	0	0	1	0	0	2	0	1	0	0	1	1
21	T. proriger	0	0	0	0	1	0	0	2	1	1	1	0	0	?
22	Y. columbianus	?	?	0	0	?	0	0	1	0	0	?	?	1	?
23	Russellosaurus coheni	0	1	0	0	?	0	0	1	0	0	?	?	?	?
24	Angolasaurus bocagei	0	1	0	0	?	0	0	2	?	0	?	?	1	?
25	E. composite YP	0	1	0	0	1	1	0	2	0	1	0	0	1	?
26	E. clidastoid	?	1	0	0	1	1	0	2	0	1	?	?	1	0
27	Tethysaurus nopscai	0	0	0	0	?	0	0	0	?	0	?	?	1	0
28	Mosasaurus	0 / 1	0	1	0	1	0	0	2	1	1	0	1	0 / 1	1
29	Plotosaurus	1	0	0	0	0	0	1	2	?	1	0	1	0	?
30	Plioplatecarpus	0 / 1	1	0	0	1	0	0	2	0	1	?	?	0	?
31	Globidens	0	0	1	1	0	0	1	1	0	1	0	1	1	?

		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	Outgroup	?	0	0	0	?	0	0	?	0 / 1	0	0	?	0	0
[illegible]	A. dalmaticus	?	0	0	1	2	?	?	0	0	0	?	?	?	?
[illegible]	A. buccichi	?	0	?	?	?	?	?	0	0	0	0	0	?	0
[illegible]	Trieste Aglalosaur	?	0	?	?	1	?	?	0	?	0	?	0	0	?
[illegible]	Dallasaurus turneri	0	0	1	1	1	1	1	0	?	?	0	?	?	?
[illegible]	Haasiasaurus gittlemani	0	0	0	0	1	0	0	0	0	0	?	0	?	?
[illegible]	Taxon novum	0	0	1	0	1	?	0	0	0	1	?	?	?	?
[illegible]	Halisaurus	0	0	1	0	0	0	1	0	1	1	1	0	1	0
[illegible]	C. liodontus	0	0	0	1	2	0	1	0	2	1	1	1	1	0
[illegible]	C. mooreville	0	0	0	1	2	?	1	0	2	1	1	1	1	?
[illegible]	C. novum sp.	0	0	?	1	2	1	1	0	?	?	1	?	1	?
[illegible]	C. propython	0	0	0	1	2	?	1	0	?	?	1	?	1	?
[illegible]	P. planifrons	0	0	0	1	1	?	?	0	?	?	?	?	?	?
[illegible]	P. tympaniticus 8769	0	0	0	1	1	?	?	0	?	?	?	?	0	?
[illegible]	P. tympaniticus 600	0	0	0	1	1	0	0	0	0	1	0	0	0	1
[illegible]	Plesio. crassidens	0	0	0	1	2	?	1	0	?	?	?	?	?	?
[illegible]	Progn. overtoni	?	0	?	1	2	?	?	?	?	?	?	?	1	?
[illegible]	Progn. rapax	0	0	0	1	2	1	1	0	?	?	?	?	1	?
[illegible]	T. nepaeolicus	0	0	0	1	1	0	0	?	?	?	?	?	?	?
[illegible]	T. novum sp.	0	?	0	?	1	?	?	0	?	?	?	?	?	?
[illegible]	T. proriger	0	0	0	1	1	0	0	0	1	1	0	0	0	1
[illegible]	Y. columbianus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Russellosaurus coheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Angolasaurus bocagei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	E. composite YP	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	E. clidastoid	1	0	0	1	?	?	?	0	?	?	?	?	?	?
[illegible]	Tethysaurus nopscai	1	1	1	0	0	0	?	?	?	?	?	?	0	?
[illegible]	Mosasaurus	0 / 1	0 / 1	0	1	2	0	1	1	2	1	1	1	1	?
[illegible]	Plotosaurus	0	1	0	1	2	0	1	1	2	?	?	1	?	?
[illegible]	Plioplatecarpus	0	0	0	1	1	0	0	0	?	?	?	?	0	?
[illegible]	Globidens	0	?	0	1	2	?	1	0	?	?	?	?	?	?

		99	100	101	102	103	104	105	106	107	108	109	[illegible]	[illegible]	[illegible]
[illegible]	Outgroup	0	0	0	?	?	0	0	0	0	0	0	0	0	0
[illegible]	A. dalmaticus	?	?	0	?	0	?	?	?	0	?	0	?	?	?
[illegible]	A. buccichi	0	0	0	?	0	0	?	0	0	?	0	?	?	?
[illegible]	Trieste Aigialosaur	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Dallasaurus turneri	?	?	0	?	0	0	?	?	0	1	?	0	0	0
[illegible]	Haasiasaurus gittlemani	?	1	1	1	0	?	1	0	0	?	0	0	0	0
[illegible]	Taxon novum	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Halisaurus	1	1	1	1	1	1	0	0	1	0	0	1	0	0
[illegible]	C. liodontus	1	0	1	1	0	0	0	0	2	1	0	1	0	1
[illegible]	C. mooreville	?	0	1	1	0	0	0	0	2	1	0	1	0	1
[illegible]	C. novum sp.	?	0	1	1	0	0	0	0	2	1	0	1	0	1
[illegible]	C. propython	?	?	?	?	?	0	0	0	2	1	0	1	0	1
[illegible]	P. planifrons	?	0	1	0	1	1	0	0	2	0	?	1	1	0
[illegible]	P. tympaniticus 8769	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	P. tympaniticus 600	0	0	1	0	1	1	0	0	2	0	?	?	1	?
[illegible]	Plesio. crassidens	?	0	1	1	0	0	1	1	3	1	2	1	0	1
[illegible]	Progn. overtoni	?	?	?	?	?	?	?	?	2	1	2	1	0	1
[illegible]	Progn. rapax	?	0	1	?	0	0	1	1	2	1	2	1	0	1
[illegible]	T. nepaeolicus	?	?	?	?	?	?	?	?	1	0	?	1	?	0
[illegible]	T. novum sp.	?	1	1	0	1	1	0	1	1	0	?	1	1	0
[illegible]	T. proriger	0	1	1	0	1	1	0	1	1	0	?	1	1	0
[illegible]	Y. columbianus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Russellosaurus coheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	Angolasaurus bocagei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
[illegible]	E. composite YP	?	?	?	?	?	1	?	?	?	?	?	?	?	?
[illegible]	E. clidastoid	?	0	1	0	1	1	0	0	2	1	?	?	?	0
[illegible]	Tethysaurus nopscai	?	1	1	1	0	0	0	0	?	?	?	?	?	0
[illegible]	Mosasaurus	?	0	1 / 2	1	0	0	0 / 1	0 / 1	3	1	1	1	0	1
[illegible]	Plotosaurus	?	0	2	1	0	0	1	1	3	1	1	1	0	1
[illegible]	Plioplatecarpus	?	0	1	0	1	1	0	0	2	0	?	1	1	0
[illegible]	Globidens	?	?	?	?	?	0	?	?	2	1	0	1	0	1

	113	114	115	116	117	118	119	120	121	122	123	124	125	126
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	?	0
A. dalmaticus	0	0	0	0	0	0	?	0	0	0	?	?	?	0
A. buccichi	0	0	0	0	0	0	?	0	0	?	?	?	?	0
Trieste Aglalosaur	0	0	0	0	?	?	?	?	?	0	1	1	?	0
Dallasaurus turneri	0	0	?	?	?	?	?	?	0	0	?	?	?	0
Haasiasaurus gittlemani	0	0	0	0	1	1	1	0	0	0	?	?	?	0
Taxon novum	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Halisaurus	0	0	1	0	1	1	1	0	0	1	1	1	?	0
C. liodontus	1	1	2	1	0	0	0	1	0	1	0	0	1	2
C. mooreville	1	1	2	1	0	0	0	1	0	1	0	0	1	2
C. novum sp.	1	1	2	1	0	0	0	1	0	?	?	?	?	2
C. propython	1	1	2	1	0	?	0	?	?	?	?	?	?	2
P. planifrons	0	?	2	0	1	1	1	0	0	?	?	?	?	1
P. tympaniticus 8769	?	?	?	?	?	?	?	?	?	?	?	?	?	?
P. tympaniticus 600	0	1	2	0	1	1	1	0	0	1	1	1	0	1
Plesio. crassidens	1	1	2	1	0	0	0	1	0	?	?	?	?	2
Progn. overtoni	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Progn. rapax	1	1	2	1	0	0	0	1	0	?	?	?	?	2
T. nepaeolicus	0	0	1	?	1	1	1	0	0	?	?	?	?	?
T. novum sp.	0	0	1	?	?	?	?	?	?	?	?	?	?	1
T. proriger	0	0	1	?	1	1	1	0	0	1	?	0	0	1
Y. columbianus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Russellosaurus coheni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Angolasaurus bocagei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
E. composite YP	?	?	?	?	?	?	?	?	?	?	?	?	?	?
E. clidastoid	0	1	2	0	1	0	1	0	0	?	?	?	?	1
Tethysaurus nopscai	1	1	?	?	?	?	?	?	?	0	0	?	?	?
Mosasaurus	1	1	2	1	0	0	0	1	1	1	0	0	1	2
Plotosaurus	1	1	2	1	0	0	0	1	1	?	?	?	?	2
Plioplatecarpus	0	1	2	0	1	1	1	0	0	?	?	?	?	1
Globidens	1	1	?	?	?	?	?	?	?	?	?	?	?	2

		127	128	129
[illegible]	Outgroup	0	0	0
[illegible]	A. dalmaticus	0	?	0
[illegible]	A. buccichi	0	?	0
[illegible]	Trieste Aigialosaur	0	?	0
[illegible]	Dallasaurus turneri	?	0	1
[illegible]	Haasiasaurus gittlemani	0	?	?
[illegible]	Taxon novum	?	0	?
[illegible]	Halisaurus	0	0	0
[illegible]	C. liodontus	0	0	1
[illegible]	C. mooreville	0	0	1
[illegible]	C. novum sp.	?	0	1
[illegible]	C. propython	?	0	1
[illegible]	P. planifrons	?	2	0
[illegible]	P. tympaniticus 8769	?	3	0
[illegible]	P. tympaniticus 600	0	3	0
[illegible]	Plesio. crassidens	?	0	?
[illegible]	Progn. overtoni	?	0	1
[illegible]	Progn. rapax	?	0	1
[illegible]	T. nepaeolicus	?	0	0
[illegible]	T. novum sp.	?	0	0
[illegible]	T. proriger	1	0	0
[illegible]	Y. columbianus	?	2	0
[illegible]	Russellosaurus coheni	?	1	?
[illegible]	Angolasaurus bocagei	?	3	0
[illegible]	E. composite YP	?	3	1
[illegible]	E. clidastoid	0	3	1
[illegible]	Tethysaurus nopscai	?	?	?
[illegible]	Mosasaurus	1	0	1
[illegible]	Plotosaurus	1	0	1
[illegible]	Plioplatecarpus	?	3	0
[illegible]	Globidens	?	0	1

GENERAL CONCLUSIONS

This study represents the first large-scale systematic analysis constructed around the semi-aquatic squamates known in general terms as aigialosaurs. Previous workers (deBraga and Carroll 1993, Bell 1993 and 1997, Polcyn and Bell in press) have included aigialosaurs as peripheral taxa in larger studies of fully aquatic mosasaurians. These studies have generally resulted in little support for the family Aigialosauridae as a monophyletic taxon, but the basal mosasauroids involved were too poorly known to make anything other than tentative evolutionary statements. An improved understanding of basal mosasauroids is essential to both mosasauroid and anguimorph systematics.

Thorough redescriptions of the monotypic taxa *Aigialosaurus dalmaticus* Kramberger, 1892 and *Opetiosaurus bucchichi* Kornhuber, 1901 have shown *Opetiosaurus* to be a junior synonym of *Aigialosaurus*. The taxa are differentiated at the species level by several equivocal characters that may or may not be a result of taphonomic forces. The redescriptions correct previous studies that provide erroneous data with regards to aigialosaur specimens (Carroll and deBraga 1992, Bell 1993, 1997)

The improved morphological understanding of *A. dalmaticus* and *A. bucchichi* allowed the genus *Aigialosaurus* to be coded into an existing anguimorph data matrix (Gao and Norell 1998). The resulting tree topologies indicate that *Aigialosaurus* (and by association mosasauroids in general) are platynotan lizards that, together with *Paravaranus*, form a sister group to the family Varanidae. This systematic analysis did not include Serpentes and thus the validity of the taxon Pythonomorpha (Pierce and Caldwell 2004) could not be tested. Inclusion of Serpentes in the data matrix would be an excellent starting point for future research in this area.

When the data matrix of Bell and Polcyn (in press) was revised to reflect the redescriptions of *A. dalmaticus* and *A. bucchichi*, the most recent hypothesis of mosasauroid relationships (Bell and Polcyn in press) was not supported. The suggestion of previous studies (Bell 1993, 1997, Bell and Polcyn in press) that aigialosaurs represent a paraphyletic assemblage is supported, although the rediagnosis of the family Aigialosauridae proposed by Bell and Polcyn (in press) would make that taxon monophyletic. While the interrelationships among the basal mosasauroids remain poorly resolved, the retrieved tree topologies indicate that the paddle-like limb commonly associated with mosasaurs evolved once in halisaurs and a second time within Natantia. This finding contradicts the suggestion by Bell and Polcyn (in press) that paddle-like limbs evolved three times within the mosasauroid lineage.

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