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**ANATOMY, FUNCTIONAL MORPHOLOGY AND
PHYLOGENY OF AİSTOPODA (TETRAPODA,
LEPOSPONDYLI)**

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JULY, 2000

A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND
RESEARCH IN PARTIAL FULFILLMENT OF THE REQUIREMENTS OF THE
DEGREE OF DOCTOR OF PHILOSOPHY.

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0-612-69965-X

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GENERAL INTRODUCTION

BACKGROUND

Modern tetrapods are subdivided into two general groups, amniotes and amphibians. Three groups comprise extant amphibians (termed Lissamphibia): salamanders, frogs and caecilians. Modern amphibians are united by structures of the middle ear and eye, and lack the multiple membranes of the amniotic egg that unite amniotes. Additionally, there is a vast assemblage of extinct archaic amphibians from the Paleozoic Era (543-250 MA) that possess traits that are also present in the sarcopterygian “fish” which gave rise to them. Paleozoic tetrapods have long been distinguished by the patterns of their vertebrae. Authors such as Romer (1945) used the size, shape and relationships of centra to identify and classify “rhachitomes” (large intercentra, small pleurocentra), “stereospondyls” (pleurocentra absent), and “anthracosaurs” (large pleurocentra, small intercentra). The clearest distinction between taxa is at a higher taxonomic level—between the multipartite centrum-bearing “labyrinthodonts” and a group of vertebrates with single, spool-shaped centrum called lepospondyls. Many features other than vertebral characters help separate these groups. “Labyrinthodonts” take their name from complex infolding of tooth dentine that appears labyrinthine in cross section. This in-folding is absent in lepospondyls. Lepospondyls also resemble one another in the absence of many other “labyrinthodont” features: an intertemporal bone, a distinct atlas intercentrum, and a squamosal, or “otic,” notch. Size is another distinguishing feature. Most labyrinthodonts are large, a meter or more in length. Lepospondyls, on the other hand, are very small. These features led Zittel (1888) to establish Lepospondyli as its own subclass, separate from the “labyrinthodonts.”

Within the lepospondyls are included a wide diversity of body types, each clearly distinct, but showing little evidence that any one group has special relationships to any other. As recently summarized by Carroll et al. (1998), there are five definite, and one possible, member of the subclass. The most generalized body plan is found in the Microsauria, which, as their name suggests, look like “little reptiles.” Microsaurs range from short bodied fully terrestrial forms to elongate forms with many vertebrae (Carroll and Gaskill, 1978). These contrast with the Nectridea, all short bodied but with distinctive deep tails for propulsion through the water (Bossy, 1976; Milner, 1978). Some nectrideans have developed oversized, boomerang shaped heads. Adelospondyli, which are only known from the Carboniferous of Scotland, are elongate and limbless. They have lost the endochondral portions of their pectoral girdle but have retained the dermal pectoral girdle (Andrews and Carroll, 1991; Carroll and Andrews, 1998). Lysorophids are also elongate, but they still possess limbs, albeit in a greatly reduced size. They also have an orbitotemporal fenestra and anteriorly sloping suspensorium (Wellstead, 1991, 1998). The only lepospondyl that lacks simple, spool-shaped centra is *Acherontiscus*, a poorly preserved specimen from Scotland that has embolomere-like pleurocentra and intercentra but a small skull and elongate trunk (Carroll, 1969).

Perhaps the most striking group of Paleozoic tetrapod is Aïstopoda. They are extremely elongate, with up to 230-250 vertebrae, and have no limbs and only traces of the pectoral girdle. Their skulls are highly fenestrate, although they retain a distinct orbit, in contrast with lysorophids. The oldest aïstopods (Fig. 1) come from the mid Viséan (340-345 MA; Wellstead, 1982) Wardie Shales and the late Viséan deposits of East Kirkton, Scotland (Milner, 1994), and the youngest come from the Lower Permian fissure

deposits at Ft. Sill Oklahoma (270-280 MA; McGinnis, 1967). Most are known from the early Westphalian D (approx. 300 MA) of Mazon Creek, Illinois and late Westphalian D (approx. 295 MA) of Linton, Ohio, and Nýřany, Czech Republic (Fritsch, 1879; Romer, 1930; Steen, 1930, 1938; Baird, 1964; Carroll, 1998b). Other aïstopods have been found in the Westphalian A of Jarrow, Ireland (Huxley and Wright, 1867; Milner, 1994), the Westphalian A-B of the Swisshelm Mountains, Arizona (Thayer, 1985), the Westphalian B of Newsham, Northumberland, England (Boyd, 1984), the Westpahlian D of Five Points, Ohio (Hook and Baird, 1993), the Stephanian (296-286 MA) of Kounova, Czech Republic (Fritsch, 1879; Schwartz, 1908), and Colorado (Vaughn, 1969). Aïstopod fragments have been reported from the Westphalian D of Cannelton, Pennsylvania (Baird, 1964), the Lower Permian Cutler Formation (Berman, 1993) and the late Carboniferous Dunkard Formation (Baird, pers. comm.).

The first aïstopods were described by Huxley and Wright (1867), who named two genera: *Ophiderpeton* and “*Dolichosoma*.” From the beginning two general morphotypes were recognized. *Ophiderpeton* has a broad skull and is thickly covered with dermal armor, while “*Dolichosoma*” (now known as *Phlegethontia*; Baird, 1964; Chapter 2), has a slender skull and fine ventral gastralia but lacks dorsal osteoderms. These two morphotypes have been recognized as families: Ophiderpetontidae (Schwartz, 1908) and Phlegethontiidae (Cope, 1875). A third family, Lethiscidae, has recently been added (Wellstead, 1982); however, it is close to the ophiderpetontid morphotype (Chapter 5).

The problem facing students of aïstopods is that they are rarely complete. Most specimens are fragmentary strings of vertebrae. Out of context, they provide relatively little information, since overall vertebral morphology is conserved within the group. This

has led to a proliferation of taxa, especially from the classic localities. However, more recently developed techniques for preparation and study of coal shale fossils (Baird, 1955) has made it possible to examine details of anatomy at fine scales. This has in recent years prompted a revision, led by Professor Robert Carroll, of all lepospondyl taxa (summarized in Carroll et al., 1998). The present revision of Aïstopoda represents the completion of this effort.

Prof. Carroll discovered new specimens from Nýřany, including complete ophiderpetontids and phlegethontiids, in the Naturhistorisches Museum in Vienna. Information from these specimens was supplemented by specimens from Mazon Creek recently donated by private collectors to Field Museum of Natural History. A wide range in body size is represented, permitting their being arranged in probable growth series. These new anatomical data were coupled with computer assisted cladistic analysis to produce a new, synthetic view of aïstopods, their biology, and their relationships.

RESEARCH DESIGN

Selection of Material

This thesis is an exercise in descriptive taxonomy, which produces all of the data used in subsequent searches for patterns of interrelatedness. It is also, in part, an exploration of the limits of higher level cladistic inference in the face of incomplete data sets.

Early in this research, it was decided that I narrow my focus to the Westphalian forms. The type material Huxley described from earlier beds in Ireland has been badly degraded due to pyrite disease (McGinnis, 1967). Since Professor Carroll had already

produced latex casts of the best Vienna material and I had borrowed “galvanotypes” of Fritsch’s specimens from Prague, I decided to focus my efforts on the North American collections. This was richly rewarding, as I was able to see newly available material from Linton at the Carnegie Museum and from Mazon Creek at the Field Museum of Natural History. However, to provide a thorough phylogenetic study, restudy of the unique type of *Lethiscus* was also necessary. Fortunately, new technology has been developed since the study of Wellstead (1982) that provided a rich source of new data.

Techniques of Study

Specimens from Linton are preserved crushed within organic rich shales called cannel coal. Because the bone is so small and friable (splitting of the shale usually cleaves the bone), and the matrix insoluble, more success is had by etching away the bone with dilute hydrochloric acid, which leaves a high quality natural mould from which latex peels may be taken (Baird, 1955). Material from Mazon Creek is preserved in three dimensions within siderite nodules. The original bone is degraded and partially replaced by the clay mineral kaolinite. The in-filling materials were removed using a pin vise under a dissecting microscope. Latex casts were produced in the same manner as done above. All casts were drawn under an oblique light using a camera lucida attached to a Wild dissecting microscope.

I studied each of the families, Phlegethontiidae, Ophiderpetontidae, and Lethiscidae, in order of the amount of previous study. I started with Phlegethontiidae, which is the most thoroughly described family. After completion of this study of the most derived group and having formulated questions about bone homologies, I began to

consider Ophiderpetontidae. It was necessary to know the anatomy of both groups before moving on to the final chapters, where I considered the anatomy of a new aïstopod, the poorly preserved type specimen of *Lethiscus* in serial x-ray sections, and produced a cladistic study in the in-group relationships.

ORGANIZATION OF CHAPTERS

In order to understand the evolution of the peculiar anatomy of aïstopods, it was first necessary to establish their relationships with other early tetrapods. This is the subject of Chapter 1. Discovering the anatomy of lepospondyls is hampered by the sometimes fragmentary nature of the fossils. However, exclusion of taxa may impact the quality of the analysis by not providing the whole distribution of characters (Novacek, 1992a, b). I developed a method whereby problematic taxa may be discovered and removed after the analysis, so that they may assist in determining tree topology. I also produced a working hypothesis of lepospondyl relationships, determining the closest out groups for use as comparison taxa in evaluating anatomy and polarity.

The anatomy and interrelationships of Phlegethontiidae are treated in Chapter 2. I was able to study a reasonably complete growth series and generate a hypothesis of a general developmental mechanism leading to such a derived condition from the very different bauplan of “labyrinthodonts.” Chapter 3 considers Ophiderpetontidae. Although the skull of ophiderpetontids has been recently studied (Milner, 1994; Carroll, 1998a), very little has been published on their postcranial anatomy. I was also fortunate to have been able to borrow the skull of the poorly known ophiderpetontid *Coloraderpeton*, which has only been described in an unpublished thesis 17 years ago (Gallup, 1983).

Chapter 4 describes a new taxon, whose distinctiveness was discovered only after preparation. It was previously described as a phlegethontiid (Turnbull and Turnbull, 1955), but it has a more complete complement of skull table bones.

Finally, in Chapter 5, I consider the poorly preserved, unique *Lethiscus*, using data from the High-Resolution Computerized Tomography facility at the University of Texas at Austin. This is followed by a cladistic analysis of the in group relationships of all aistopods and a new classification. The final classification was presented in both a Linnean and phylogenetic format. There is an ongoing debate within the systematic community regarding the degree to which Linnean taxonomy must be altered in order to directly reflect phylogeny (see <http://www.ohiou.edu/phylocode/> for a newly proposed “Phylocode of Zoological Nomenclature”). Some are even questioning the Linnean binomial (Pleijel, 1999; Cantino et al., 1999). While I believe that abandoning the binomial would cause more confusion than may be justified, I do agree that Linnean ranks do not easily fit into a system based on monophyly. I abandon them in my phylogenetic taxonomy (Chapter 5)

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FIGURE 1. Geological timescale showing the lineage duration of all lepospondyl groups. Localities indicated by an * are where aistopods have been discovered. From Carroll et al. (1998).

[illegible]

CHAPTER 1

A PHYLOGENETIC ANALYSIS OF LEPOSPONDYLI

In press in *Systematic Biology* as: Jason S. Anderson. The phylogenetic trunk: maximal inclusion of taxa with missing data in an analysis of the Lepospondyli (Vertebrata, Tetrapoda).

PREAMBLE CHAPTER 1

Before I began my investigation of the anatomy and interrelationships of aïstopods, I felt it important that they be placed within a larger phylogenetic context. This is necessary to interpret the relative importance of various aïstopod anatomical features. Indeed, it is sometimes impossible to identify positively bones of extinct animals unless they can be compared with similar elements in related species. This is particularly a problem for animals with highly divergent body plans such as aïstopods. Rigorous cladistic methods have only recently been applied to the lepospondyls, so many outstanding questions exist regarding the details of their sister-group relationships. Lepospondyls are difficult to study and not all are thoroughly known. The two previous analyses attempted to compensate for this lack of detail by using higher taxa as their operational taxonomic units, with the best-known species included where possible. I approached this question from the opposite direction. Since I had no a priori method for determining how detrimental an incomplete taxon might be to the outcome of an analysis, I decided to include all taxa and remove the troublesome species a posteriori, when they were recognized as problematic. This approach required developing a procedure that would make the identification of the most problematic taxa more objective. The following chapter presents my phylogenetic hypothesis of the placement of the aïstopods within the Lepospondyli, employing this method to achieve maximal inclusion of incomplete taxa.

ABSTRACT

The importance of fossils to phylogenetic reconstruction is well established. However, analyses of fossil data sets are confounded by problems related to the incomplete nature of the specimens. Taxa that are incompletely known are problematic because of the uncertainty of their placement within a tree, leading to a proliferation of most parsimonious solutions because of wild card behavior. Problematic taxa are commonly deleted based on a priori criteria of completeness. Paradoxically, a taxon's problematic behavior is tree dependent, and levels of completeness are not necessarily associated with problematic behavior. Exclusion of taxa based on completeness eliminates real character conflict and, by not allowing incomplete taxa to determine tree topology, the phylogenetic hypothesis is diminished.

A method is proposed to allow optimization of taxonomic inclusion and tree stability. It identifies and removes taxa causing multiple most parsimonious solutions, producing a more stable topology, called the phylogenetic trunk. This method is used in an analysis of the Paleozoic Lepospondyli. A single most parsimonious tree, or trunk, was found after removal of one taxon identified as being problematic. The 38 trees found one additional step from this primary trunk are reduced to two by removal of one additional taxon. These trunks are compared to the trees found by excluding taxa with various degrees of completeness. Effects of incomplete taxa are explored by comparison with the stable tree. Correlated characters associated with limblessness are discussed regarding the assumption of character independence. Inclusion of intermediate taxa is found to be the single best method for breaking down long branches.

INTRODUCTION

Perhaps the primary difficulty of phylogenetic analysis of fossil data sets comes from information missing due to non-preservation or inaccessibility (Rowe, 1988; Nixon and Wheeler, 1992; Novacek, 1992b; Grande and Bemis, 1998). Taxa that are not coded for particular character states have those states reconstructed, based upon the distribution of the states present in other taxa (Maddison and Maddison, 1992). This may produce a kind of "circularity of reasoning" (Grande and Bemis, 1998). Thus, missing data allows incomplete taxa to act as wild cards within the analysis (Nixon and Wheeler, 1992), proliferating the number of most parsimonious trees (MPTs) since the problem taxon fits several positions on the tree (Huelsenbeck, 1991; Novacek, 1992b).

Maddison (1993) distinguished several types of missing data: (1) the data are missing, (2) the character is missing, and (3) the character is polymorphic. Programs such as PAUP (Swofford, 1998) are able to accommodate polymorphic characters, and they will be not be considered further. Missing characters and missing data are treated in the same way by phylogenetic analysis software, so throughout this paper "missing data" refers to both cases, unless otherwise stated.

The common method for controlling the influence of missing data has been *a priori* elimination of potential problem taxa based upon arbitrary criteria of completeness (e.g., taxa over 12% incomplete are removed from the analysis; Rowe, 1988; Grande and Bemis, 1998). However, elimination of taxa *a priori* prohibits those taxa from determining topology, thus removing potentially important character conflicts from the analysis (Novacek, 1992b; Kearney, 1998). It assumes that all incomplete taxa are equally problematical, which is not the case (Kearney, 1998). Further, since a taxon's stability depends on the shape of the tree, not allowing that taxon to help determine topology prohibits it from finding a stable position. It is therefore necessary to optimize inclusion of incomplete taxa while maintaining a reasonably well-resolved tree.

Previous studies of the effects of missing data have considered one or two incomplete taxa within a matrix of otherwise complete taxa (Novacek, 1992a; Grande and Bemis, 1998). Not adequately addressed is the problem in which a matrix contains many incomplete taxa. In these instances, it can be predicted that there will be interaction of characters, resulting from the way in which phylogenetic programs treat missing data, and that deletion of taxa could radically shift topology and change tree lengths. A method is needed to investigate the alternatives that a deleted taxon has upon tree topology.

A procedure that does so is outlined below. It involves the systematic discovery and removal of problem taxa subsequent to a phylogenetic analysis. This procedure, termed the phylogenetic trunk method (since a stable "trunk" is sought amongst the swaying "branches" of multiple MPTs), permits all incomplete taxa to determine tree topology and facilitates identification, removal and *a posteriori* exploration of effects caused by problematic taxa. It is applied to an analysis of the Lepospondyli and the general problem of Paleozoic tetrapod relationships.

To avoid confusion in terminology, I should state that I follow Ahlberg and Clack (1998) in using Tetrapoda as a stem taxon comprised of all taxa crown-ward of Elpistostegalia, rather than the crown definition of Gauthier et al. (1988b) and Laurin (1998), for two reasons. One, this definition is closer to the traditional meaning of Tetrapoda (taxa with digitized limbs). Second, I do not adhere to the principle of priority of explicit phylogenetic definition advocated by Laurin when applied to historically laden names. Instead, I follow de Querioz and Gauthier (1990, 1992, 1994) who advocate following the first use of a name with a specific clade, which in this case would be Gaffney's (1979) use of Tetrapoda. This criterion accommodates phylogenetic taxonomies that predate current conventions. Furthermore, while never explicitly stated, it is clear from his figure that Gaffney's Neotetrapoda is a crown taxon, and thus takes priority over a crown-based definition of Tetrapoda.

"Labyrinthodonts" and Lepospondyls

Paleozoic tetrapods have been traditionally separated into two groups based upon vertebral morphology: the "Labyrinthodontia" (now considered paraphyletic) and Lepospondyli (Romer, 1945; Carroll, 1988). "Labyrinthodonts" are characterized by large size, the retention of labyrinthine in-folding of tooth dentine and multipartite vertebrae (of intercentra, pleurocentra and neural arch) from their osteolepiform ancestors.

Lepospondyls, known from the Viséan to Lower Permian of North America and Europe and persisting into the Upper Permian of North Africa, are small tetrapods that possess a single spool-shaped centrum. They lack labyrinthodont infolding of the teeth and various cranial ossifications of primitive "labyrinthodonts" are lost (Carroll et al., 1998). The current concept of this taxon includes five orders. The largest and most diverse is the Microsauria, ranging in morphotype from short, terrestrially-adapted forms so convergent with reptiles that they have at times been included with them (Dawson, 1863; Gregory, 1965; Carroll and Baird, 1968; Carroll, 1991; Reisz and Modesto, 1996), to elongate forms with reduced limbs (Case, 1929; Gregory et al., 1956; Carroll and Gaskill, 1978; Carroll, 1998b). The members of the Nectridea are, with one exceptional family, aquatic amphibians, distinguished by unique caudal vertebrae with large symmetric neural and haemal arches fused to the centra (Baird, 1965; Bossy, 1976; Milner, 1978, 1980; Bossy and Milner, 1998). The Adelospondyli are known only from Scotland. Although they possess pronounced dermal pectoral girdle elements, there is no trace of either endochondral girdle ossifications or limbs (Andrews and Carroll, 1991; Carroll and Andrews, 1998). Members of the Aistopoda are superficially snake-like in appearance with highly fenestrated skulls, no limbs, only a vestige of pectoral girdle elements and up to 230 vertebrae (Baird, 1964; McGinnis, 1967; Carroll, 1998a). Lysorophids are also elongate tetrapods, but they still possess limbs, albeit reduced in size and composition similar in proportions to those of *Amphiuma* (Wellstead, 1991, 1998).

Lepospondyls are typically much smaller than "labyrinthodonts." This has led some authors to hypothesize that the Lepospondyli could be an unnatural collection associated by characters attributable to small size, especially considering the divergent cranial anatomy among the constituents (Carroll, 1989, 1999). For example, labyrinthine infolding of tooth dentine is present in a large microsauro (Carroll and Gaskill, 1978) and a large sauropleurine nectridean (Baird, pers. comm.), and is absent in small and larval temnospondyls (Bolt, 1969, 1979). Reduction of cranial ossifications, common in lepospondyls, is a characteristic of extant miniaturized salamanders (Hanken, 1984). It is argued that since these characters seem to be correlated with small size, establishing the homology of the loss is difficult if not impossible (Carroll, 1986, 1995, 1999).

Modern amphibians, the Lissamphibia, have been somewhat uncomfortably incorporated within this scheme. Lissamphibians possess holospondylous vertebrae, but few other characters that unite them with any Paleozoic group. Romer (1945) placed frogs with the "labyrinthodonts" and caecilians and salamanders with lepospondyls. In 1963, Parsons and Williams argued for lissamphibian monophyly, which has been widely accepted (but see Carroll and Currie, 1975; Carroll and Holmes, 1980). Bolt (1969, 1977) described many similarities between lissamphibians and dissorophoid temnospondyls, particularly *Dolesempetron*, listing nine synapomorphies arguing for a temnospondyl origin of modern amphibians (Bolt, 1991). As a result lissamphibians have either been placed within the Temnospondyli (Milner, 1988; Trueb and Cloutier, 1991), or, more conservatively, as a separate subclass of equal rank (Carroll, 1988).

Until recently, phylogenetic hypotheses of Paleozoic tetrapods have not supported lepospondyl monophyly (Fig. 1). Indeed, various studies have placed lepospondyls next to every conceivable "labyrinthodont" group. A series of papers in the mid 1980s placed nectrideans as sister taxa to colosteids, which in turn were out group to a microsauro-temnospondyl dichotomy (Fig. 1 c) comprising a higher taxon named the Batrachomorpha (Panchen, 1980; Smithson 1985; Milner et al., 1986; Panchen and

Smithson 1987, 1988; Milner, 1993). A close relationship between microsaur and temnospondyls has also been suggested by recent studies of Devonian and Carboniferous tetrapods (Lebedev and Coates, 1995; Coates, 1996; Ahlberg, 1998).

The recent large scale, computer assisted cladistic analyses by Michel Laurin and Robert Reisz (Laurin and Reisz, 1997; Laurin, 1998; subsequently "Laurin and Reisz" is used to refer to both papers unless otherwise specified) elaborated upon Carroll's (1995) analysis of Paleozoic tetrapods, expanding its scope to include lissamphibians (Fig. 1 d). In their hypothesis, a monophyletic Lissamphibia is deeply nested within the Lepospondyli, which is in turn sister group to amniotes and their stem (to the exclusion of *Seymouria* and other anthracosaurs), thus departing from the reptilomorph-batrachomorph view. If this hypothesis were correct, lepospondyls would become crucial to understanding the phylogenetic relationships of frogs, salamanders and caecilians, and, as second outgroup, to amniotes, i.e. all extant tetrapods. Yet, surprisingly, there has been no detailed phylogenetic test of lepospondyl monophyly. The only cladistic analyses with an exclusively lepospondyl focus were three small studies of limited scope; one of nectridean relationships by Milner (1980; it also appears in a somewhat modified form in Milner, 1993), another of tuditanomorph microsaur by Schultze and Foreman (1981), and the third of the lepospondyl orders using only vertebral characteristics by Carroll and Chorn (1995).

Carroll and Laurin and Reisz included primarily familial or ordinal level taxa in their analyses, assuming their monophyly. This is potentially problematical because, as Nixon and Davis (1991) observed, errors are introduced into an analysis when nonmonophyletic groups are used as operational taxonomic units, especially when defined on the basis of pre-existing, typological taxonomy. Laurin and Reisz included only two lepospondyl species. One, *Rhynchonkos stovalli*, was included because of previous hypotheses of its close relationship with caecilians (Carroll and Currie, 1975). The other, the morphologically divergent *Pantylus cordatus*, was included because it is

relatively completely known (Carroll, 1968; Romer, 1969a). I hope to be able to produce a more reliable phylogeny by including all recognized species. This, however, raises the problem of the many gaps in the data matrix that will be produced by the inclusion of incompletely known species.

MATERIALS AND METHODS

Because the degree of completeness is not necessarily correlated with the degree to which an incomplete taxon will act as a wild card (Kearney, 1998), I propose a new method for considering taxa with high amounts of missing data within a phylogenetic analysis which allows their input in tree construction. The first step is the inclusion of all taxa in a matrix, which is analyzed and consensus trees produced to identify areas where problem taxa are present. Adams consensus is particularly useful, since it maintains stable component topology while reducing unstable taxa to their most inclusive group. The unstable taxa identified in the Adams consensus tree are ranked according to the number of different positions in which they occur within the component trees. The most variable taxon is removed from the matrix and the analysis rerun. Should two taxa have an equal variability score, each in turn is excluded to determine the taxon whose elimination produces the fewest MPTs. If eliminating both taxa produces the same number of MPTs, the analysis bifurcates and subsequent steps are performed on both sets of trees. Should the variable taxon be a clade, the most incomplete member of that clade is removed. Iterations are performed until no greater resolution can be gained (or until a level of stability satisfactory to the investigator is achieved). This tree, the phylogenetic trunk, forms the basis for further experimentation. Problem taxa may then be examined by reintroducing them to the analysis and changes to the trunk thus produced explored individually. Examination of character conflict in this manner is easier to understand than the cacophony of confounded signals produced by simultaneous consideration of several

problem taxa, as is the case with current consensus methods. This method permits maximal inclusion of incomplete, but stable, taxa which would otherwise have been eliminated under an arbitrary cut-off criterion, making the final phylogenetic hypothesis richer and more complete (Novacek, 1992a; Halanych, 1998).

This method assumes that the amount of taxon variability is strongly correlated with production of more MPTs, which is true for the example at hand, but this assumption remains to be tested using computer simulations. An alternative method that avoids this assumption involves the systematic deletion of all variable taxa to find the one whose deletion produces the fewest MPTs. Further iterations are performed using this procedure until the desired level of resolution is achieved.

The proposed method is similar to some consensus methods such as the Reduced Adams consensus (Wilkinson, 1994) and the Maximum Agreement Subtree (Kubicka et al., 1995), which also seek to remove problematic taxa. However, these methods focus on portraying shared topology within all component trees, and usually prune all unstable taxa. By ranking the degree of instability, the phylogenetic trunk method allows for less variable taxa to settle when more disruptive wild cards are removed. Further, by reanalyzing the matrix after each pruning cycle, the phylogenetic trunk method permits the discovery of a topology different from those within the component trees.

Analysis

The phylogenetic trunk method was used to analyze the lepospondyls. Forty-two fossil lepospondyls were coded for 182 osteological characters, including all characters that have been mentioned as distinctive in various descriptive works, citations to which can be found in Carroll et al. (1998). Taxa were coded from the literature and from specimens when possible (Table 1). Characters used in previous lepospondyl analyses (Milner, 1980; Schultze and Foreman, 1981; Carroll and Chorn, 1995) were included in one form or another (see Appendix 1). The guiding principle was total evidence (Gauthier

et al., 1988a; Kluge, 1989); any character that was present in at least two taxa and that could not be shown to be non-homologous by pre-analysis criteria of homology (e.g., de Pinna, 1991) was included. The operational taxonomic level was the species (Bininda-Emonds et al., 1998; Weins, 1998), with the exception of *Brachydectes*, which was included as a composite of *B. elongatus* and *B. newberryi*. Use of species introduces additional uncertainty, as most lepospondyls (indeed, most Paleozoic tetrapods) are not completely known. Many of the included species are known from single or a few incomplete specimens, sometimes of questionable association, leaving many characters uncodable. Unlike Grande and Bemis (1998), no distinction was made between characters uncodable due to lack of preservation or inaccessibility (where a character is potentially codable but unobservable as preserved); both received a "?." Inapplicable characters, which are inevitable given lepospondyl morphologic diversity, were coded "-", although current phylogenetic programs treat missing and inapplicable characters equally. Polymorphisms and partial uncertainty were coded according to Maddison and Maddison (1992).

The holotype of *Micraroter erythrogeios* (Carroll and Gaskill, 1978) was removed (Wilkinson, 1995) because it is essentially identical for codable characters with the more complete specimen in the collections in the Bernard Price Institute of Paleontological Research, Johannesburg (BPI 3839), here assumed to be conspecific. Adelogyrinids are represented by the best known species *Adelogyrinus simorhynchus*, since *Adelospondylus watsoni* is similarly redundant.

The Jurassic caecilian *Eocaecilia micropodia* (Jenkins and Walsh, 1993) was included because its primitive characters (not found in any other caecilian) closely resemble characteristics of microsaurs. It fits the criteria for a fossil that is potentially informative in an analysis of extant forms. It is clearly a caecilian, sharing several synapomorphies (pseudodentary, medial process of the pseudodentary, os basiale, long retroarticular process, intravertebral foramina for the spinal nerves, and pedicellate,

labiolingually-oriented bicuspid teeth), but retains many primitive characters shared with microsaur (several centers of ossification of the skull, limbs, pattern of dermal skull roof, odontoid process on the atlas with laterally expanded proximal articular surface). A test of lissamphibian monophyly is beyond the scope of the current study, the primary purpose being the establishment of the basic pattern of lepospondyl phylogeny.

No one group of “labyrinthodonts” is an obvious sister group of the lepospondyls, so five different taxa are included in the study. They are the embolomere *Proterogyrinus scheelei* (Romer, 1970; Holmes, 1980, 1984), the primitive temnospondyls *Balanerpeton woodi* (Milner and Sequeira, 1994) and *Dendrerpeton acadianum* (Godfrey et al., 1987; Holmes et al., 1998), the colosteid *Greererpeton burkemorani* (Romer, 1969b, 1972; Smithson, 1982; Godfrey, 1989), the seymouriamorph *Seymouria baylorensis* (White, 1939; Berman et al., 1987; Laurin, 1995, 1996), and the stem amniote *Limnoscelus paludis* (Williston, 1911, 1912; Romer, 1946; Fracasso, 1984; Berman and Sumida, 1990). The whole assemblage was rooted on *Acanthostega gunnari* (Clack, 1994, 1998; Coates 1996; Ahlberg and Clack, 1998). Not considered were baphetids (loxommatids) or *Crassigyrinus* because most recent phylogenies place them far stemward from lepospondyls. Where necessary, characters were polarized using *Ichthyostega* (Jarvik, 1996a), and *Eustenopteron* (Andrews and Westoll, 1970; Jarvik, 1996b) as successively further outgroups.

Consistent in Carroll’s (1995) most parsimonious trees was the sister group relationship between aistopods and adelospondylids. He attributed this to convergence due to elongation and limb loss. Fifteen characters in his matrix grouped limbless taxa, which could potentially swamp the phylogenetic signal in a matrix with a large amount of homoplasy and missing data. In an attempt to limit character non-independence due to convergence, limb loss characters (e.g., humerus present or absent) were eliminated. Elongation, which is correlated with limblessness (Gans, 1975, 1986; Lande, 1978;

Greer, 1991), is still accounted for in the matrix (character 180, number of presacials; character 182, skull-to-trunk ratio).

All characters were reexamined. Previous analyses (Laurin and Reisz, 1997; Laurin, 1998) coded brachystelechid microsaurs (*Batropetes*, *Carrolla*, *Quasicaecilia*) as having open interpterygoid vacuities, although their palatal region is very incompletely known. However, when basal skull length is regressed upon area of the interpterygoid vacuity (Fig. 2), brachystelechids fall on a regression line with all other microsaurs, which is a different line than that of the true open palated temnospondyls, suggesting that the "open" condition in brachystelechids is apparent, due to allometric scaling. All microsaurs are therefore coded "0" as having closed palates. Indeed, the term closed palate is misleading; primitive tetrapods have narrow, slit-like openings which run along the cultriform process (Clack, 1994). *Greererpeton* is coded as having the primitive closed morphology for similar reasons (Holmes et al., 1998). True palatal closure only occurs when the pterygoids suture at the midline (as in baphetids, *Batrachiderpeton* and *Keraterpeton*; Fig. 3) or in the formation of a secondary palate. Only temnospondyls and various nectrideans were coded as having open palates.

In adelospondylids, tabular articulations were coded using the tabular-squamosal despite the fusion of these two bones, assuming that the tabular and squamosal portions of this single ossification maintain their usual positions relative to each other.

Utaherpeton was coded as not having an articulation between the tabular and postfrontal despite our lack of knowledge of the tabular because the postorbital precludes the possibility by its attachment to the parietal. Codings for aïstopods incorporate as yet unpublished observations (e.g., the "frontoparietal" described by McGinnis (1967) is comprised by the fused frontals only, presence of an odontoid process on the atlas, and single median proatlas in *Phlegethontia*) made by myself during the course of my ongoing revision of the group.

The definition of double occipital condyles is of concern. In the analyses of Carroll (1995) and Laurin and Reisz, all microsaurs and nectrideans were coded as possessing double condyles. This misses important anatomical details. The condyle of microsaurs, like the condyle of more primitive tetrapods (Fig. 4) involves the exoccipitals and basioccipital. Primitively, in *Proterogyrinus* (Fig. 4a), the condyle is semispherical beneath the foramen magnum. Microsaurs (Fig. 4c), being much smaller, have a relatively larger foramen magnum, which presumably forces the condyle to spread laterally beneath it in order to maintain a sufficient articular surface for the atlas, producing the strap-shaped morphology noted by Carroll and Gaskill (1978). The basioccipital of microsaurs is recessed from the level of the exoccipitals but *retains its articulation with the atlas* because of the anteriorly projecting "odontoid" process of the atlas (Carroll and Gaskill, 1978; Panchen and Smithson, 1988). Thus, the condyle of microsaurs (including *Eocaecilia*) is single because it is one continuous point of articulation. Double condyles are here defined as two physically separate points of articulation between the occiput and atlas (Fig. 4d). More specific distinctions are captured by other characters (e.g., character 133 for the strap-shaped morphology; character 134 for the odontoid process).

Character 43, Tabular horns, is restricted to diplocaulid nectrideans. The superficially similar posterior projection of the tabular (and other bones) present in adelogyrinids and embolomeres is here considered part of the squamosal (or otic) notch complex and is not considered homologous (Fig. 5).

The data were analyzed using PAUP* 4.0b4a (Swofford, 1998) using a heuristic search employing TBR branch-swapping over 100 replicates. Characters were unordered and equally weighted. Trees were examined using MacClade 3.07 (Maddison and Maddison, 1997). Tree statistics were derived from MacClade because of its ability to accommodate a combination of polymorphism and partial uncertainty in the matrix. Characters supporting each node were determined using MacClade's branch list function, which finds unambiguous state transformations.

RESULTS

Analysis of the complete matrix produced two MPTs. These varied only in the position of *Lepterpeton*. It was placed either as a basal sauropleurine nectridean (most likely position) or as the basal most urocordylid nectridean. When it was removed from consideration, a single tree was obtained (Fig. 6). It has a consistency index of 0.29 and a retention index of 0.58. It is the primary phylogenetic trunk of this collection of taxa.

To further illustrate this method, I relaxed parsimony slightly, accepting trees one step longer than the trunk. The Adams consensus tree of these 38 trees is shown in Figure 7. The most variable taxon is identified as *Sparodus validens*, which occupies 8 separate positions within the component trees. When it is deleted and the analysis rerun, two trees are found. These vary in the position of *Cardiocephalus sternbergi*, which is either sister group to *C. peabodyi* and *Euryodus*, or a monophyletic genus with *C. peabodyi*, which is sister group to *Euryodus*. Deletion of *C. sternbergi* obtains a single MPT. It is interesting to note that about half of the 664 trees found two steps from the trunk are eliminated by the removal of *C. sternbergi*.

Following the alternative approach, where the taxon whose removal produces the fewest MPTs is removed, the Mazon Creek microsauro is selected for elimination. Its deletion produces a single MPT, while removing *Sparodus* produces two. Other details of topology are the same. This tree will serve as the secondary trunk for the discussion that follows.

Relaxing parsimony a further step from the secondary trunk, 38 additional trees are found. They vary in the precise order of the Hapsidopariontidae, the placements of *Cardiocephalus sternbergi*, *Microbrachis*, *Hylopleuron*, *Odonterpeton*, *Utaherpeton*, *Stegotretus*, *Tuditatus*, *Asaphestera*, and *Sparodus*, the ordering within the Brachystelechidae, and the placement of *Ctenerpeton* within the Urocordylidae. With the

elimination of the previously identified *Cardiocephalus sternbergi*, *Sparodus* and *Odonterpeton*, and the further removal of *Asaphestera*, *Hapsidoparion*, *Hyloplesion*, and *Quasicaecilia* (using the alternative method), a single MPT is found with the same topology as the primary trunk, which is stable until two additional steps from post parsimonious are accepted, at which point 86 trees are found.

In these examples I have attempted to ignore a fundamental stability to illustrate the operation of this method. This method works best when one is working towards stability from a large number of trees. Unless one can effectively ignore the most parsimonious topology (in this case the primary trunk), it cannot be discounted that the stable arrangement will effect the outcome of the application of this method. This may be why I keep getting a topology identical to the primary trunk, and why I found the same number of trees when relaxing parsimony the first and second time.

This procedure illustrates the difficulty of identifying which taxa are varying (Fig. 8). Given three taxa with the basal two alternating in their positions, which is unstable? There are two approaches to this question. The most conservative answer is to count both as variable, having in this case two alternate positions. This is how taxa were scored above. The other approach is to examine overall stability. If a taxon is always basal to a clade found to be invariant in the Adams consensus tree, except when a taxon is placed just basal to it in a subset of component trees, one could argue that its position is stable. Using this criterion, *Sparodus validens* scores equally variable as *Odonterpeton triangulare*. Deletion of *Sparodus* still produces two MPTs, while pruning *Odonterpeton* obtains four. Following the steps for finding the phylogenetic trunk outlined above, *Sparodus* would be selected for removal.

DISCUSSION

The trunk has been rooted based upon *Acanthostega*. This places *Greererpeton* at the base of the tree, followed by a monophyletic Temnospondyli, and a succession of *Proterogyrinus*, *Seymouria*, and *Limnoscelis*. This succession of outgroups, and the placement of lepospondyls as sistergroup to amniotes (*Limnoscelis*), closely follows the pattern of Carroll (1995) and Laurin and Reisz. It should be noted that my focus in character selection was on finding lepospondyl apomorphies; this study was not intended to be an overall analysis of Paleozoic tetrapod relationships. The topology is consistent with that found by Carroll and Laurin and Reisz; however, the relatively low bootstrap support and rapid proliferation of trees found as one moves away from most parsimonious (due to homoplasy, the lack of plesiomorphic forms between each group of lepospondyls, and confounded by high amounts of missing data) suggest that we are far from a final solution to the problem of Paleozoic tetrapod relationships.

The Lepospondyli is confirmed to be monophyletic, most obviously diagnosed by the presence of an odontoid process on the atlas (subsequently reduced and lost in nectrideans). The Microsauria is found paraphyletic. The most basal lepospondyls are *Utaherpeton* and *Hylopleuron*, followed by a dichotomy, placing the remaining microbrachimorphs (less the brachystelechids) as sister group to adelospondylids, nectrideans, aïstopods and lysorophids. The nectrideans are possibly paraphyletic; the clade comprised by lysorophids and aïstopods is placed within Nectridea, as sister group to the diplocaulids. There is little bootstrap support for this topology, and it is lost one step from most parsimonious. Close relations between nectrideans and aïstopods has long been accepted, based upon the fused vertebrae, articulations accessory to the zygapophyses, and the presence of intravertebral spinal nerve foramina (present in aïstopods and the nectrideans *Sauroplorea bairdi* (Bossy and Milner, 1998) and *Crossotelos*, which could be conspecific (Carlson, 1999). Additionally, the oldest

aïstopod, *Lethiscus stocki*, and the ophiderpetontid *Coloraderpeton*, neither included in the present study, have crenulated neural spines, broadly similar to the morphology found in nectrideans. The question of whether aïstopods belong within Nectridea aside, very close relationships between the two groups seems likely.

On the other side of the dichotomy lie the tuditanomorph microsaurs. At its base are *Odonterpeton*, the Hapsidopariontidae, *Tuditanus* and *Asaphestera*, and a clade of microsaurs with overturned snouts comprised of *Micraroter*+*Pelodosotis*, the gymnarthrids, pantylids, and goniorhynchids+caecilians+brachystelechids. *Eocaecilia* is well established as a tuditanomorph. As hypothesized by Carroll and Currie (1975), its immediate outgroup is *Rhynchonkos*, and despite approximately 60 million years of divergent evolution, it is consistently placed as sister group to the brachystelechid microsaurs, sharing characters associated with skull and jaw consolidation, and multicuspid teeth. This whole assemblage is placed as sister group to the gymnarthrids.

Bolt (1991) distinguished between the multicuspid teeth of lissamphibians and brachystelechids. He noted that the cusps of brachystelechids run anterior-posteriorly, while those of lissamphibians are placed labio-lingually. This he correlated with tooth pedicelly, which is absent within brachystelechids but present in dissorophoid temnospondyls and lissamphibians, including *Eocaecilia*. This hypothesis suggests that multicuspid teeth were acquired in the most recent ancestor of caecilians and brachystelechids, and pedicelly was either lost in brachystelechids or acquired in caecilians. In the future, inclusion of other lissamphibians may shed additional light on this question. The present hypothesis, which tentatively suggests an origin of caecilians separate from frogs (assuming a temnospondyl origin), has received support from molecular (Feller and Hedges, 1998) and developmental (Carroll et al., 1999) studies.

This tree contrasts with the results obtained from arbitrary taxonomic exclusion. Excluding taxa with greater than 10% missing data (a level equivalent to that used in the literature; Rowe, 1988; Grande and Bemis, 1998) produces a single tree (C. I.=0.56, R.

$I=0.47$; Fig. 9) that only includes six lepospondyl taxa and all out groups except *Dendrerpeton*. A monophyletic Anthracosauria is found, with temnospondyls as its out group. This assemblage is sister group to *Greererpeton* and the lepospondyls. The topology does not achieve the arrangement of the trunk until a completeness criterion of 60% is employed, which demonstrates that taxa over 50% incomplete are contributing to determining the tree shape accepted as the trunk. Applying arbitrary completeness criteria reduces both the taxonomic scope of the study and topological variants.

Exploration of the Effect of Problem Taxa

Two problem taxa were responsible for producing many additional MPTs. Whether this is due to real character conflict or the effect of missing data needs to be examined. If caused by the former, the problem taxa should be retained, if the latter, we should understand how the missing data is operating.

The effect of *Lepterpeton* is clear from the initial most parsimonious trees. It is equally parsimonious to place it in two different positions on the tree (Fig. 10), in a typical "wild card" fashion (Nixon and Wheeler, 1992). Examination of the specimen shows that it is most likely a poorly preserved sauropleurine, and its removal obtains a single tree.

Accepting all trees one step from most parsimonious from this trunk produces 38 trees. They fall into two major groupings: those with nodes A and B in the same position as in the trunk, and where they switch positions. The former is the only variant found when *Sparodus* is removed, while the latter is the only variant produced by the removal of *Odonterpeton*. In the alternate topology (Fig. 10b), the tuditanomorphs become paraphyletic. This reversal is assisted in part by the highly incomplete Mazon Creek microsaurs and the fairly incomplete *Adelogyrinus* creating character ambiguity. Removal of the Mazon Creek microsaurs eliminates this topologic variant even when both *Odonterpeton* and *Sparodus* are retained. It also produces only a single MPT, which is

the solution found following the alternative procedure outlined above. In matrices with a high proportion of missing data, absence or presence of a single taxon may produce a radical shift in topology.

The fact that elongate morphotypes (aïstopods and lysorophids) cluster despite the attempted elimination of the correlated character complex is not surprising. Lee (1999), in an analysis of squamate phylogeny, found a well-supported elongate-limbless clade of snakes, amphisbaenids and dibamids. Upon inclusion of important fossils (mosasauroids, *Sineoamphisbaena* and *Pachyrhachis*), the snakes were pulled away from the limbless clade. Yet, when Lee attempted various differential weighting schemes he always recovered the limbless clade *unless the fossils were included*. Inclusion of appropriate taxa, with the differing character suites that diagnose them, would seem to be the only mechanism for correct determination of phylogeny in these instances (Gauthier et al., 1988a; Graybeal, 1998; Halanych, 1998). In the absence of these fossils, one can only indicate clades that may be due to such a morphotypic clustering, and reexamine included taxa in light of the resultant phylogeny. For this reason, it is hoped that careful re-examination of the oldest and presumably more primitive aïstopod *Lethiscus* will illuminate whether the aïstopod-lysorophid clade is realistic.

Donoghue et al. (1989) and Novacek (1992a) stated that fossils were most likely to change tree topology when there are large morphologic gaps, or branches with numerous apomorphies. A long branch, they argue, should not only be considered the result of anagenesis; a series of species or even whole clades could fit into that position. This is the situation found by Lee (1999), where the well supported dibamid-amphisbaenid-snake clade (Bremer index of 25, bootstrap support of 100%) separated upon inclusion of all relevant taxa. Caution should be taken when interpreting nodes with such values.

CONCLUSIONS

The Lepospondyli is a monophyletic taxon with some well-established internal branches. This cladogram shows lepospondyl relationships with stem amniotes, similar to the findings of Carroll (1995) and Laurin and Reisz (1997). The Microsauria is found a paraphyletic grade, and the Nectridea may include the Aïstopoda, although bootstrap analysis shows little support for this exact topology. This study creates a basic framework for future morphologic and phylogenetic studies of these groups.

Taxa with significant missing data may be incorporated into the tree construction phase by use of the iterative phylogenetic trunk method. Any effect of a problematic taxon may be examined in light of the stable trunk and the biological possibility of proposed different topologies established in a relatively controlled manner. Given the large amount of missing data in this matrix (21.8% of the matrix is coded “?”; 26.8% unknown or inapplicable) and the quantity of homoplasy to be expected amongst a large number of relatively similar species, the resolution found with the inclusion of so many taxa is satisfying. Within the urocordylid nectrideans, *Ctenerpeton* has 76.9% unknown characters, yet its placement is stable. *Lepterpeton*, on the other hand, has 67.6% unknown characters and causes instability. Arbitrary exclusion of incomplete taxa is thus not the most effective use of the relevant information.

Despite attempts to remove influences of correlated character complexes, a limbless clade of lysorophids and aïstopods is found. Differential weighting schemes, of which exclusion is one extreme, have previously been attempted with similar results (Lee, 1999). Inclusion of transitional fossils seems to be the only way to break the attraction of long branches (Gauthier et al., 1988a; Lee, 1999). However, nodes where transitional forms may be hypothesized to have an effect on branch length are those which are found to be well-supported via decay indices, so caution is urged in their interpretation.

Several areas for further study are revealed by this analysis. Generally, the anatomy of included taxa may be re-examined in light of this hypothesis. The aïstopod-lyisorophid clade can be tested by the inclusion of the oldest aïstopod (indeed, oldest lepospondyl) *Lethiscus* (Wellstead, 1982). Further preparation of the type of *Utaherpeton* would enable more complete character coding, and might restore microsaurian monophyly. Insight into the origin of caecilians is provided by this hypothesis. Re-examination of the critical but very poorly known *Acherontiscus* (Carroll, 1969, 1998c) might help fill in the morphologic gap between "labyrinthodonts" and lepospondyls. Inclusion of the newly described oldest microsauro from Goreville, Illinois (Lombard and Bolt, 1999) will no doubt refine our views of early lepospondyl evolution.

ACKNOWLEDGMENTS

I would like to thank Maureen Kearney, whose well-timed questions and comments improved my critical thinking about the problem of missing data. Christopher Brochu, Joseph Felsenstein and Thomas Holtz helped me become oriented within the systematics literature, although I am solely responsible for any omissions. Various versions of the manuscript have benefited from review by Michael Caldwell, Robert Carroll, Robert Holmes, Michel Laurin, Alison Murray, Gavin Naylor, Richard Olmstead, and Joseph Slowinski. This research was supported by the Natural Science and Engineering Research Council of Canada.

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APPENDIX I

Characters and data matrix used in this study, with a brief description where necessary.

Dermal skull:

1. **Intertemporal.** 0: present; 1: absent.
2. **Supratemporal.** 0: present; 1: absent.
3. **Supratemporal exposure on occiput.** 0: absent; 1: present.
4. **Postorbital-tabular contact.** 0: absent 1: present
5. **Postfrontal-tabular contact.** 0: absent; 1: present.
6. **Squamosal-tabular contact.** 0: absent; 1: present; 2: fused.
7. **Nature of squamosal-temporal contact.** 0: weakly overlapping; 1: sutural. This character has been worded as to avoid functional interpretations. In addition, the usual character was subdivided (characters 7 and 8) to capture variation in the anterior extent of the presumed line of kinesis, as some nectrideans do not possess an articulation between the lacrimal and prefrontal which would result in mobility (Bossy, 1976).
8. **Nature of lacrimal-prefrontal contact.** 0: overlapping; 1: sutural.
9. **Lacrimal.** 0: present; 1: absent.
10. **Lacrimal participation in border of external naris.** 0: present; 1: absent.
11. **Lacrimal participation in border of orbit.** 0: absent; 1: present.
12. **Lacrimal orbital processes.** 0: only ventral present; 1: dorsal and ventral present.
From Schultze and Foreman (1981) for gymnarthrids.
13. **Quadratojugal.** 0: present; 1: absent.
14. **Jugal-quadratojugal contact.** 0: present; 1: absent.
15. **Maxilla-quadratojugal contact.** 0: present; 1: absent.
16. **Frontals.** 0: paired; 1: fused.

17. **Frontal participation in border of orbit.** 0: absent; 1: present.
18. **Nasals.** 0: present; 1: absent.
19. **Alary processes of premaxilla.** 0: absent; 1: present.
20. **Septomaxilla.** 0: ossified; 1: unossified.
21. **Prefrontal participation in border of external naris.** 0: distant from; 1: near; 2: present. Character 1, figure 6, of Schultze and Foreman (1981).
22. **External naris in dorsal view.** 0: exposed; 1: not exposed.
23. **Dorsal exposure of premaxilla.** 0: broad; 1: narrow; 2: none. This character refers to the dorsal width of the nasal ramus of the premaxilla.
24. **Dorsal shape of skull.** 0: triangular; 1: diamond.
25. **Posterior skull margin.** 0: concave; 1: straight; 2: convex; 3: undulating. From Schultze and Foreman (1981), who correlated it to locomotor patterns.
26. **Antorbital region.** 0: blunt; 1: pointed.
27. **Antorbital region.** 0: short; 1: long.
28. **Quadrate braced by an internal flange of squamosal.** 0: absent; 1: present. This flange reinforces the quadrate ramus of the pterygoid. As such this character must be distinguished from the similarly named character of Laurin and Reisz (1997; character 38) which is ascribed to most taxa.
29. **"Otic" or Squamosal notch.** 0: present; 1: absent.
30. **Raised orbital rim.** 0: absent; 1: present. Carroll and Gaskill (1978) associated this character with depth of overlying integument, but it seems to be present within taxa with both shallow and deep tissue (as indicated by degree of dermal ornamentation).
31. **Postorbital.** 0: present; 1: absent.
32. **Jugal-postorbital tongue-in-groove joint.** 0: absent; 1: present. Bossy (1976) cited this as part of the kinetic system of the urocordylid nectridean skull. This may be homologous with the similar joint in some aïstopods, but in their case the

dorsal participant is the postfrontal; the postorbital presumably having been lost.

(This character was thus coded as inapplicable in aïstopods.)

33. **Postorbital participation in the orbital margin.** 0: present; 1: absent.
34. **Parietal-postorbital contact.** 0: absent; 1: present.
35. **Parietal-squamosal contact.** 0: absent; 1: present.
36. **Parietal-tabular contact.** 0: absent; 1: present.
37. **Postparietals.** 0: paired; 1: fused; 2: absent.
38. **Parietal foramen.** 0: present; 1: absent.
39. **Postparietals.** 0: moderate; 1: large. Large is at least 75% the size of the parietals.
40. **Postparietal-squamosal contact.** 0: absent; 1: present.
41. **Jugal-squamosal contact.** 0: present; 1: absent.
42. **Tabular.** 0: present; 1: absent. *Adelogyrinus* was coded for some tabular characters on the assumption that the "tabular" and "squamosal" elements of the tabular-squamosal maintained their usual topographical position relative to each other.
43. **"Tabular horns."** 0: absent; 1: present. This character is restricted to the posterior/posterolateral projecting structures on the skulls dorsal margin. The projection of the tabular (and other bones) seen in adelospondyls and embolomeres is here considered part of the "otic notch" complex.
44. **Tabular horns.** 0: parallel or slightly divergent; 1: widely divergent.
45. **Squamosal forms base of tabular horn.** 0: absent; 1: present.
46. **Lateral line canal grooves.** 0: present; 1: absent. Present in any stage on ontogeny.
47. **Dermal sculpturing.** 0: deep circular pits; 1: shallow ridges and grooves; 2: little to none.
48. **Premaxilla anterior margin.** 0: vertical; 1: overturned.
49. **Maxillary participation in border of orbit.** 0: absent; 1: present.
50. **Maxilla participation in margin of external naris.** 0: present; 1: absent.

51. **Maxilla forms entire ventral margin of the external naris.** 0: absent; 1: present.
52. **Maxilla.** 0: longer than palatine; 1: shorter than palatine.
53. **Marginal teeth.** 0: vertical; 1: turned medially.
54. **Marginal teeth largest anteriorly.** 0: absent; 1: present. Tooth sizes decreases evenly from the premaxilla to the rear of the maxilla (as in sauropleurine nectrideans; Bossy, 1976; Milner and Bossy, 1998).
55. **Marginal teeth.** 0: pointed pegs; 1: blunt pegs; 2: large cones.
56. **Number of premaxillary teeth.** 0: ≥ 10 ; 1: 5-9; 2: < 5 .
57. **Number of maxillary teeth.** 0: ≥ 30 ; 1: 20-29; 2: < 20 .
58. **Teeth laterally compressed.** 0: absent; 1: present.
59. **Caniform teeth mid-row.** 0: absent; 1: present. The whole row (premaxilla and maxilla) is here considered. This is a conservative character allowing the "canine"-like tooth of *Hyloplesion* equivalence with the enlarged tooth of *Euryodus primus*, which may not be likely. This biases the study toward finding close relationships between microsaur and amniotes.
60. **Teeth.** 0: simple points; 1: multiple cusps.
61. **Multiple cusp orientation.** 0: labiolingual; 2: antero-posterior.
62. **Enamel fluting.** 0: absent; 1: present.
63. **Labyrinthine in-folding.** 0: present; 1: absent.

Occiput:

64. **Occipital profile.** 0: low and wide (height/width <0.42); 1: high and wide (height/width 0.42-0.50); 2: high and narrow (height/width >0.50).
65. **Supraoccipital.** 0: absent; 1: present.
66. **Occipital condyle.** 0: concave; 1: convex.
67. **Occipital condyle.** 0: single; 1: double.
68. **Jugular foramen.** 0: between opisthotic and exoccipital; 1: through exoccipital.

69. **Braincase articulation with skull roof.** 0: strongly integrated; 1: loosely articulated.
70. **Jaw articulation.** 0: posterior to occiput; 1: even with occiput; 2: anterior to occiput; 3: far anterior (>20% BSL). The subdivision of the state "anterior to occiput" per Schultze and Foreman (1981).

Palate and braincase:

71. **Internal nares.** 0: widely separated; 1: narrowly separated.
72. **Palatine teeth.** 0: present; 1: absent. Teeth are here distinguished from denticles based on size, degree of elaboration, and pattern of implantation.
73. **"Palatal" teeth.** 0: single pit-pairs; 1: multiple, in rows; 2: multiple, random.
74. **Vomerine teeth.** 0: present; 1: absent.
75. **Denticles on pterygoid.** 0: present; 1: absent.
76. **Teeth on pterygoid.** 0: absent; 1: present.
77. **Denticles on vomers.** 0: present; 1: absent.
78. **Denticles on palatines.** 0: present; 1: absent.
79. **Denticles on parasphenoid.** 0: present; 1: absent.
80. **Palatal teeth.** 0: larger than marginals; 1: equal to marginals; 2: smaller than marginals.
81. **Parasphenoid.** 0: medial to stapes; 1: extends laterally under footplate of stapes.
82. **Basipterygoid articulation.** 0: loose; 1: sutured or fused.
83. **Stapes.** 0: perforated stem; 1: imperforate stem; 2: no stem.
84. **Footplate of stapes.** 0: oval; 1: round; 2: palmate.
85. **Dorsal process of stapes.** 0: absent; 1: present.
86. **"Accessory ossicle."** 0: absent; 1: present.
87. **Pleurospenoid.** 0: unossified; 1: ossified.
88. **Sphenethmoid.** 0: ossified; 1: unossified.

89. **Interpterygoid vacuities.** 0: narrow ("closed"); 1: wide; 2: sutured at midline.
90. **Pterygoids contact anteriorly.** 0: present; 1: absent.
91. **Pterygoid-exoccipital contact.** 0: absent; 1: present.
92. **Ectopterygoid.** 0: present; 1: absent.
93. **"Pharangobranchial pouches."** 0: absent; 1: present. These are large chambers behind the quadrate ramus of the pterygoids and the opisthotic present in *Diplocaulus* and *Diploceraspis* (Beerbower, 1963).

Jaw:

94. **Dentary relative to jaw length.** 0: long; 1: short. Long is at least two thirds of the entire jaw length.
95. **Dentary forms "coronoid process."** 0: absent; 1: present. Refers only to the dentary participation in this structure.
96. **Surangular.** 0: normal; 1: reduced; 2: absent.
97. **Angular.** 0: narrow; 1: deep. Deep is over half the entire jaw height.
98. **Number of splenals.** 0: 2; 1: 1; 2: 0.
99. **Lateral Splenal exposure.** 0: present; 1: absent.
100. **Number of Meckelian fossae.** 0: 2 or more; 1: 1; 2: 0.
101. **Ventral border of Meckel's fossa/ae.** 0: splenal; 1: angular.
102. **Retroarticular process.** 0: absent; 1: present.
103. **Retroarticular process.** 0: straight; 1: hooked.
104. **Mandible articulation to tooth row.** 0: above; 1: equal; 2: below.
105. **Anterior extent of angular in lateral view.** 0: posterior tooth row; 1: middle of tooth row.
106. **Number of coronoids.** 0: 3; 1: 2; 2: 1; 3: 0.
107. **Coronoid teeth.** 0: present; 1: absent.

108. **Coronoid teeth.** 0: larger than marginals; 1: equal to marginals; 2: smaller than marginals.
109. **Symphysis.** 0: dentary alone; 1: dentary and splenial.
110. **Jaw sculpture.** 0: present; 1: absent.
111. **Ossified hyoids.** 0: present; 1: absent.

Vertebrae and ribs:

112. **Number of vertebral accessory articulations.** 0: 0; 1: 1; 2: 2 or more.
113. **Strong lateral ridge between pre- and postzygopophyses.** 0: absent; 1: present.
114. **Caudal processes on centra between depressions.** 0: absent; 1: present. Per Bossy (1976).
115. **Trunk intercentra.** 0: present; 1: absent.
116. **Atlas-axis intercentra.** 0: present; 1: absent.
117. **Trunk neural arch to centrum.** 0: loosely articulated; 1: sutured; 2: fused.
118. **Base of neural spine.** 0: equal to or wider than base of the haemal spine; 1: smaller than haemal spine.
119. **Height of neural spines.** 0: even throughout; 1: alternating.
120. **Dorsal neural spine.** 0: narrow and smooth; 1: laterally broad and sculpted.
121. **Neural spine shape.** 0: ant-post sides parallel (rectangular); 1: strongly non-parallel (triangular).
122. **Dorsal neural spine.** 0: smooth; 1: crenulated.
123. **Haemal arches.** 0: present; 1: absent.
124. **Haemal arches.** 0: intercentral; 1: fused to mid-length of centrum.
125. **Haemal arches.** 0: longer than or equal to neurals; 1: shorted than neurals.
126. **Haemal accessory articulations.** 0: none; 1: one; 2: two.
127. **Haemal arch shape.** 0: non-parallel (triangular); 1: parallel (rectangular).
128. **Tail.** 0: tapers; 1: deep throughout with a sudden end.

129. **Trunk neural arches.** 0: paired; 1: fused.
130. **Spinal nerve foramina.** 0: absent; 1: present.
131. **Transverse processes.** 0: short; 1: extended (more than twice the lateral distance covered by the zygapophyses).
132. **Transverse process.** 0: on arch pedicle; 1: on centrum.
133. **Anterior articulating surface of atlas.** 0: equal in diameter to posterior; 1: laterally expanded.
134. **Atlas centrum.** 0: multipartite; 1: single notochordal; 2: single odontoid.
135. **Atlas neural arch.** 0: loosely articulated; 1: sutured to centrum; 2: fused to centrum.
136. **Atlas parapophyses.** 0: on centrum; 1: on transverse process; 2: absent.
137. **Atlas neural arch.** 0: paired; 1: sutured at midline; 2: fused at midline.
138. **Atlas accessory articulation.** 0: absent; 1: zygosphenes; 2: zygantra.
139. **Proatlas.** 0: present; 1: absent.
140. **Second cervical neural arch.** 0: expanded relative to more posteriornural arches; 1: equal to more posterior; 2: shorter than more posterior.
141. **Atlas ribs.** 0: one pair; 1: two pairs; 2: absent.
142. **Cervical rib distal shape.** 0: spatulate; 1: pointed.
143. **Ribs immediately anterior to sacrum.** 0: shorter than more anterior ribs; 1: as long as more anterior ribs.
144. **Costal process at rib head.** 0: absent; 1: present. This process in advanced aistopods give the rib head a distinctive "k-shape".
145. **Number of sacrals.** 0: 1; 1: 2; 2: 3.
146. **Sacral parapophysis.** 0: on centrum; 1: on transverse process.
147. **Number of pairs of caudal ribs.** 0: 5 or more; 1: 4; 2: 3; 3: 2 or fewer.

Pectoral girdle and limbs:

- 148. **Interclavicle posterior stem.** 0: absent or short; 1: long.
- 149. **Interclavicle posterior stem.** 0: wide; 1: narrow.
- 150. **Interclavicle.** 0: diamond shaped; 1: t-shaped.
- 151. **Interclavicle anterior plate.** 0: broad; 1: narrow.
- 152. **Interclavicle shape-diamond.** 0: broad diamond; 1: narrow diamond. Only diamond-shaped interclavicles were coded.
- 153. **Interclavicle anterior fimbriation.** 0: present; 1: absent.
- 154. **Interclavicle sculpture.** 0: present; 1: absent.
- 155. **Cleithrum.** 0: rounded or pointed dorsally; 1: t- or y-shaped dorsally.
- 156. **Clavicle blades.** 0: widely separate; 1: articulate medially; 2: interdigitate.
- 157. **Supraglenoid foramen.** 0: present; 1: absent.
- 158. **Number of coracoid foramina.** 0: 0; 1: 1; 2: 2.
- 159. **Scapulocoracoid occification.** 0: present; 1: scapula only; 2: absent.
- 160. **Entepicondylar foramen.** 0: present; 1: absent.
- 161. **Torsion in humerus.** 0: absent; 1: less than 80 degrees; 2: more than 80 degrees.
- 162. **Deltapectoral crest.** 0: weak; 1: intermediate; 2: prominent.
- 163. **Supinator process.** 0: absent; 1: present.
- 164. **Humerus length.** 0: long; 1: short. Long is defined as equal or greater than the length of 4 dorsal vertebrae.
- 165. **Humerus:radius.** 0: ≥ 0.7 ; 1: 0.5-0.7; 2: < 0.5 . These (and all continuously distributed characters) are divided based upon gaps in the distribution of values.
- 166. **Olecranon process.** 0: unossified; 1: ossified.
- 167. **Carpals.** 0: fully or partially ossified; 1: unossified.
- 168. **Number of digits in manus.** 0: 5 or more; 1: 4; 2: 3.

Pelvis girdle and limbs:

169. **Pelvis.** 0: elements fused; 1: sutured; 2: poorly ossified.
170. **Ilium.** 0: 2 dorsal processes; 1: narrowly bifurcate; 2: single blade.
171. **Pubo-ischiadic plate extent.** 0: 6 vertebrae; 1: 5 vertebrae; 2: 4 vertebrae; 3: 3 vertebrae.
172. **Internal trochanter-articulation.** 0: distinct; 1: continuous.
173. **Femoral shaft.** 0: robust; 1: slender. Slender is $\text{width:length} < 0.20$
174. **Femur.** 0: long; 1: short. Long is defined as long or longer than 4 vertebral centra.
175. **Distal tibia.** 0: expanded; 1: not expanded.
176. **Tarsals.** 0: ossified; 1: unossified. Any ossified podial constituted a score of "0".
177. **Number of distal tarsals.** 0: 6; 1: 5 or fewer.
178. **"Astragulus."** 0: absent; 1: present.
179. **Number of digits, pes.** 0: 5 or more; 1: 4 or less.

Body size and proportion:

180. **Number of presacral vertebrae.** 0: 25-35; 1: <25; 2: >35. This division was intended to capture general elongation (or reduction) trends while avoiding the issue of limbless ecomorph long branch attraction (Lee, 1999).
181. **Basal skull length.** 0: >70mm; 1: 50-70mm; 2: 30-50mm; 3: <30mm. This character is split along gaps in the distribution.
182. **Skull:trunk.** 0: ≥ 0.45 ; 1: 0.30-0.45; 2: 0.20-0.29; 3: <0.20.

Taxa	Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
<i>Acanthostega</i>		1	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Adelogyrinus</i>		1	1	-	1	0	2	1	-	1	-	-	-	0	0	0	0	0	0	0	1	1	0	0	0	0	0
<i>Asaphestera</i>		1	1	-	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>Balanerpeton</i>		0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
<i>Batrachiderpeton</i>		1	1	-	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
<i>Batropetes</i>		1	1	-	1	0	1	1	1	0	0	1	0	?	?	?	0	1	0	0	1	2	1	2	1		
<i>Brachydectes</i>		1	1	-	-	-	1	1	1	0	0	1	1	1	-	-	0	0	0	1	2	0	0	0	-		
<i>Cardiocephalus peabodyi</i>		1	1	-	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	1	1	1	1	1		
<i>Cardiocephalus sternbergi</i>		1	1	-	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	0			
<i>Carrolla</i>		1	1	-	?	0	?	?	1	0	0	1	1	1	-	-	0	1	0	0	0	2	0	0	1		
<i>Cienerpeton</i>		1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Denderpeton</i>		0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>Diceratosaurus</i>		1	1	-	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0
<i>Diplocaulus magnicornis</i>		1	1	-	0	0	1	1	1	0	0	0	-	0	0	1	1	1	1	0	1	1	1	0	0	0	0
<i>Diplocaulus primus</i>		1	1	-	0	0	1	1	1	0	0	0	-	0	0	1	1	1	1	0	1	1	0	0	0	0	0
<i>Diploceraspis</i>		1	1	-	0	0	1	1	-	1	-	-	-	0	0	1	1	1	1	0	1	2	0	0	0	0	0
<i>Eocaecilia</i>		1	1	-	-	0	1	1	-	1	-	-	-	0	0	0	0	0	0	0	1	2	1	1	1		
<i>Euryodus dalyae</i>		1	1	-	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	1	1	2	0		
<i>Euryodus primus</i>		1	1	-	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	2	1		
<i>Greererpeton</i>		1	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
<i>Hapsidoparion</i>		1	1	-	0	1	1	0	1	0	0	1	0	1	-	-	0	0	0	0	0	1	0	0	0	0	0
<i>Hylopleuron</i>		1	1	-	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Keraterpeton galvani</i>		1	1	-	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0
<i>Lepterpeton</i>		1	?	?	?	?	?	0	0	0	0	1	1	?	?	?	?	?	?	?	?	2	0	0	0	0	0
<i>Limnascelis</i>		1	0	1	0	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Llistrofus</i>		1	1	-	1	1	1	0	1	0	0	1	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0
<i>Mazon Creek</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Micraroter</i>		1	1	-	1	1	1	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Microbrachis</i>		1	1	-	1	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>Odonterpeton</i>		1	1	-	-	-	-	1	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0
<i>Oestocephalus</i>		1	0	0	-	0	1	0	1	0	0	1	0	0	1	1	0	0	0	0	1	2	1	1	0		
<i>Pantylus</i>		1	1	-	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	1	0		
<i>Pelodosotis</i>		1	1	-	1	1	1	1	1	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0
<i>Phlegethontia</i>		1	1	-	-	-	-	1	-	-	-	-	-	-	-	1	1	0	0	1	2	0	0	0	0	0	0
<i>Proterogyrinus</i>		0	0	0	0	0	0	0	0	0	1	?	0	0	1	0	0	0	0	?	0	0	0	0	0	0	0
<i>Ptyonius</i>		1	0	1	0	0	1	0	1	0	0	1	1	0	0	1	0	0	0	0	1	2	0	0	0	0	0
<i>Quasicaecilia</i>		1	1	-	-	-	-	?	1	0	0	1	0	1	-	-	0	1	0	?	1	1	1	2	1		
<i>Rhynchonkos</i>		1	1	-	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	1	2	1		
<i>Sauroplorea bairdi</i>		?	?	?	?	?	?	?	0	0	0	1	?	?	?	?	1	?	0	0	1	2	0	0	0	0	0
<i>Sauroplorea pectinata</i>		1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	2	0	0	0	0	0
<i>Sauroplorea scalaris</i>		1	0	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1	2	0	0	0	0	0
<i>Saxonerpeton</i>		1	1	-	1	1	1	1	1	0	0	1	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0
<i>Scincosaurus</i>		1	1	-	1	1	1	1	1	0	0	1	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0
<i>Seymouria baylorensis</i>		0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Sparodus</i>		1	1	-	1	1	1	1	?	0	?	1	1	0	0	1	?	0	?	?	?	?	?	?	?	?	?
<i>Stegotretus</i>		1	1	-	1	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0		
<i>Tuditanus</i>		1	1	-	1	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Urocordylus</i>		1	0	?	?	0	?	0	0	0	0	1	1	0	0	?	?	?	?	?	?	?	?	0	0	0	0
<i>Utaherpeton</i>		?	?	?	?	0	?	?	1	0	0	1	1	?	?	?	0	0	0	0	?	2	0	0	0	0	0

Taxa	Characters	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4	4	4	4	4	4
		5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	
<i>Acanthostega</i>		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	-	-	0	0	0	
<i>Adelogyrinus</i>		3	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0/1	0	-	-	0	1	0	
<i>Asaphestera</i>		3	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	-	-	0/1	1	0	
<i>Balanerpeton</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1	0	0	
<i>Batrachiderpeton</i>		0	0	0	1	1	0	0	0	0	1	1	1	0	0	1	0	0	0	1	1	0	0	1	0	
<i>Batropetes</i>		3	0	0	0	1	0	0	0	0	1	1	1	2	0	-	-	0	0	0	-	-	1	2	1	
<i>Brachydectes</i>		2	0	0	0	1	0	1	-	-	-	1	1	0	1	1	1	-	0	0	-	-	1	2	0	
<i>Cardiocephalus peabodyi</i>		2	1	0	0	1	1	0	0	0	0	0	1	0	0&1	1	0	0	0	0	-	-	1	2	1	
<i>Cardiocephalus sternbergi</i>		2	1	0	0	1	1	0	0	0	0	0	1	0	0&1	1	0	0	0	0	-	-	1	2	1	
<i>Carrolla</i>		3	0	0	0	1	0	0	0	0	1	1	?	2	0	-	-	?	?	0	-	-	1	2	1	
<i>Ctenerpeton</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Denderpeton</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	-	1	0	0	
<i>Diceratosaurus</i>		0	0	0	1	1	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	0	0	1	0	
<i>Diplocaulus magnicornis</i>		0	0	0	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1	0	
<i>Diplocaulus primus</i>		0	0	0	1	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1	0	
<i>Diploceraspis</i>		0	0	0	0	1	0	0	0	1	1	1	1	0	0	1	0	0	0	1	1	1	0	1	0	
<i>Eocaecilia</i>		2	1	0	0	1	1	1	-	-	-	1	1	0	1	1	1	0	0	0	-	-	1	2	0	
<i>Euryodus dalyae</i>		1	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	1	2	1	
<i>Euryodus primus</i>		1	1	0	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	0	-	-	?	?	1	
<i>Greererpeton</i>		3	0	0	0	1	0	0	0	0	1	0	0	0	0	0&1	0	0	0	0	-	-	0	0	0	
<i>Hapsidoparion</i>		1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	-	-	1	2	0	
<i>Hyloplesion</i>		1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	1	0	0	0	-	-	1	2	0	
<i>Keraterpeton galvani</i>		0	0	0	?	1	0	0	0	0	1	1	1	0	0	1	0	0	0	1	0	1	0	1	0	
<i>Lepterpeton</i>		?	1	1	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	0	-	-	?	?	0	
<i>Limnoscelis</i>		0	1	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0	-	-	1	2	1	
<i>Llistrofus</i>		1	0	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	-	-	1	1	?	
<i>Mazon Creek</i>		?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Micraroter</i>		3	0	0	0	1	1	0	0	0	0	0	1	0	1	0&1	0	1	0	0	-	-	1	2	1	
<i>Microbrachis</i>		1	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	-	-	0	1	0	
<i>Odonterpeton</i>		2	0	0	0	1	1	0	0	0	1	1	-	1	0	0	0	0	1	-	-	-	1	2	0	
<i>Oestocephalus</i>		2	0	0	0	1	0	1	-	-	-	0	0	0	0	1	0	1	0	0	-	-	1	2	0	
<i>Pantylus</i>		1	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	0	0	0	-	-	1	0	1	
<i>Pelodosotis</i>		3	1	0	0	1	0	0	0	0	0	0	1	0	1	1	0	1	0	0	-	-	1	2	1	
<i>Phlegethontia</i>		2	1	0	0	1	0	1	-	-	-	-	2	1	-	-	0	1	0	-	-	-	1	2	0	
<i>Proterogyrinus</i>		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	-	0	0	0	
<i>Ptyonius</i>		1	1	0	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	-	-	1	1	0	
<i>Quasicaecilia</i>		3	0	0	0	1	1	0	0	0	1	?	-	2	0	-	-	?	1	0	-	-	1	2	1	
<i>Rhynchonkos</i>		2	1	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	1	2	1	
<i>Sauropleura bairdi</i>		?	1	1	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	
<i>Sauropleura pectinata</i>		0	1	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	-	-	1	1	0	
<i>Sauropleura scalaris</i>		0	1	1	0	1	0	0	1	0	1	0	1	0	0	0	0	0	0	0	-	-	1	1	0	
<i>Saxonerpeton</i>		1	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	-	-	0	2	0	
<i>Scincosaurus</i>		1/3	0	0	1	1	0	0	0	0	0	0	1	2	0	-	-	0	0	0	-	-	0	1	0	
<i>Seymouria baylorensis</i>		1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	-	-	0	0	0	
<i>Sparodus</i>		2	?	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	1	1	?	
<i>Stegotretus</i>		1	0	0	0	1	1	0	0	0	0	0	1	0	0	1	0	0	0	0	-	-	1	1	1	
<i>Tuditanus</i>		0	0	0	0	1	1	0	0	0	0	0	1	?	0	0	0	0	0	0	-	-	1	1	0	
<i>Urocordylus</i>		?	1	0	0	1	0	0	1	0	1	?	?	?	?	?	?	?	?	0	-	-	1	1	0	
<i>Utaherpeton</i>		?	0	0	0	1	0	0	0	0	1	?	?	?	?	?	?	?	?	0	-	-	1	2	0	

Taxa	Characters	4	5	5	5	5	5	5	5	5	5	5	6	6	6	6	6	6	6	6	6	7	7	
		9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1
<i>Acanthostega</i>		0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	-	-	0	0	0	0
<i>Adelogyrinus</i>		1	?	?	?	0	0	0	?	0	0	0	0	-	0	1	0	0	0	0	1	?	2	?
<i>Asaphostera</i>		0	0	0	0	0	1	0	1	0	0	0	0	-	0	1	2	1	0	0	0	1	2	0
<i>Balanerpeton</i>		0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	?	?	0	0	0	0
<i>Batrachiderpeton</i>		1	0	0	1	0	0	0	1	2	0	0	0	-	0	1	1	?	1	1	?	0	2	0
<i>Batropetes</i>		0	1	-	?	1	0	0	1	2	0	0	1	1	0	1	1	1	0	-	0	3	?	
<i>Brachydectes</i>		1	0	0	0	0	0	0	1	2	0	0	0	-	0	1	2	1	0	0	0	0	3	1
<i>Cardiocephalus peabodyi</i>		0	0	0	?	1	0	2	2	2	1	1	0	-	1	1	0	0	0	0	0	0	3	?
<i>Cardiocephalus sternbergi</i>		1	0	0	0	1	0	2	2	2	1	1	0	-	1	1	0	0	0	0	0	0	3	0
<i>Carrolla</i>		0	0	?	0	1	0	0	2	2	1	0	1	1	0	1	1	0	1	0	1	0	3	0
<i>Cienerpeton</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Denderpeton</i>		0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	?	?	?	?	?	0	0
<i>Diceratosaurus</i>		1	0	0	?	0	0	?	?	?	?	0	0	-	0	1	0	?	1	1	?	?	2	?
<i>Diplocaulus magnicornis</i>		0	0	0	1	0	0	0	1	2	0	0	0	-	0	1	0	0	1	1	0/1	0	3	0
<i>Diplocaulus primus</i>		0	0	0	?	0	0	0	1	2	0	0	0	-	0	1	0	?	1	1	?	0	3	0
<i>Diploceraspis</i>		0	0	0	1	0	0	0	1	2	0	0	0	-	0	1	0	0	1	1	0	0	3	0
<i>Eocaecilia</i>		1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	-	0	3	0
<i>Euryodus dalyae</i>		0	0	0	0	1	0	2	2	2	0	1	0	-	0	1	0	0	0	0	0	1	2	0
<i>Euryodus primus</i>		0	0	0	0	1	0	2	2	2	0	1	0	-	1	1	0	0	0	0	1	1	2	0
<i>Greererpeton</i>		0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	?	1	0	0
<i>Hapsidoparion</i>		0	0	1	0	0	0	0	1	1	0	0	0	-	0	1	0	1	1	0	0	1	2	0
<i>Hyloplezion</i>		0	0	0	1	0	0	0	1	1	0	1	0	-	0	1	0	1	0	0	?	?	1&2	0
<i>Keraterpeton galvani</i>		0	0	0	?	0	0	0	2	2	0	0	0	-	0	1	0	?	1	1	?	?	2	0
<i>Lepterpeton</i>		1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
<i>Limnoscelis</i>		0	0	0	0	0	1	0	2	2	0	1	0	-	0	0	0	1	0	0	0	0	1	1
<i>Llistrofus</i>		0	0	1	?	0	0	0	?	1	0	0	0	-	0	1	1	?	?	?	?	?	2	?
<i>Mazon Creek</i>		?	?	?	?	?	0	?	?	?	0	0	0	-	0	1	?	?	?	?	?	?	?	?
<i>Micraroter</i>		1	0	0	0	1	0	1	1	2	0	1	0	-	0	1	0	1	0	0	1	1	2	0
<i>Microbrachis</i>		0	0	0	0	0	0	0&1	1	1	0	0	0	-	0	1	0	?	0	0	?	0	2	0
<i>Odonterpeton</i>		0	0	0	0	0	0	0	1	2	0	0/1	0	-	0	1	1	?	?	?	?	0	?	1
<i>Oestocephalus</i>		1	0	0	1	0	0	0	1	0	0	0	0	-	0	1	2	0	0	0	0	0	0	0
<i>Pantylus</i>		0	0	0	0	0	0	2	2	2	0	1	0	-	0	1	0	1	0	0	0	0	1	1
<i>Pelodosotis</i>		0	1	-	0	1	0	0	1	2	0	1	0	-	0	1	2	1	0	0	0	1	2	?
<i>Phlegethontia</i>		1	0	1	-	0	0	0	2	2	0	0	0	-	0	1	2	0	0	0	-	0	2	?
<i>Proterogyrinus</i>		0	0	0	0	0	0	0	1	0	0	0	0	-	0	0	2	0	0	0	0	0	0	0
<i>Ptyonius</i>		0	0	0	0	0	0	0	1	2	0	0	0	-	0	1	1	?	?	?	?	0	0	0
<i>Quasicaecilia</i>		0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	?	0	-	0	3	?
<i>Rhynchonkos</i>		0	0	0	0	1	0	0	1	2	0	0	0	-	0	1	0	1	1	0	1	0	3	1
<i>Sauroplesura bairdi</i>		1	1	-	?	0	1	0	1	?	0	?	0	-	0	1	?	?	?	?	?	?	?	?
<i>Sauroplesura pectinata</i>		1	1	-	0	0	1	0	0	1	0	0	0	-	0	0&1	2	?	?	?	?	?	0	0
<i>Sauroplesura scalaris</i>		1	0&1	0	0	0	1	0	1	2	0	0	0	-	0	1	1	?	?	?	?	?	0	0
<i>Saxonerpeton</i>		0	0	1	0	0	0	0	1	1	0	0	0	-	0	1	1	0	?	0	?	1	2	0
<i>Scincosaurus</i>		1	0	0	0	0	0	0	1	2	0	0	0	-	0	1	?	?	1	1	?	?	3	0
<i>Seymouria baylorensis</i>		0	0	0	0	0	0	0	1	2	0	1	0	-	0	0	0	0	0	0	0	0	0	0
<i>Sparodus</i>		0	?	?	?	?	0	2	2	2	0	1	0	-	1	1	?	?	?	?	?	?	3	?
<i>Stegotretus</i>		0	0	1	0	1	0	2	2	2	0	1	0	-	0	1	0	1	0	0	0	0	2	1
<i>Tuditanus</i>		0	0	0	?	0	0	0	1	1	0	0	0	-	0	1	1	?	?	?	?	?	1	0
<i>Urocordylus</i>		0	?	?	?	0	1	0	?	?	0	0	0	-	0	1	?	?	?	?	?	?	0	0
<i>Utaherpeton</i>		1	0	?	?	0	0	1	?	1	0	0	0	-	0	1	?	?	?	?	?	?	1/2	?

	7	7	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	8	9	9	9	9	9	9			
Taxa	Characters	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5		
<i>Acanthostega</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Adelogyrinus</i>		1	-	1	0	?	0	0	1	-	0	0	?	?	?	?	?	?	0	0	?	?	0	0	0	0	
<i>Asaphestera</i>		0	1	0	0	1	0	0	?	0	?	0	?	?	?	?	0	0	1	0	1	0	?	0	0	?	
<i>Balanerpeton</i>		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0		
<i>Batrachiderpeton</i>		0	1	0	0	0	0	1	1	1	?	1	?	?	?	?	?	0	0	2	0	0	1	0/1	1	0	
<i>Batropetes</i>		?	?	?	1	0	1	1	0	-	1	0	1	0	0	0	0	0	0	?	0	?	?	0	0	1	
<i>Brachydectes</i>		1	1	0	1	0	1	1	1	1	1	?	1	1	0	0	1	0	0	1	0	1	0	1			
<i>Cardiocephalus peabodyi</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1		
<i>Cardiocephalus sternbergi</i>		0	1	0	1	1	1	1	1	2	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	
<i>Carrolla</i>		1	-	1	1	0	1	1	1	-	0	0/1	0	0	0	0	1	0	0	1	0	0	0	0	?	?	
<i>Ctenerpeton</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Denderpeton</i>		0	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?	?	0	?	1	1	0	0	0	0	
<i>Diceratosaurus</i>		?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	0	0	0	0	1	?	0	0	0
<i>Diplocaulus magnicornis</i>		0	1	0	1	0	1	1	1	1	0	1	?	?	?	?	?	?	0	0	1	1	1	1	1	0	0
<i>Diplocaulus primus</i>		0	1	0	1	0	1	1	1	1	0	1	?	?	?	?	?	?	0	0	1	1	1	?	1	0	0
<i>Diploceraspis</i>		0	1	1	1	0	1	1	1	1	0	1	?	?	?	?	?	?	0	0	1	1	1	0	1	0	1
<i>Eocaecilia</i>		0	1	0	0	0	1	1	0	1	1	0	0	0	0	?	?	?	0	0	1	0	1	0	0	-	
<i>Euryodus dalyae</i>		0	1	0	0	0	0	0	0	2	1	0	0	0	0	1	0	?	0	0	0	0	0	0	0	1	
<i>Euryodus primus</i>		0	1	0	0	0	0	0	1	2	1	0	?	?	?	?	?	?	0	?	0	0	0	0	0	1	
<i>Greererpeton</i>		0	0&1	0	0	0	1	1	0	0&1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<i>Hapsidoparion</i>		0	1	1	0	0	1	1	0	1	0	0	1	1	0	1	0	?	?	0	1	0	0	0	0	1	
<i>Hyloplesion</i>		1	-	1	0	0	0	0	0	-	0	0	1	1	0	0	?	?	?	0	1	0	0	0	0	1	
<i>Keraterpeton galvani</i>		0	1	1	0	0	0	1	1	1	?	?	?	?	?	?	?	?	0	2	0	?	?	?	0	1	0
<i>Lepterpeton</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	
<i>Limnoscelis</i>		1	-	1	0	1	0	0	0	1	0	0	?	?	?	?	0	0	0	0	1	0	0	0	0	0	
<i>Llistrofus</i>		0	1	0	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1
<i>Mazon Creek</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Micraroter</i>		0	1	0	0	0	0	0	0	2	0	0	0	1	0	1	0	?	?	0	0	0	0	0	0	1	
<i>Microbrachis</i>		1	-	1	0	0	0	0	0	-	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	
<i>Odonterpeton</i>		0	1	1	0	0	0	0	0	1/2	1	0	2	0	0	1	0	1	0	0	0	0	0	0	0	1	
<i>Oestocephalus</i>		0	1	?	1	0	?	1	0	1	?	0	?	?	?	?	?	?	0	0	0	0	0	1	0	0	
<i>Pantylus</i>		0	2	0	0	0	0	0	1	1	1	0	1	0	1	1	?	?	0	0	0	0	1	0	0	1	
<i>Pelodosotis</i>		0	1	?	0	0	?	?	0	2	1	0	1	2	1	1	0	0	0	1	0	?	?	0	0	0/1	
<i>Phlegethontia</i>		?	?	?	1	0	?	?	1	?	0	0	2	0	0	0	0	0	0	?	?	0	1	0	0	0	
<i>Proterogyrinus</i>		0	0	?	0	0	?	1	0	0	0	0	?	?	?	?	?	0	0	0	0	0	0	0	0	0	
<i>Ptyonius</i>		0	1	0	1	0	0	1	1	2	0	0	?	?	?	?	?	?	0	1	1	0	0	0	0	0	
<i>Quasicaecilia</i>		?	?	?	1	0	?	?	1	?	0	0	1	0	1	?	1	0	?	1	0	?	?	?	?	?	
<i>Rhynchonkos</i>		0	1	0	1	0	1	1	0	1	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	1	
<i>Sauroplesura bairdi</i>		?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Sauroplesura pectinata</i>		0	1	0	0	1	0	1	1	2	0	0	?	?	?	?	?	0	0	0	?	0	1	0	0	0	
<i>Sauroplesura scalaris</i>		0	1	1	0	1	1	1	1	2	0	0	?	?	?	?	?	0	0	0	?	0	1	0	0	0	
<i>Saxonerpeton</i>		1	-	1	0	0	0	0	0	-	?	0	?	?	?	?	?	?	1	0	1	0	0	0	0	1	
<i>Scincosaurus</i>		1	-	1	1	0	1	0	1	-	0	1	?	?	?	?	?	?	0	0	0	1	0	1	0	?	0
<i>Seymouria baylorensis</i>		0	0	0	0	0	0	0	0	1	0	0	1	?	?	?	?	0	1	0	2	0	0	0	0	0	
<i>Sparodus</i>		0	1	?	0	1	?	0	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0
<i>Stegotretus</i>		0	2	0	0	1	0	0	0	1	1	0	?	?	?	?	?	?	0	0	0	0	0	1	0	0	1
<i>Tuditanus</i>		?	?	?	0	0	0	0	0	?	0	0	2	0	0	0	0	?	0	0	0	?	?	0	1	0	
<i>Urocordylus</i>		0	1	?	0	0	?	1	?	2	?	0	?	?	?	?	?	?	0	0	0	0	?	?	0	0	0
<i>Utaherpeton</i>		?	?	1	0	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0

		9	9	9	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

[illegible]

APPENDIX II

Node support for Lepospondyli as determined by MacClade 3.07. All characters unambiguous. Note that character reconstructions are not sensitive to inapplicable data. Previously named clades, except monotypic families, are indicated. Para- or polyphyletic taxa indicated by quotation marks.

Terminal Apomorphies:

Greererpeton

Total changes along branch: 21

10. Present->absent; 20. Ossified->unossified; 21. Distant from->present; 25. Concave->undulating; 29. Present->absent; 69. Strongly integrated->loosely articulated; 77. Present->absent; 78. Present->absent; 106. 3->2; 108. Larger than marginals->equal to marginals; 131. Absent->present; 142. Spatulate->pointed; 143. Short->long; 151. Broad->narrow; 156. Widely separate->articulate medially; 157. Present->absent; 164. Long->short; 171. 6 vertebrae->4 vertebrae; 176. Ossified->unossified; 180. 25-35->>35; 182. ≥ 0.45 ->0.20-0.29

Balanerpeton

Total changes along branch: 3

20. Ossified->unossified; 97. Narrow->deep; 129. Fused->paired

Dendrerpeton

Total changes along branch: 4

99. Present->absent; 101. Splenial->angular; 171. 6 vertebrae->5 vertebrae; 173. Slender->robust

Proterogyrinus

Total changes along branch: 2

64. Low and wide->high and narrow; 78. Present->absent

Seymouria baylorensis

Total changes along branch: 5

87. Unossified->ossified; 89. Narrow ->fused at midline; 156. Widely separate->articulate medially; 174. Long->short; 180. 25-35-><25

Limnoscelis

Total changes along branch: 10

3. Absent->present; 26. Blunt->pointed; 37. Paired->fused; 48. Vertical->overtured; 54. Absent->present; 56. 5-9-><5; 71. Widely separated->narrowly separated; 76. Absent->present; 120. Narrow and smooth->laterally broad and sculpted; 178. Absent->present

Utaherpeton

Total changes along branch: 9

12. Only ventral present->dorsal and ventral present; 21. Distant from->present; 49. No->yes; 55. Pointed pegs->blunt pegs; 105. Posterior tooth row->middle of tooth row; 159. Both->scapula only; 165. 0.5-0.7->=0.7; 176. Ossified->unossified; 180. 25-35-><25

Hylopleuron

Total changes along branch: 8

40. Absent->present; 52. Longer than palatine->shorter than palatine; 84. Oval->round; 131. Absent->present; 160. Present->absent; 165. 0.5-0.7-><0.5; 171. 6 vertebrae/5 vertebrae->4 vertebrae; 182. 0.30-0.45->0.20-0.29

Tuditanus

Total changes along branch: 8

12. Only ventral present->dorsal and ventral present; 25. Undulating->concave; 70. Anterior to occiput->even with occiput; 90. Absent->present; 94. Long->short; 105. Posterior tooth row->middle of tooth row; 110. Absent->present; 159. Both->absent

Asaphestera

Total changes along branch: 10

54. Absent->present; 57. 20-29->>=30; 64. High and wide->high and narrow; 76.

Absent->present; 151. Narrow->broad; 154. Absent->present; 162. Prominent->intermediate; 169. Sutured->poorly ossified; 181. <30mm->30-50mm; 182. 0.30-0.45->0.20-0.29

Pantylus

Total changes along branch: 12

30. Present->absent; 38. Present->absent; 53. Turned medially->vertical; 70. Far anterior ->even with occiput; 110. Absent->present; 111. Absent->present; 119. Even->alternating; 143. Short->long; 156. Articulate medially->interdigitate; 160. Absent->present; 172. Distinct->continuous; 181. <30mm->50-70mm

Stegotretus

Total changes along branch: 5

70. Far anterior ->anterior to occiput; 102. Present->absent; 104. Below->above; 156. Articulate medially->widely separate; 169. Sutured->poorly ossified

Sparodus

Total changes along branch: 9

24. Triangular->diamond; 62. Absent->present; 95. Present->absent; 99. Absent->present; 100. 1->0; 151. Narrow->broad; 165. <0.5->0.5-0.7; 171. 6 vertebrae->5 vertebrae; 181. <30mm->30-50mm

Cardiocephalus sternbergi

Total changes along branch: 5

49. No->yes; 75. Present->absent; 76. Absent->present; 77. Present->absent; 78. Present->absent

Cardiocephalus peabodyi

Total changes along branch: 2

159. Both->scapula only; 169. Sutured->poorly ossified

Euryodus primus

Total changes along branch: 4

15. Absent->present; 38. Present->absent; 68. Between opisthotic and exoccipital->through exoccipital; 102. Absent->present

Euryodus dalyae

Total changes along branch: 1

62. Present->absent

Rhynchonkos

Total changes along branch: 3

71. Widely separated->narrowly separated; 99. Absent->present; 178. Present->absent

Eocaecilia

Total changes along branch: 14

9. Present->absent; 31. Present->absent; 38. Present->absent; 48. Overturned->vertical; 49. No->yes; 53. Turned medially->vertical; 56. 5-9->>=10; 57. <20->>=30; 92. Present->absent; 130. Absent->present; 132. On arch pedicle->on centrum; 146. On centrum->on transverse process; 168. 4->3; 179. 5 or more->4 or less

Batropetes

Total changes along branch: 2

50. Present->absent; 98. 0->1

Carrollia

Total changes along branch: 4

12. Only ventral present->dorsal and ventral present; 20. Unossified->ossified; 22. Not exposed->exposed; 23. None->broad

Quasicaecilia

Total changes along branch: 3

21. Present->near; 64. High and wide->high and narrow; 85. Absent->present

Pelodosotis

Total changes along branch: 11

12. Only ventral present->dorsal and ventral present; 21. Distant from->near; 30. Present->absent; 50. Present->absent; 64. Low and wide->high and narrow; 85. Absent->present; 98. 2->1; 135. Fused to centrum->sutured to centrum; 143. Short->long; 157. Present->absent; 169. pelvis: sutured->fused

Micraroter

Total changes along branch: 7

49. No->yes; 55. Pointed pegs->blunt pegs; 68. Between opisthotic and exoccipital->through exoccipital; 83. Imperforate stem->perforated stem; 90. Absent->present; 145. 2->3; 172. Distinct->continuous

Hapsidoparion

Total changes along branch: 6

4. Present->absent; 13. Present->absent; 64. High and wide->low and wide; 102. Present->absent; 111. Absent->present; 117. Sutured->loosely articulated

Llistrofus

Total changes along branch: 5

39. Moderate->large; 40. Absent->present; 47. Little to none->shallow ridges and grooves; 74. Absent->present; 104. Below->equal

Saxonerpeton

Total changes along branch: 3

46. Absent->present; 65. Present->absent; 72. Present->absent

Odonterpeton

Total changes along branch: 15

25. Straight->convex; 37. Paired->fused; 42. Present->absent; 57. 20-29-><20; 71. Widely separated->narrowly separated; 81. Medial of stapes->under footplate of stapes; 83. Imperforate stem->no stem; 90. Absent->present; 107. Present->absent; 129.

Fused->paired; 134. Single odontoid->single notochordal; 137. Fused at midline->sutured at midline; 141. One pair->two pairs; 159. Both->absent; 160. Present->absent

Microbrachis

Total changes along branch: 4

170. Single blade->narrowly bifurcate; 175. Expanded->not expanded; 180. 25-35->>35; 182. 0.30-0.45->0.20-0.29

Mazon Creek

Total changes along branch: 4

90. pterygoids contact anteriorly: absent->present; 147. number pairs of caudal ribs: 3->2 or fewer; 169. pelvis: sutured->poorly ossified; 176. tarsals: ossified->unossified

Sauroplorea pectinata

Total changes along branch: 1

56. 5-9->>=10

Sauroplorea bairdi

Total changes along branch: 1

130. Absent->present

Sauroplorea scalaris

Total changes along branch: 5

74. Present->absent; 138. Zygantra->zygosphenes; 163. Absent->present; 167.

Unossified->fully or partially ossified; 169. Poorly ossified->fused

Ptyonius

Total changes along branch:

no unambiguous changes

Ctenospondylus

Total changes along branch: 1

169. Poorly ossified->fused

Urocordylus

Total changes along branch: 7

125. Longer than or equal to neurals->shorter than neurals; 162. Weak->prominent; 165. ≥ 0.7 -> $0.5-0.7$; 166. Unossified->ossified; 169. Poorly ossified->sutured; 173. Slender->robust; 182. $0.30-0.45$ -> $0.20-0.29$

Keraterpeton galvani

Total changes along branch: 3

49. Yes->no; 56. $5-9$ -> <5 ; 74. Present->absent

Batrachiderpeton

Total changes along branch: 5

21. Present->near; 64. Low and wide->high and wide; 133. Same size as posterior->laterally expanded; 140. Equal to more posterior->shorter than more posterior; 147. 2 or fewer->4

Diceratosaurus

Total changes along branch:

no unambiguous changes

Diplocaulus magnicornis

Total changes along branch: 2

22. Exposed->not exposed; 97. Deep->narrow

Diplocaulus primus

Total changes along branch:

no unambiguous changes

Diploceraspis

Total changes along branch: 8

9. Present->absent; 28. Present->absent; 74. Present->absent; 92. Absent->present; 95. Absent->present; 112. 1->2 or more; 126. None->one; 134. Single notochordal->single odontoid

Brachydectes

Total changes along branch: 19

12. Only ventral present->dorsal and ventral present; 13. Present->absent; 40. Absent->present; 65. Absent->present; 70. Anterior to occiput->far anterior ; 71. Widely separated->narrowly separated; 72. Present->absent; 81. Medial of stapes->under footplate of stapes; 84. Oval->round; 87. Unossified->ossified; 90. Present->absent; 94. Long->short; 95. Absent->present; 112. 1->0; 117. Fused->sutured; 129. Fused->paired; 134. Single notochordal->single odontoid; 135. Fused to centrum->sutured to centrum; 137. Fused at midline->paired

Oestocephalus

Total changes along branch: 8

2. Absent->present; 7. Sutural->weakly overlapping' 22. Exposed->not exposed; 23. Broad->narrow; 41. Present->absent; 57. $<20->=30$; 70. Anterior to occiput->posterior to occiput; 79. Absent->present

Phlegethontia

Total changes along branch: 9

9. Present->absent; 16. Paired->fused; 17. No->yes; 26. Blunt->pointed; 37. Paired->absent; 42. Present->absent; 51. Absent->present; 56. $5-9-><5$; 100. 1->0

Scincosaurus

Total changes along branch: 16

5. Absent->present; 28. Absent->present; 34. Present->absent; 37. Paired->absent; 67. Single, with basioccipital->double; 70. Anterior to occiput->far anterior ; 82. Loose->sutured or fused; 118. Equal to or wider than haemal->smaller than haemal spine; 121. Non-parallel->ant-post sides parallel; 125. Longer than or equal to neurals->shorter than neurals; 156. Widely separate->interdigitate; 162. Weak->prominent; 164. Short->long; 171. 3 vertebrae->4 vertebrae; 172. Continuous->distinct; 182. $0.30-0.45-><0.20$

Adelogyrinus

Total changes along branch: 8

6. Present->fused; 9. Present->absent; 15. Absent->present; 29. Absent->present; 33. Present->absent; 68. Between opisthotic and exoccipital->through exoccipital; 159. Both->absent; 181. <30mm->30-50mm

Node Support

Node 1

Total changes along branch: 5

11. Absent<->present; 105. Middle of tooth row<->posterior tooth row; 158. 0<->1; 165. ≥ 0.7 <->0.5-0.7; 170. 2 dorsal processes<->single blade

Node 2

Total changes along branch: 5

1. Absent->present; 6. Present->absent; 8. Mobile ->sutural; 34. Present->absent; 172.

Distinct->continuous

Node 3

Total changes along branch: 6

7. Weakly overlapping->sutural; 19. Absent->present; 46. Present->absent; 89. Narrow ->wide; 90. Present->absent; 180. 25-35-><25

Node 4

Total changes along branch: 5

36. Absent->present; 56. ≥ 10 ->5-9; 158. 1->2; 170. Single blade->narrowly bifurcate; 182. ≥ 0.45 ->0.30-0.45

Node 5

Total changes along branch: 6

57. ≥ 30 -<20; 80. Larger than marginals->equal to marginals; 108. Larger than marginals->smaller than marginals; 139. Present->absent; 145. 1->2; 149. Wide->narrow

Node 6

Total changes along branch: 11

1. Present->absent; 6. Absent->present; 29. Present->absent; 34. Absent->present; 46. Present->absent; 47. Circular pits->little to none; 65. Absent->present; 72. Present->absent; 74. Present->absent; 90. Present->absent; 110. Present->absent

Node 7

Total changes along branch: 6

57. <20->20-29; 63. Present->absent; 115. Present->absent; 116. Present->absent; 164. Long->short; 181. >70mm-<30mm

Node 8

Total changes along branch: 6

95. Absent->present; 121. Ant-post sides parallel->non-parallel; 145. 2->1; 147. 5 or more->3; 162. Prominent->weak; 170. Narrowly bifurcate->single blade

Node 9

Total changes along branch: 3

4. Absent->present; 102. Absent->present; 109. Dentary and splenal->dentary alone

Node 10

Total changes along branch: 6

30. Absent->present; 64. Low and wide->high and wide; 72. Absent->present; 86. Absent->present; 99. Present->absent

106. 3->2

Node 11

Total changes along branch: 3

34. Present->absent; 35. Present->absent; 164. Short->long

Node 12

Total changes along branch: 7

25. Straight->undulating; 74. Absent->present; 135. Sutured to centrum->fused to centrum; 136. Absent->on centrum; 145. 1->2; 162. Weak->prominent; 178. Absent->present

Node 13

Total changes along branch: 5

47. Little to none->shallow ridges and grooves; 86. Present->absent; 99. Absent->present; 117. Sutured->fused; 170. Single blade->2 dorsal processes

Node 14

Total changes along branch: 7

39. Moderate->large; 48. Vertical->overtured; 53. Vertical->turned medially; 57. 20-29-><20; 64. High and wide->low and wide; 88. Unossified->ossified; 115. Absent->present

Node 15

Total changes along branch: 5

22. Exposed->not exposed; 25. Undulating->convex; 69. Loosely articulated->strongly integrated; 70. Anterior to occiput->far anterior; 160. Present->absent

Node 16

Total changes along branch: 4

55. Pointed pegs->large cones; 56. 5-9-><5; 90. Absent->present; 106. 2->1

Node 17

Total changes along branch: 5

71. Widely separated->narrowly separated; 92. Present->absent; 109. Dentary alone->dentary and splenial; 115. Present->absent; 180. >35-><25

Node 18

Total changes along branch: 3

76. Absent->present; 116. Present->absent; 170. Single blade->2 dorsal processes

Node 19

Total changes along branch: 5

62. Absent->present; 65. Present->absent; 80. Equal to marginals->smaller than marginals; 100. 1->0; 102. Present->absent

Node 20

Total changes along branch: 2

21. Distant from->near; 97. Narrow->deep

Node 21

Total changes along branch: 6

23. Narrow->none; 25. Convex->straight; 69. Strongly integrated->loosely articulated; 70. Far anterior ->anterior to occiput; 117. Sutured->fused; 181. <30mm->30-50mm

Node 22

Total changes along branch: 8

24. Triangular->diamond; 66. Concave->convex; 68. Between opisthotic and exoccipital->through exoccipital; 77. Present->absent; 78. Present->absent; 104. Below->equal; 117. Sutured->fused; 175. Expanded->not expanded

Node 23

Total changes along branch: 9

5. Present->absent; 20. Ossified->unossified; 21. Distant from->present; 35. Absent->present; 60. Simple points->multiple cusps; 98. 2->0; 106. 2->0; 145. 2->1; 174. Long->short

Node 24

Total changes along branch: 5

17. No->yes; 25. Convex->undulating; 26. Pointed->blunt; 37. Paired->absent; 64. Low and wide->high and wide

Node 25

Total changes along branch: 2

79. Present->absent; 81. Under footplate of stapes->medial of stapes

Node 26

Total changes along branch: 8

14. Present->absent; 38. Present->absent; 41. Present->absent; 80. Equal to marginals->smaller than marginals; 111. Absent->present; 119. Even->alternating; 159. Both->scapula only; 181. <30mm->50-70mm

Node 27

Total changes along branch: 3

7. Sutural->weakly overlapping; 51. Absent->present; 96. Normal->reduced

Node 28

Total changes along branch: 2

30. Present->absent; 41. Present->absent

Node 29

Total changes along branch: 6

46. Absent->present; 47. Little to none->shallow ridges and grooves; 104. Below->above; 110. Absent->present; 111. Absent->present; 171. 6 vertebrae/5 vertebrae->3 vertebrae

Node 30

Total changes along branch: 1

131. Absent->present

Node 31

Total changes along branch: 4

49. No->yes; 79. Present->absent; 95. Present->absent; 141. One pair->absent

Node 32

Total changes along branch: 4

92. Present->absent; 112. 0->1; 122. Smooth->crenulated; 134. Single odontoid->single notochordal

Node 33

Total changes along branch: 11

4. Present->absent; 72. Absent->present; 74. Absent->present; 78. Present->absent; 90. Absent->present; 131. Absent->present; 160. Present->absent; 161. More than 80 degrees->absent; 165. 0.5-0.7->>=0.7; 167. Fully or partially ossified->unossified; 169. Sutured->poorly ossified

Node 34

Total changes along branch: 10

2. Absent->present; 7. Sutural->weakly overlapping; 12. Only ventral present->dorsal and ventral present; 26. Blunt->pointed; 32. Absent->present; 64. Low and wide->high and wide; 70. Anterior to occiput->posterior to occiput; 80. Equal to marginals->smaller than marginals; 138. Absent->zygantra; 181. <30mm->30-50mm

Node 35

Total changes along branch: 7

15. Absent->present; 16. Paired->fused; 27. Short->long; 76. Absent->present; 147. 3/2 or fewer->4; 152. Broad diamond->narrow diamond; 180. <25->25-35

Node 36

Total changes along branch: 2

113. Absent->present; 120. Narrow and smooth->laterally broad and sculpted

Node 37

Total changes along branch: 5

49. Yes->no; 103. Straight->hooked; 112. 1->2 or more; 114. Absent->present; 118. Equal to or wider than haemal->smaller than haemal spine

Node 38

Total changes along branch: 2

143. Short->long; 179. 5 or more->4 or less

Node 39

Total changes along branch: 3

39. Moderate->large; 153. Present->absent; 166. Unossified->ossified

Node 40

Total changes along branch: 8

28. Absent->present; 43. Absent->present; 67. Single, with basioccipital->double; 82.

Loose->sutured or fused; 106. 0->1; 138. Absent->zygosphenes; 155. Rounded or pointed dorsally->t- or y-shaped; 156. Widely separate->interdigitate

Node 41

Total changes along branch: 5

89. Narrow ->fused at midline; 94. Long->short; 103. Straight->hooked; 105. Posterior tooth row->middle of tooth row; 125. Longer than or equal to neurals->shorter than neurals

Node 42

Total changes along branch: 4

91. Absent->present; 97. Narrow->deep; 120. Narrow and smooth->laterally broad and sculpted; 121. Non-parallel->ant-post sides parallel

Node 43

Total changes along branch: 13

16. Paired->fused; 17. No->yes; 18. Present->absent; 33. Present->absent; 49. Yes-

>no; 70. Anterior to occiput->far anterior; 89. Narrow ->wide; 90. Present->absent; 93.

Absent->present; 132. On arch pedicle->on centrum; 133. Same size as posterior-

>laterally expanded; 140. Equal to more posterior->shorter than more posterior; 146. On centrum->on transverse process

Node 44

Total changes along branch: 2

21. Present->near; 99. Present->absent

Node 45

Total changes along branch: 8

31. Present->absent; 47. Shallow ridges and grooves->little to none; 64. Low and wide->high and narrow; 99. Present->absent; 110. Present->absent; 122. Crenulated->smooth; 180. $<25->>35$; 182. $0.30-0.45-><0.20$

Node 46

Total changes along branch: 9

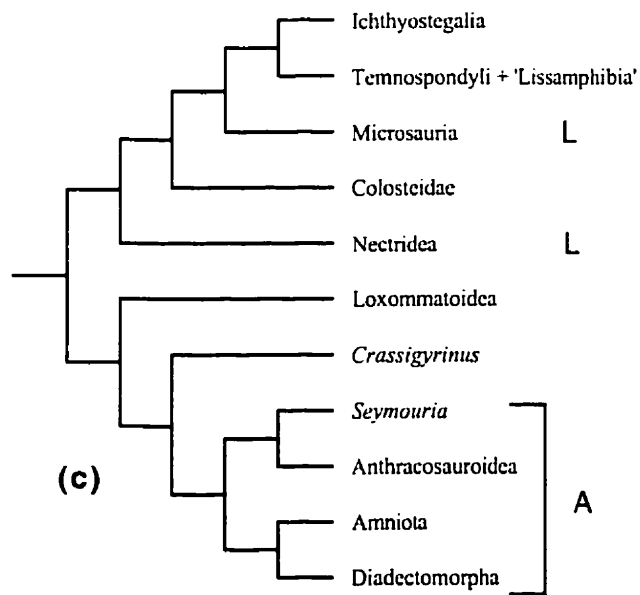
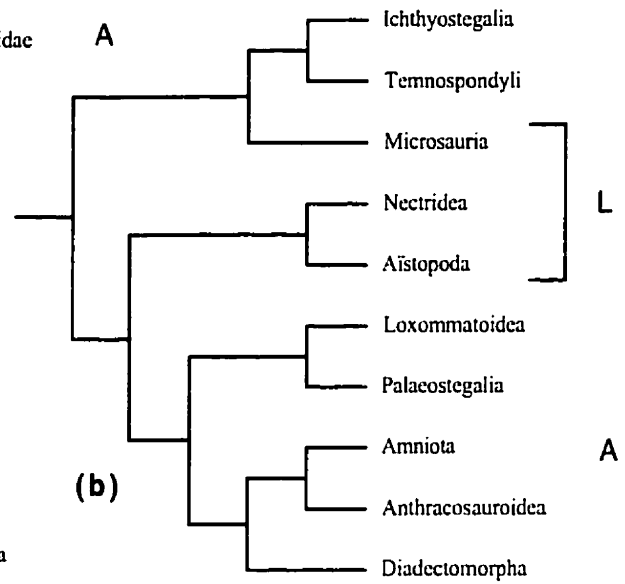
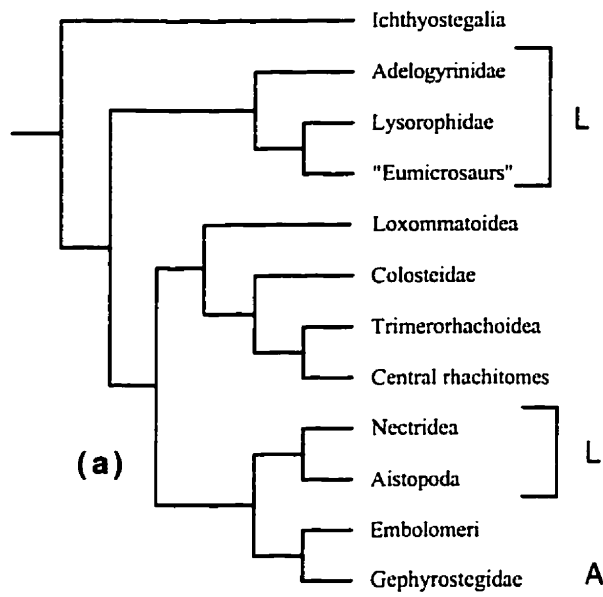
102. Present->absent; 111. Present->absent; 121. Non-parallel >ant-post sides parallel; 123. Present->absent; 130. Absent->present; 139. Absent->present; 144. Absent->present; 147. 2 or fewer->5 or more; 181. $<30\text{mm}->30-50\text{mm}$

TABLE 1. Taxa included in all analyses, with counts of all missing ("?") and inapplicable ("-") characters, giving an indication of completeness. Total unknown refers to the sum of missing and inapplicable characters, as both are treated equally by PAUP. Institutional abbreviations: AMNH, American Museum of Natural History; BYU, Brigham Young University, Salt Lake City; CGH, National Museum, Prague; FMNH, Field Museum of Natural History; MCP, Mazon Creek Collection, Northeastern Illinois University; MCZ, Museum of Comparative Zoology, Harvard; NMW, Naturhistorisches Museum, Wien; NSM, Nova Scotia Museum, Halifax; TMM, Texas Memorial Museum, The University of Texas at Austin; UMMP, The University of Michigan Museum of Paleontology, Ann Arbor; YPM, Yale Peabody Museum.

Taxon	"?"	"-"	Total Unknown	% Unknown	% ?"	Specimen Examined
<i>Acanthostega gunnari</i>	1	6	7	3.8	0.5	
<i>Adelogyrinus simorhynchus</i>	58	11	69	37.9	31.9	
<i>Asaphestera intermedia</i>	43	5	48	26.4	23.6	
<i>Balanerpeton woodi</i>	5	5	10	5.5	2.7	
<i>Batrachiderpeton reticulatum</i>	34	3	37	20.3	18.7	
<i>Batropetes fritschi</i>	19	9	28	15.4	10.4	
<i>Brachydectes</i>	2	15	17	9.3	1.1	
<i>Cardiocephalus peabodyi</i>	54	6	60	33.0	29.7	
<i>Cardiocephalus sternbergi</i>	69	6	75	41.2	37.9	
<i>Carrolla craddocki</i>	83	8	91	50.0	45.6	TMM 40031-54
<i>Ctenerpeton alveolatum</i>	138	2	140	76.9	75.8	
<i>Dendrerpeton acadianum</i>	22	4	26	14.3	12.1	NSM 987GF 99.1, NSM 978GF 53.1
<i>Diceratosaurus brevirostris</i>	28	7	35	19.2	15.4	AMNH 6836
<i>Diplocaulus magnicornis</i>	9	6	15	8.2	4.9	UMMP 3852
<i>Diplocaulus primus</i>	56	3	59	32.4	30.8	
<i>Diploceraspis burkei</i>	33	7	40	22.0	18.1	
<i>Eocaecilia micropoda</i>	26	20	46	25.3	14.3	
<i>Euryodus dalyae</i>	46	8	54	29.7	25.3	
<i>Euryodus primus</i>	44	8	52	28.6	24.2	
<i>Greererpeton burkemorani</i>	3	7	10	5.5	1.6	
<i>Hapsidoparion lepton</i>	51	8	59	32.4	28.0	
<i>Hyloplesion longicostatum</i>	22	7	29	15.9	12.1	CGH 3028
<i>Keraterpeton galvani</i>	21	5	26	14.3	11.5	NMW 1983.32.9

<i>Lepterpeton dobbsii</i>	119	4	123	67.6	65.4	
<i>Limnoscelis paludis</i>	7	5	12	6.6	3.8	YPM 811
<i>Llistrofus pricei</i>	88	4	92	50.5	48.4	
Mazon Creek	120	3	123	67.6	65.9	FMNH PR 981
<i>Micraroter erythrogeios</i>	29	5	34	18.7	15.9	
<i>Microbrachis pelikani</i>	3	8	11	6.0	1.6	CGH 727
<i>Odonterpeton triangulare</i>	47	10	57	31.3	25.8	
<i>Oestocephalus</i>	6	49	55	30.2	3.3	AMNH 6857, MCP 323
<i>granulosum</i>						
<i>Pantylus cordatus</i>	2	5	7	3.8	1.1	
<i>Pelodosotis elongatum</i>	22	7	29	15.9	12.1	
<i>Phlegethontia longissima</i>	10	67	77	42.3	5.5	AMNH 2564, MCZ 2204
<i>Proterogyrinus scheelei</i>	11	4	15	8.2	6.0	
<i>Ptyonius marshi</i>	17	6	23	12.6	9.3	AMNH 6871
<i>Quasicaecilia texana</i>	118	12	130	71.4	64.8	
<i>Rhynchonkos stovalli</i>	20	5	25	13.7	11.0	
<i>Sauropleura bairdi</i>	143	2	145	79.7	78.6	
<i>Sauropleura pectinata</i>	16	9	25	13.7	8.8	
<i>Sauropleura scalaris</i>	12	6	18	9.9	6.6	
<i>Saxonerpeton geinitzi</i>	19	12	31	17.0	10.4	
<i>Scincosaurus crassus</i>	27	9	36	19.8	14.8	NMW 1983.32.6, CM 711
<i>Seymouria baylorensis</i>	3	4	7	3.8	1.6	
<i>Sparodus validens</i>	68	6	74	40.7	37.4	
<i>Stegotretus agyrus</i>	35	6	41	22.5	19.2	
<i>Tuditanus punctulatus</i>	17	14	31	17.0	9.3	
<i>Urocordylus wandesfordii</i>	50	6	56	30.8	27.5	
<i>Utaherpeton franklini</i>	70	8	78	42.9	38.5	BYU 3050
Totals	1946	44	2388	26.8	21.8	
		2				

FIGURE 1. Recent phylogenetic hypotheses relating the Lepospondyli to various Paleozoic tetrapods. (a) Thompson and Bossy, 1970. (b) Smithson, 1985. (c) Panchen and Smithson, 1988. (d) Laurin and Reisz, 1997. An "L" denotes lepospondyls while an "A" shows the placement of amniotes.



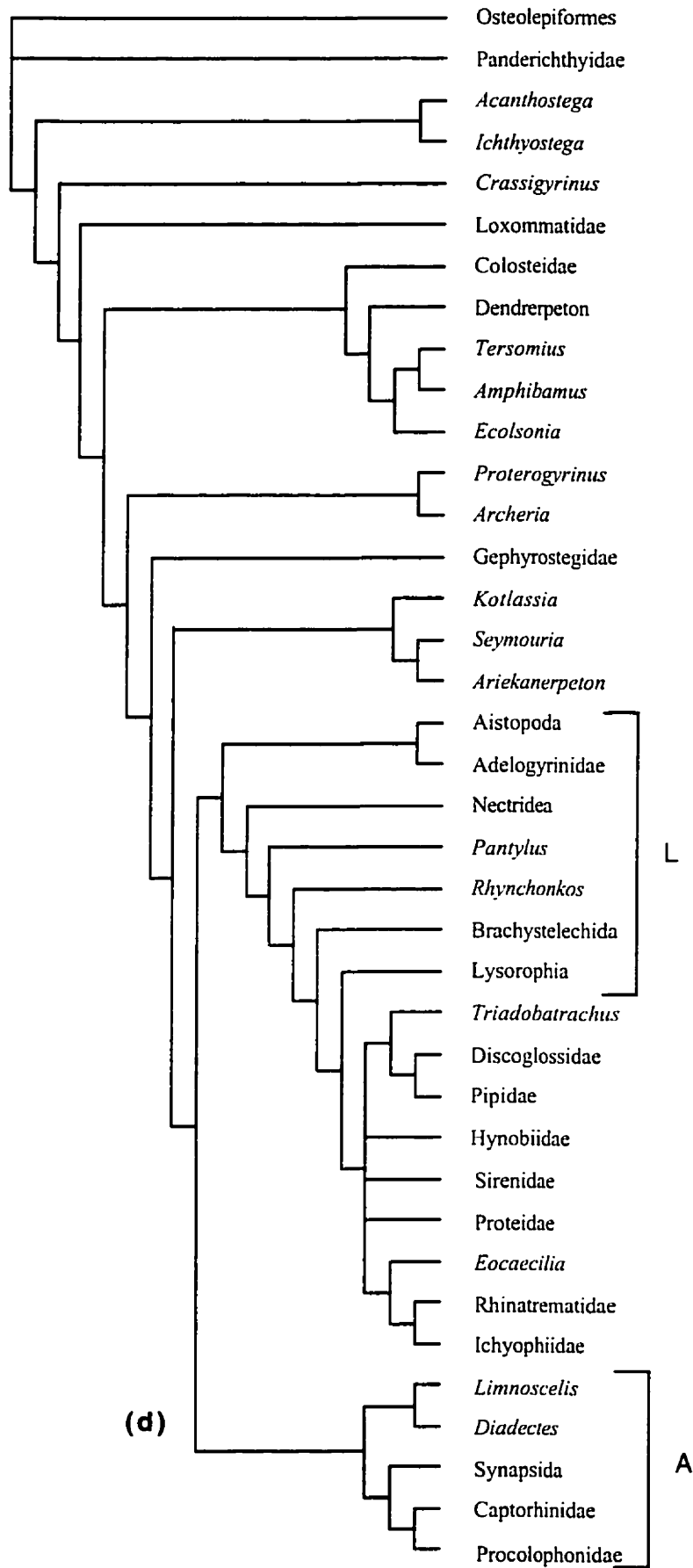


FIGURE 2. Regression of an estimate of area (length by width) of the interpterygoid vacuities upon basal skull length (rostrum to occipital condyle) for temnospondyls (open circles) and microsaurs (closed circles) in millimetres, natural log transformed. Regressions are significant for $p < 0.001$. Populations are significantly different from each other (Two way t-Test $p < 0.001$). Microsaur interpterygoid fenestrae are absolutely smaller than those of temnospondyls.

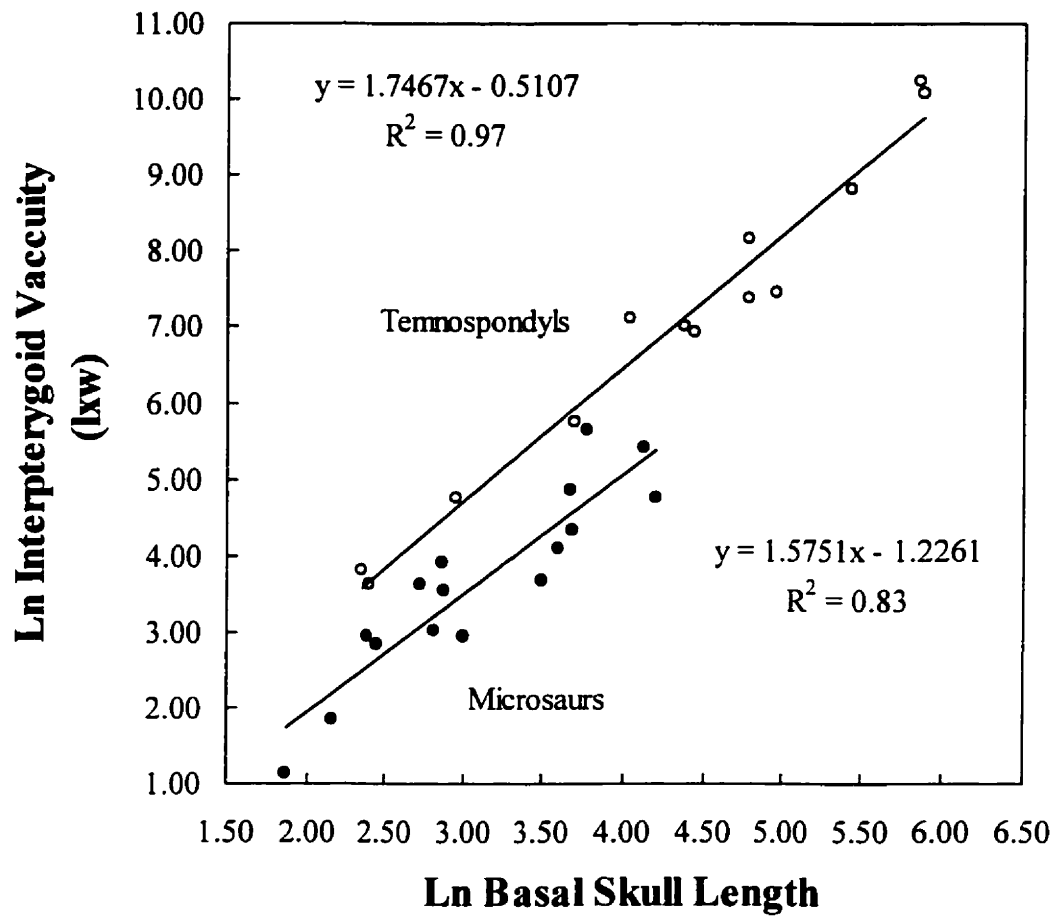


FIGURE 3. Interpterygoid vacuity states. (a) Primitive "closed" palate, with narrow openings lateral to the cultriform process. This taxon is most "open" of those with "closed" palates. *Greererpeton*, from Smithson, 1982. (b) Open palate, where the pterygoids expand laterally, narrowing near the palatines in a continuous arc. This is the most "closed" of taxa with open palates. *Ptyonius*, a urocordylid nectridean. (c) True closed palate, where the pterygoids suture at the midline. *Batrachiderpeton*, a diplocaulid nectridean. (b) and (c) from Bossy and A. C. Milner, 1998.

Abbreviations: Ipt. Vac. = interpterygoid vacuity.

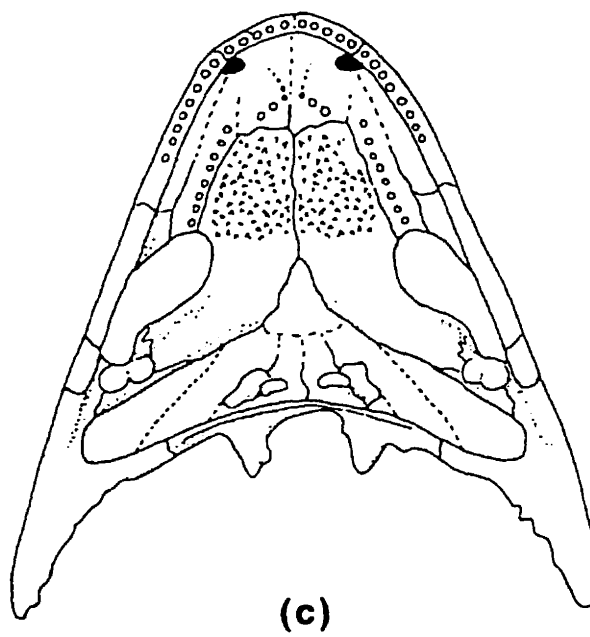
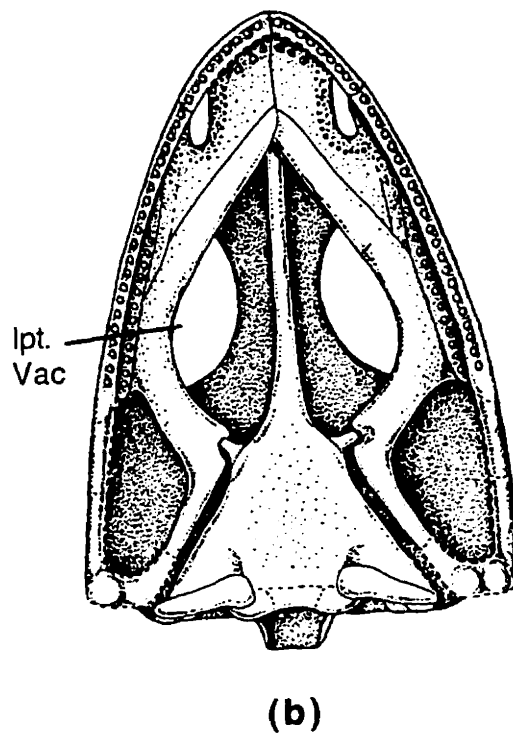
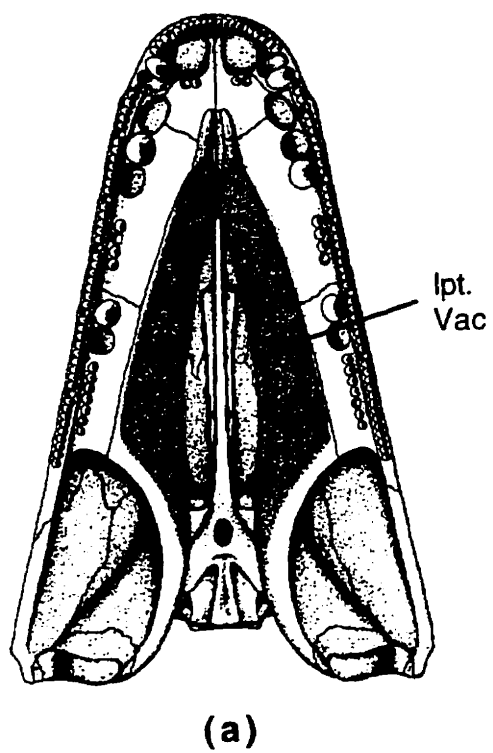


FIGURE 4. Occipital condyles. (a) *Proterogyrinus*, an embolomere. The primitive state is a spherical condyle of both the exoccipital and basioccipital. (b) *Brachydectes*, a lysorophid. This slight modification, where the condyle is now ovoid, is necessary due to the small skull size. Constituent bones remain the same and of the same proportions. (c) *Micraroter*, a microsauro. The condyle has assumed the "strap-shaped" morphology, and exoccipitals have become the dominant ossification, and the basioccipital has recessed from the level of the exoccipitals, but it continues to be a site of articulation with the atlas. (a)-(c) are single condyles. (d) True double condyles, where the basioccipital no longer serves as a site of articulation. *Diploceraspis*, a diplocaulid nectridean, from Bossy and A. C. Milner (1998). Abbreviations: BO=basioccipital, EO=exoccipital.

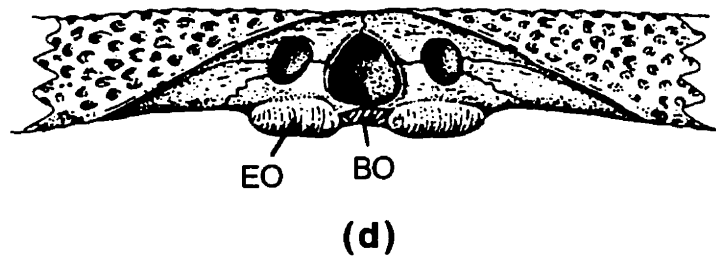
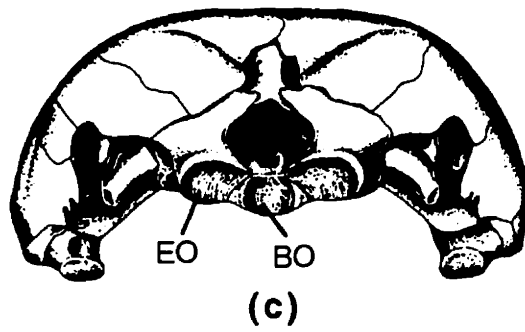
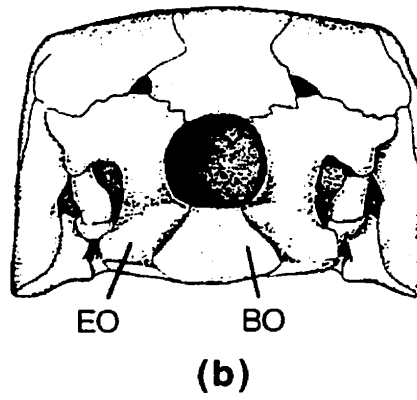
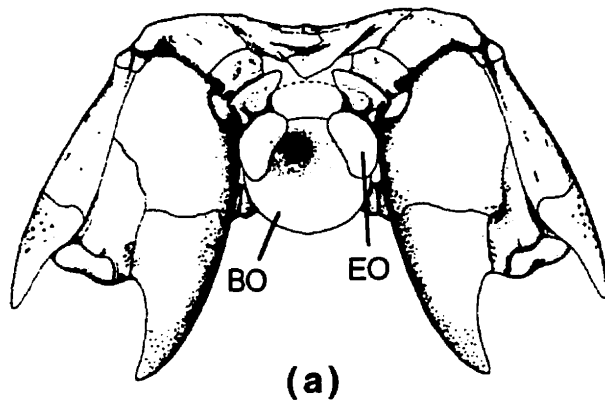
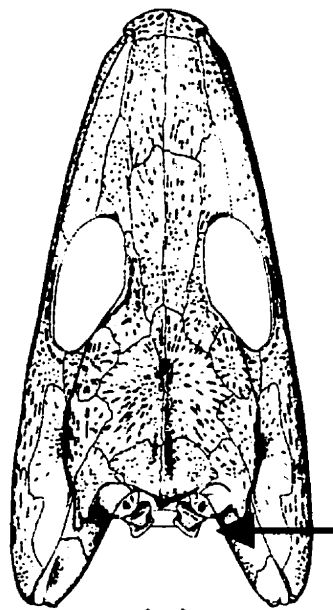
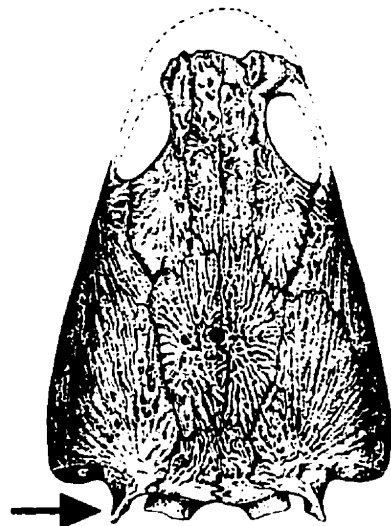
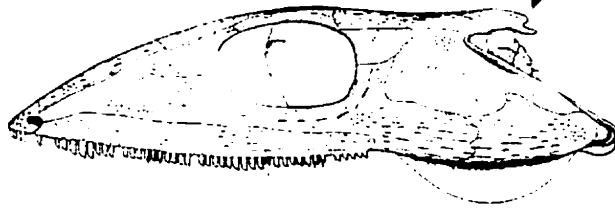


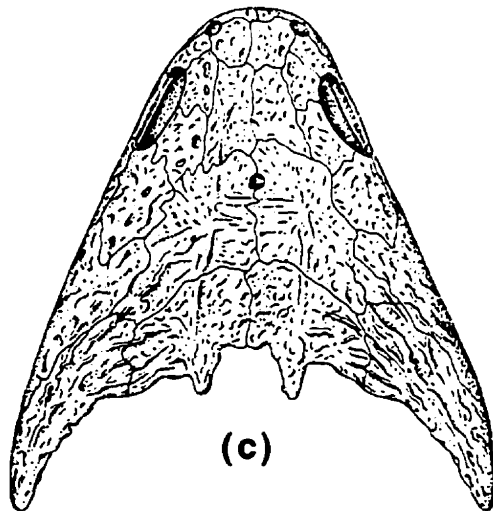
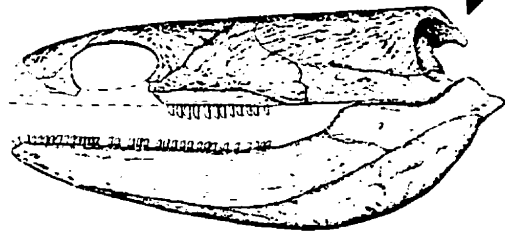
FIGURE 5. Tabular horns, indicated by arrows. (a) *Proterogyrinus*, from Holmes (1984) and (b) *Adelospondylus*, from Carroll and Andrews (1998). There is a posterior projection of the tabular, but when seen from lateral view it is evident that it forms the dorsal margin of the "otic notch." (c) *Batrachiderpeton*, from Bossy and A. C. Milner (1998). True tabular horns are large posterior projections unassociated with an otic notch (absent in nectrideans).



(a)

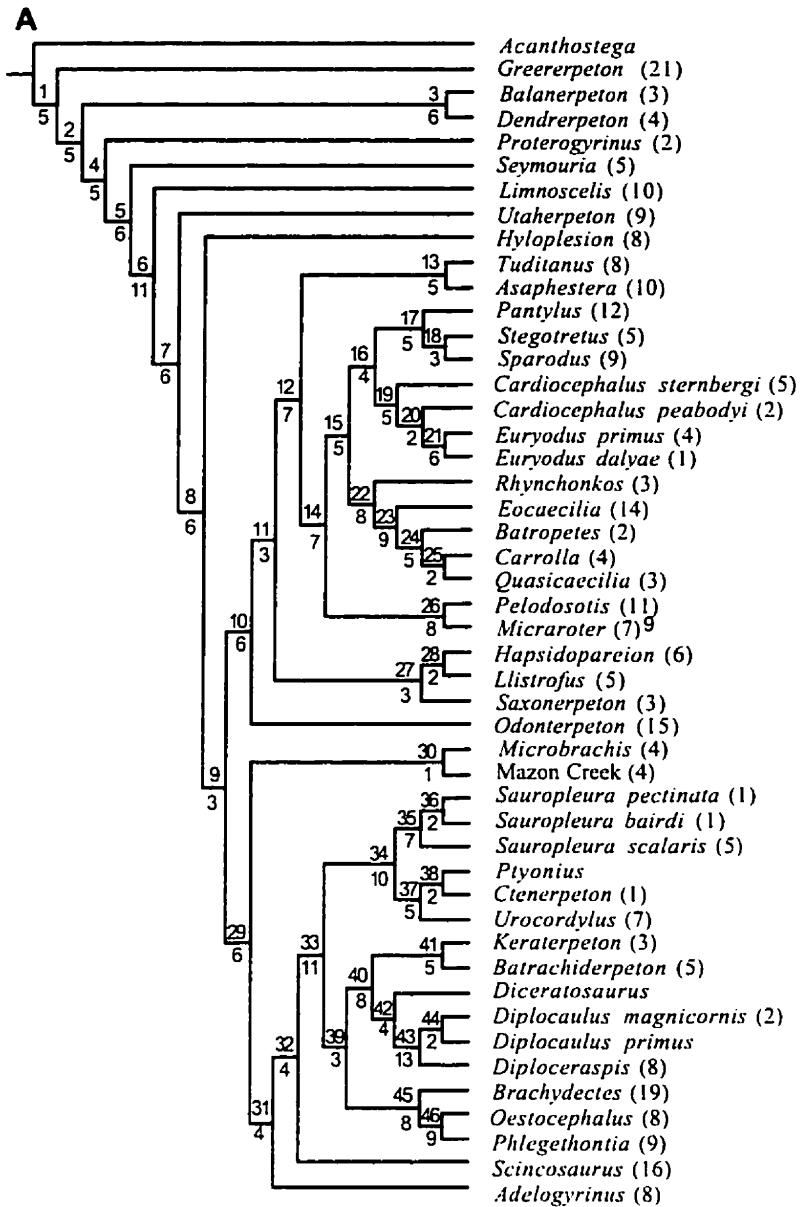


(b)



(c)

FIGURE 6. The phylogenetic trunk. Single most parsimonious tree (917 steps, C.I.=0.29, R.I.=0.58) found after deletion of the problem taxon *Lepterpeton*. Numbers to the side of taxon names are terminal apomorphies (see Appendix 3). A) Numbers above line identify the nodes as discussed in Appendix 3; numbers below the line are the amount of unambiguous character transformations, as identified by MacClade 3.07. B) Numbers above the line are the results from a decay analysis (e.g., Laurin and Reisz, 1995); numbers below the line are bootstrap frequencies above 50%. A and B are the nodes discussed in Figure 10.



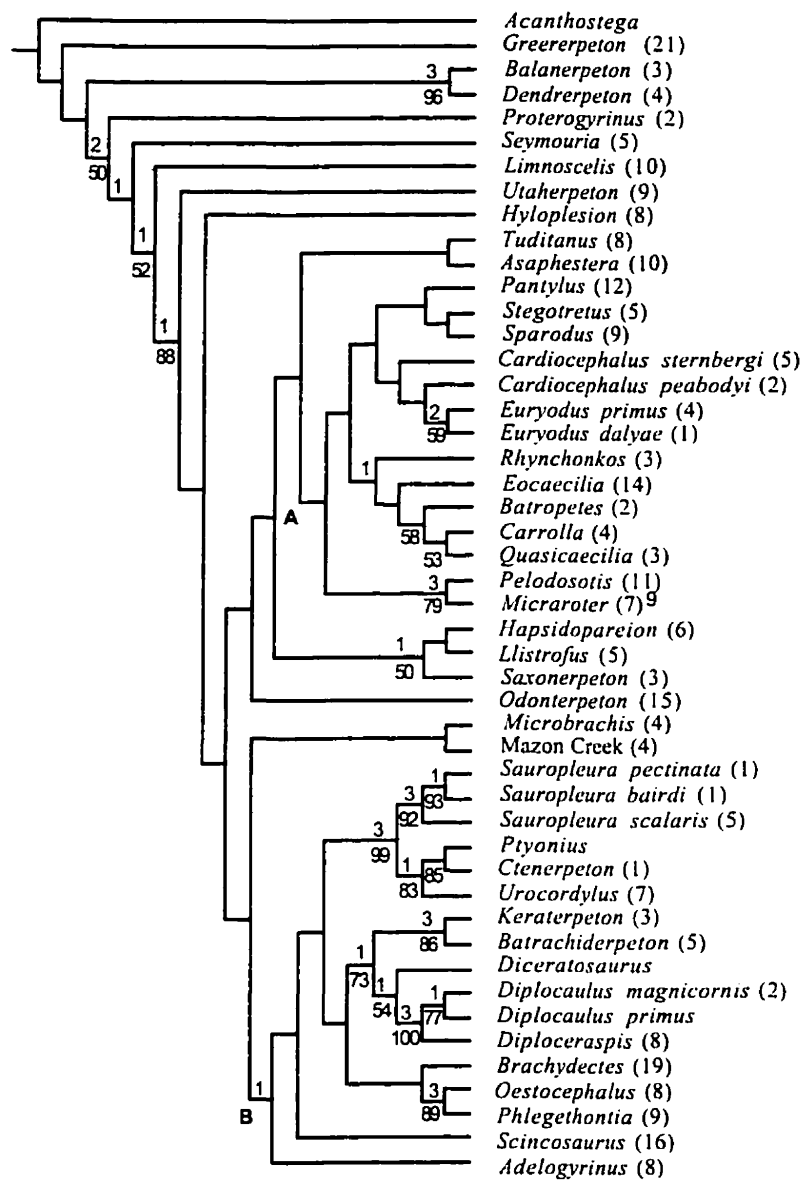
B

FIGURE 7. Adams consensus of 38 MPTs at one step from the trunk. Variable taxa are listed with the number of positions they occupy in the component trees.

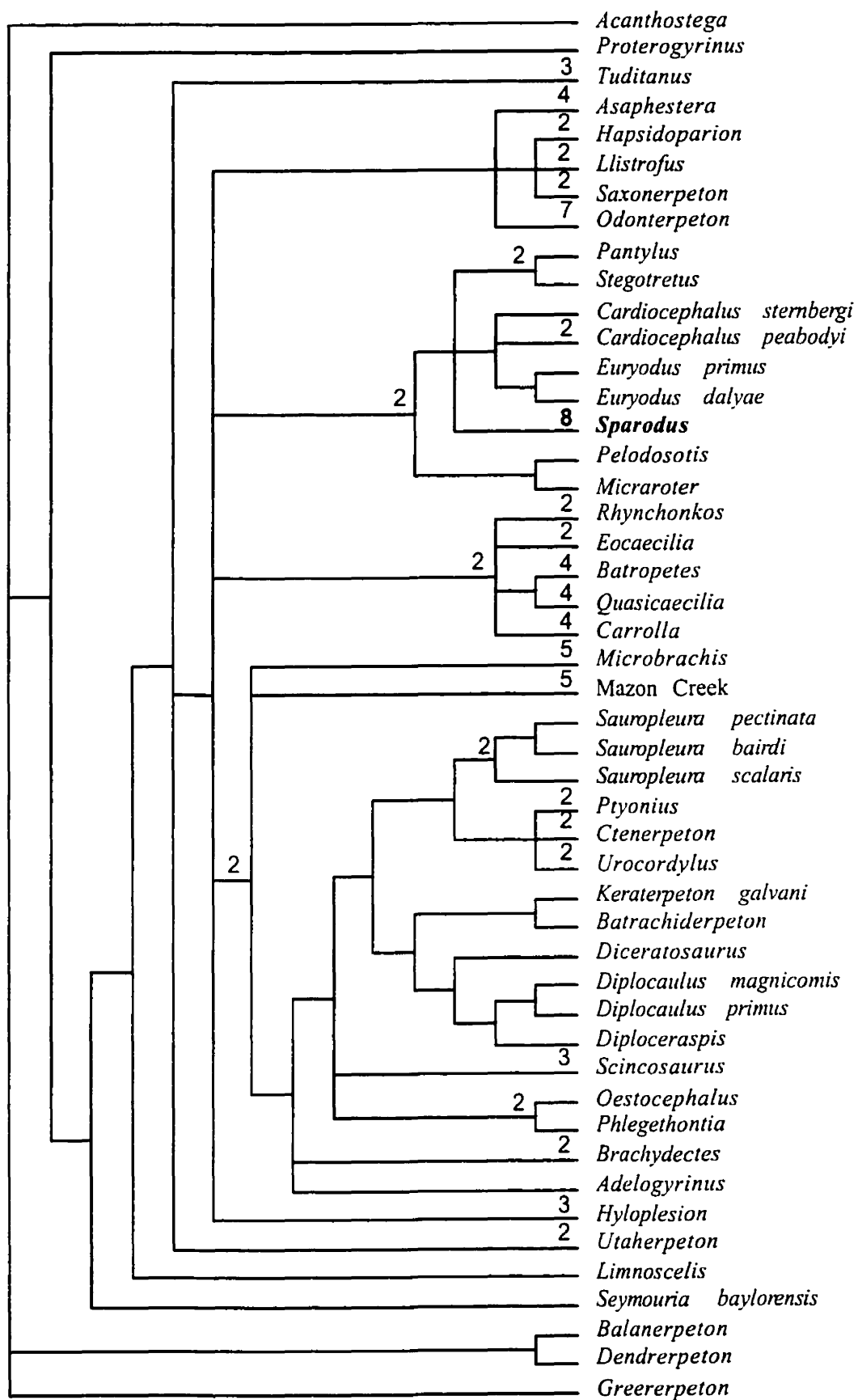


FIGURE 8. Given the alternate topologies in (a) and (b), which taxon is variable?

The conservative approach adopted here counts both taxon A and B as variable for two positions. If these two taxa were the most variable in the data set, they would each be excised to see which would produce the fewest MPTs upon removal. An alternate approach would examine all component trees; if taxon A is always just outside clade X (as in b), then taxon B would be scored as variable, while A would be considered stable since B has been interpolated between A and X in variant (a).

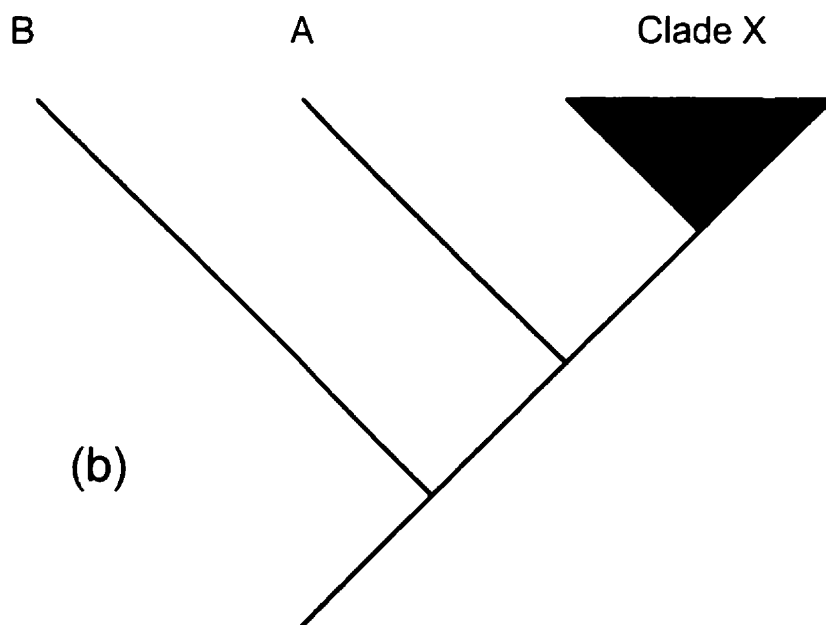
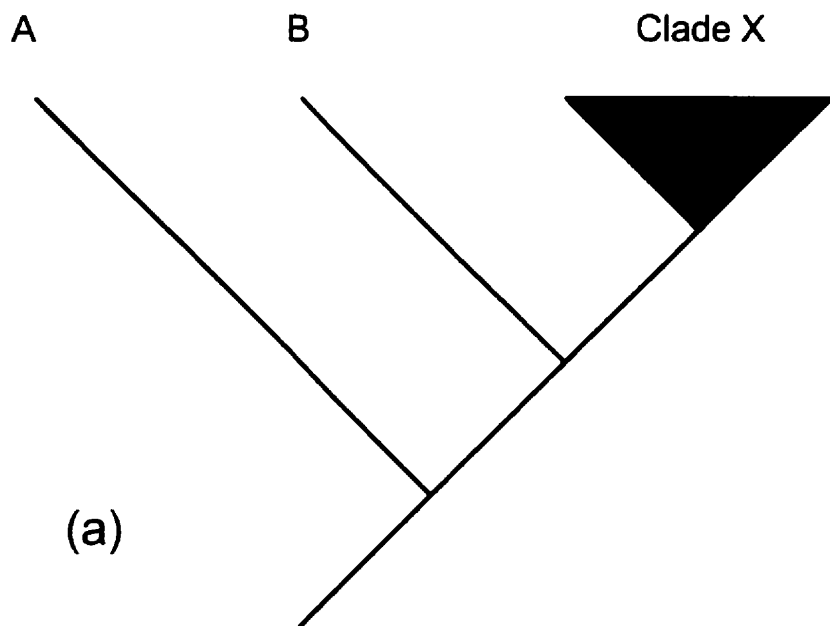


FIGURE 9. Single MPT (376 steps, C.I.=0.56, R.I.=0.47) produced by excluding all taxa with greater than 10% missing data. This tree differs from the trunk by finding a traditional Anthracosauria (*Proterogyrinus*, *Seymouria* and *Limnoscelis*), placing *Greererpeton* as outgroup to lepospondyls rather than temnospondyls (*Balanerpeton*), and rearranging lepospondyl relationships. Taxa with high amounts (over 70%) of missing data still help determine tree shape, so arbitrarily excluding them from an analysis is potentially misleading.

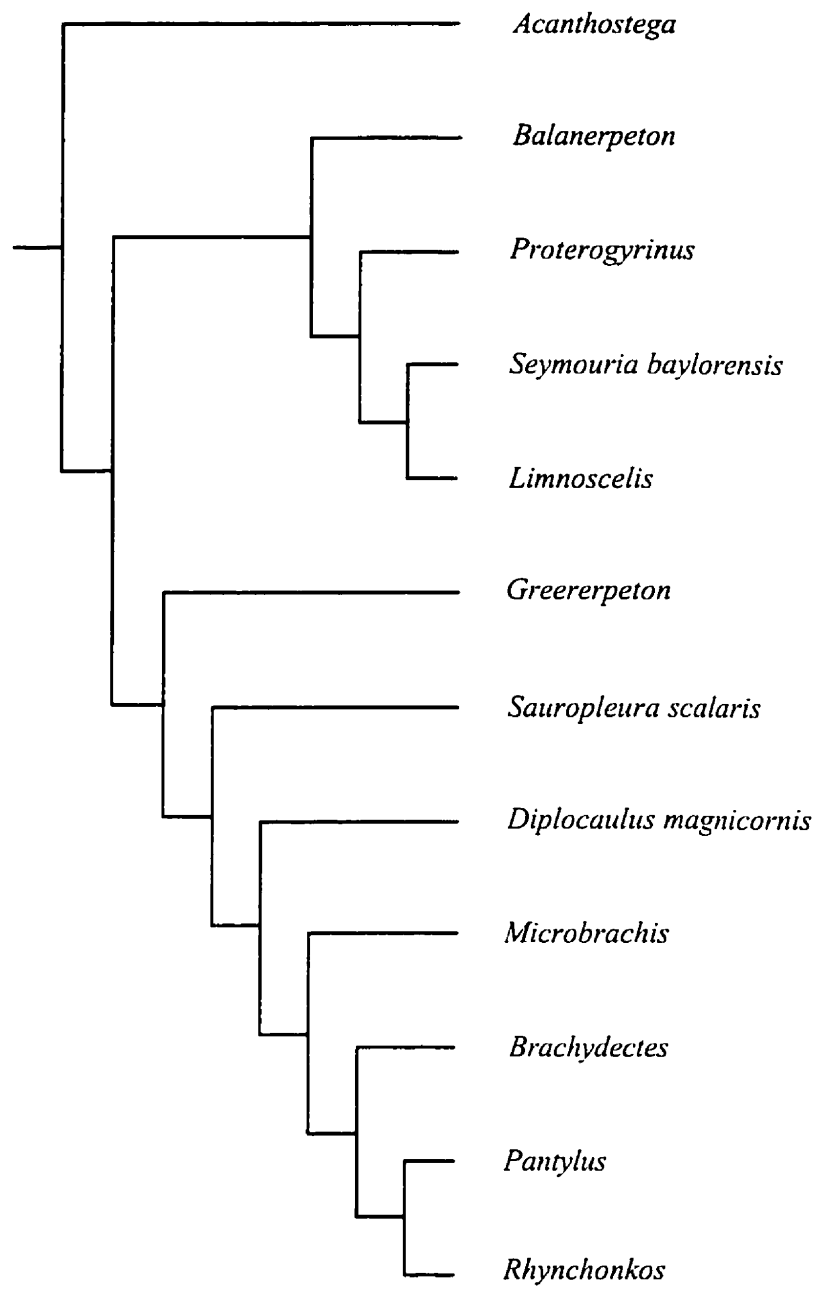
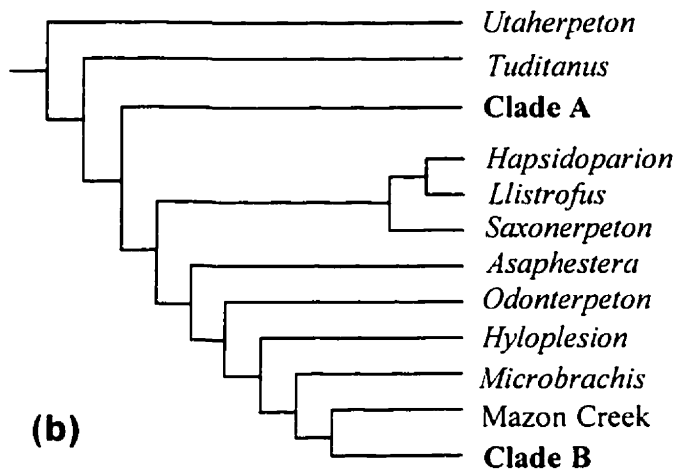
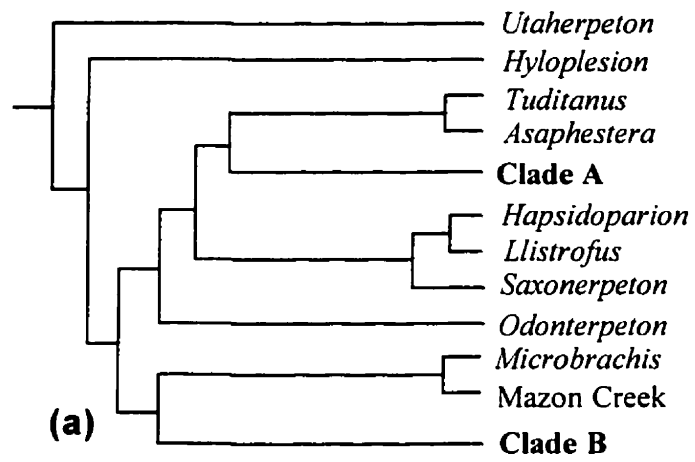


FIGURE 10. Two topological variants found within the 38 MPTs at an additional step away from the trunk. (a) Clade A is within a succession of tuditanomorph microsaurs. (b) Clade A is outgroup to most tuditanomorph microsaurs, which are attracted to *Microbrachis*, Mazon Creek, and Clade B. This is possible because of the large amount of missing data in the Mazon Creek microsaurs and *Adelogyrinus* (most basal member of Clade B) create sufficient ambiguity to allow the tuditanomorphs to "evolve" towards a Clade B condition. Removal of the Mazon Creek microsaurs eliminates variant (b).



CHAPTER 2

REVISION OF THE PHLEGETHONTIIDAE

To be submitted as: Jason S. Anderson. Revision of the Phlegethontiidae (Tetrapoda; Lepospondyli; Aïstopoda). Prepared for the Zoological Journal of the Linnean Society.

PREAMBLE CHAPTER 2

With my phylogenetic framework developed, I began examining aïstopods in detail. I decided to consider each recognised family in turn, and the logical place to begin was Phlegethontiidae. Phlegethontiid aïstopods have received some of the most thorough previous study, and as a result there was more of a foundation upon which to begin my work. They are a monophyletic assemblage, while ophiderpetontids are more likely paraphyletic. New specimens allowed me to examine areas unavailable to previous workers, and consider postcrania in greater detail. Preparation of specimens also led to the discovery of new features, including a new taxon that will be considered in Chapter 4. The anatomy of phlegethontiids is crucial to the formulation of my hypothesis of the developmental factors contributing to the acquisition of aïstopod traits.

ABSTRACT

The aïstopod family Phlegethontiidae is restudied in light of new specimens from Mazon Creek, Illinois, and Nýřany, Czech Republic. Phlegethontiids have highly fenestrate skulls, with orbits placed just anterior to the mid point. Dermal skull bones are greatly reduced in number and limited in extent, while the endochondral braincase has become hyperossified. The frontals are fused medially and encompass the parietal foramen and sagittal crest. The quadrate, pterygoid, and epipterygoid are fused into a palatoquadrate, which is common to all aïstopods. Details of the skull's anatomy are found to contradict previous kinetic models by severely limiting its potential mobility. Remnants of the pectoral girdle are present, perhaps due to the presence of an operculum-opercularis like connection to the stapes. No remnants of the pelvis remain.

Three species are recognised within the family. *Phlegethontia linearis* has short anterior vertebrae, high neural spines on at least the anterior four vertebrae, and between 230-250 vertebrae in total. *Phlegethontia longissima* has low neural spines throughout the column, anterior vertebrae that are twice as long as *P. linearis*, and only 200-210 total vertebrae. *Sillerpeton permianum*, known only from the braincase, can be distinguished from *Phlegethontia* by the retention of a separate foramen for the passage of the oculomotor nerve. "*Phlegethontia phanerhalpa*," from the Swisshelm Mountains of Arizona, is a tiny braincase fragment. It differs from the other species of *Phlegethontia* only in the placement of the jugular foramen relative to the centre of the foramen magnum, which is probably size related. It is considered a nomen dubum.

INTRODUCTION

The famous localities of Linton, Ohio, Nýřany, Czech Republic, and Mazon Creek, Illinois, have produced some of the most exquisite fossil vertebrates known, and remain among the best windows into the flora and fauna of the Upper Carboniferous. Countless descriptions have depended upon the fine degree of preservation found at these localities. Indeed, in these early days of a new synthesis between evolutionary and developmental biology, growth series from Linton and Nýřany have already played a role (Carroll, Kuntz and Albright, 1999).

However, not all taxa are equally represented. These deposits were aquatic, variously estuarine and freshwater oxbow lakes (Baird et al., 1985, 1986; Hook and Baird, 1986, 1988). The relative terrestrial or aquatic habits of the animals found preserved have been evaluated by their diversity of representation, assuming that animals from environments less like the depositional facies will be found less frequently (Milner, 1980; Milner, 1993). A more problematic bias in representation comes from the body form itself. Small, compact forms are more likely to be found complete, while large or elongate creatures have a greater likelihood of breakage occurring mid body. Further compounding this outcome is the fact that the majority of specimens from Nýřany and Linton were found during mining activities rather than concerted scientific exploration. This bias seems borne out in fact; the small temnospondyl *Amphibamus* is frequently found complete while an as yet undescribed embolomere (R. Holmes, pers. comm.) is only known from short sections of trunk and isolated bones.

Fragmentary specimens have been a particular problem for those attempting to study the Aïstopoda. Aïstopods are elongate, limbless lepospondyls, known from the Lower Carboniferous to the Lower Permian of Euramerica (Baird, 1964; Carroll, 1998b). They are rarely complete, and are usually represented by isolated strings of articulated vertebrae. This has resulted in an artificial proliferation of taxa, with new species (even multiple species) being named on a by-locality basis. Romer (1930), Steen, (1930) and Baird (1964) began to bring order to this assemblage by restricting the number of species at each locality to one, while admitting they could discern no appreciable differences between the recognized species.

Three families are currently recognized: Phlegethontiidae, Ophiderpetontidae, and Lethiscidae. These familial names are used throughout this paper for ease of discussion, but their monophyly and validity are not stipulated. The anatomy of each family will be considered in turn (this paper, Chapters 3, 4 and 5), and a phylogenetic analysis will accompany the final paper (on Lethiscidae; Chapter 5).

Professor Robert Carroll produced high-resolution latex peels (following the method of Baird, 1955) from a previously unstudied collection of Carboniferous coal-shales from Nýřany, Czech Republic, now in the Naturhistorisches Museum, Vienna. In this collection were several complete aïstopods. Additionally, new complete specimens, including juveniles, are now known from Mazon Creek, permitting consideration of species resolution versus ontogenetic changes between the different localities on a comparative basis for the first time. This material prompted my current revision of Aïstopoda, the final order of lepospondyl tetrapods to receive such treatment within recent years. The present paper considers Phlegethontiidae, the most thoroughly studied

family, as the starting point of an exploration of the anatomy and phylogeny of this curious collection of amphibians.

Phlegethontiidae

Of the three recognised families of aïstopods, the phlegethontiids are the most derived both from the typical “labyrinthodont” and lepospondyl conditions. Because of this divergent morphology it has attracted the most previous study, and is the logical place to begin a revision of the order. The first aïstopods were described from the coal shales of Jarrow, Ireland by Huxley and Wright (1867). Two genera were named, *Ophiderpeton* (which will be considered further in Chapter 3; see Milner, 1994 and Carroll, 1998a for recent discussions), and “*Dolichosoma*.” However, these specimens were never adequately prepared, and have been reported to have degraded dramatically due to pyrite disease (McGinnis, 1967:37). Cope (1868, 1871, 1874, 1875) named many species of aïstopods, two of which concern us here: *Phlegethontia linearis* and *P. serpens*, from Linton, Ohio. Fritsch (1875, 1879) named several additional species of “*Dolichosoma*” from the “Gaskohle” deposits of Nýřany and Kournova, Czech Republic, (further discussed by Schwartz, 1908). These specimens added many anatomical details unavailable in the specimens from Jarrow. The Nýřany species were reduced to one by (Steen, 1938), although she acknowledged that there were few differences between the species of *Phlegethontia* and “*Dolichosoma*” from any of the localities. Cope (1875) established the family Phlegethontiidae, to which Turnbull and Turnbull (1955) assigned “*Dolichosoma*”, citing the similarly proportioned skulls and similar dermal ossification, as well as the priority Cope’s name has over Lydekker’s (1889) Dolichosomatidae.

Gregory (1948) named the next new species of phlegethontid, *Phlegethontia mazonensis*, from the slightly older deposits of Mazon Creek, Illinois. Unlike the coal shales of Linton and Nýřany, which preserve fossils flattened dorsoventrally and sometimes laterally, Mazon Creek's nodules preserve fossils in three dimensions, frequently with impressions of soft tissues. Again, while he opted to name a separate species, Gregory acknowledged that apparent difference between the Linton phlegethontiids and the specimen from Mazon Creek might be preservational in nature. He wrote, "...it seems highly probable that *Phlegethontia mazonensis* was closely related to if not identical with *P. linearis* [from Linton]. The new specific name is given in recognition of the slight difference in age and locality, and to designate this far better preserved specimen." In 1955, Turnbull and Turnbull described a second specimen from Mazon Creek that displayed areas not preserved in the type specimen. Further preparation of this specimen reveals it to be a new species that will be described in Chapter 4.

A review of ařstopods was provided by Baird (1964). In it he clarified many taxonomic issues. First, he treated "*Dolichosoma*" as a nomen nudum, citing the inadequate description of the type by Huxley (through a layer of matrix), and transferred Fritch's "*Dolichosoma*" *longissima* to *Phlegethontia*. He also reduced *Phlegethontia* "*serpens*" to a junior synonym of *P. linearis*.

Shortly after Baird published his review of the order, McGinnis (1967) released her study of a new phlegethontiid from the Lower Permian fissure fill deposits of Ft. Sill (or Richard's Spur), Oklahoma, which included a revision of the family. She completed the pendulum swing from the extreme splitting of Cope and Fritsch to the more conservative (and justified) lumping of all North American species within the single

provisional species *Phlegethontia* cf. *longissima*, in her opinion the first adequately described species. Lund (1978) subsequently transferred these to *P.* cf. *linearis*, the species name with priority. McGinnis observed little difference between specimens from the various localities, and could not see any biological meaning for the separation of species simply because they are found in different locations.

The paper addressing phlegethontiids by Lund (1978) named two new genera. One, *Sillerpeton*, is based upon the braincase from Ft. Sill described by McGinnis, and the other, *Aornerpeton*, represents the recognition of the Mazon Creek phlegethontiid as a distinct genus. He also proposed an elaborate system of cranial kinesis, inspired perhaps by the rather snake-like skull of phlegethontiids. Finally, Thayer (1985) described a very small, fragmentary braincase from the Swisshelm Mountains in Arizona that he named *Phlegethontia phanerhalpha*. This specimen is notable in that it may preserve sutures in the occiput; all other phlegethontiids have no trace of sutures anywhere in the braincase.

The new complete specimens from the Czech Republic and all available North American phlegethontiids, as well as galvanotypes of Fritsch's material, were studied at the Redpath Museum of McGill University, Montreal. Specimens underwent further preparation and new latex peels were produced when the existing peels were too degraded for study. Specimens were drawn under a Wild dissecting microscope with a camera lucida. Growth series were established to determine patterns of allometry and development. With these new specimens the picture of phlegethontiid diversity and evolution is becoming clearer.

MATERIALS AND METHODS

Abbreviations

Institutional

AMNH: American Museum of Natural History.

CM: Carnegie Museum of Natural History.

CGH: National Museum, Pilzen.

FMNH: Field Museum of Natural History.

MCZ: Museum of Comparative Zoology, Harvard University.

NMNH: National Museum of Natural History, Smithsonian Institution.

NMW: Naturhistorisches Museum Wien.

UCMP: University of California Museum of Paleontology, Berkeley.

UMMP: University of Michigan Museum of Paleontology, Ann Arbor.

Anatomical—ak, anterior keel of braincase; ang, angular; bpp, basipterygoid process; dps, dorsal process of squamosal; ca, foramen for the carotid artery; clei, cleithrum; cltp, cultriform process; cp, costal process of rib; d, dentary; ecpt, ectopyerygoid; en, external naris; ep, epipterygoid portion of palatoquadrate; exn, external naris; gas, gastralia; II, foramen for the optic nerve; III, foramen for oculomotor nerve; j, jugal; jf, foramen for the jugular vein; lr, lateral ridge; m, maxilla; mfn, median frontal notch; mhg, medial haemal groove; n, nasal; nc, nuchal crest; ns, neural spine; oc, occipital complex; op, odontoid process of the atlas; orb, orbit; ot, foramen for the olfactory tract; p, parietal; pa, proatlas; parf, parietal foramen; pe, posteriomedial element; pf, postfrontal; pm,

premaxilla; po, postorbital; pop, posterior process of rib; poz, postzygopophysis; pp, postparietal; pq, palatoquadrate; prf, prefrontal; prz, prezygopophysis; ps, parasphenoid; pv, pituitary vein; pz, postzygopophysis; qc, quadrate condyle; qj, quadratojugal; sa, surangular; sc, sagittal crest; snf, foramen for the spinal nerve; sq, squamosal; st, stapes; tp, transverse process; tub, tuberculum; v, foramen for the trigeminal nerve; vf, ventral flange of the frontal; vsn, ventral notch for the squamosal.

Specimens studied

Phlegethontia linearis

Linton, Jefferson Co., Ohio. Canneloid shale below Upper Freeport Coal, Allegheny Group, late Westphalian D.

AMNH 6966 (Counterpart 6886, Turnbull, 1958). Complete specimen (type).

Phlegethontia ("Dolichosoma") *longissima*

Nýřany (Nürschan) Plzen Basin, Bohemia, Czech Republic, late Westphalian D.

NMW 1896 II 34 Nearly complete specimen, part and counterpart.

UMMP 22278 Galvanotype of CGH 129, skull and anterior 16 vertebrae.

UMMP 22289 Galvanotype of CGH 129 (figured by Fritsch to be in two pieces), 130 vertebrae in a broken series.

Linton, Jefferson Co., Ohio. Canneloid shale below Upper Freeport Coal, Allegheny Group, late Westphalian D. ("*Phlegethontia linearis*")

AMNH 2564 Skull and anterior 38 vertebrae.

AMNH 6899 Type of *Phlegethontia "serpens."*

AMNH 6913 Vertebrae and ribs.

CM 44759 Small skull and attached jaws in lateral view, part and counterpart.

CM 68307 Forty-one vertebrae and ribs.

CM 68336 Disarticulated skull, part and counterpart.

CM 68338 Disarticulated skull and 14 vertebrae.

MCZ 2038 Skull and anterior 4 vertebrae, part and counterpart.

MCZ 2334 Ventral view of braincase and skull roof.

USNM 4484 Disarticulated skull and anterior vertebrae

Mazon Creek, Grundy Co., and Braidwood, Will Co., Illinois. Francis Creek Shale above Morris (no. 2) Coal, Carbondale Formation, Westphalian C-D boundary.

FMNH PR 1358 (Part and counterpart) Skull and anterior vertebrae in lateral view, in epoxy.

FMNH PR 624 (Part and counterpart) Skull and anterior half of specimen.

FMNH PR 831 (Part and counterpart) Nearly complete specimen, diminutive individual.

FMNH PR 1145 (Part and counterpart) Skull and anterior half of specimen, faint body impression, diminutive individual.

MCZ 2204 Skull and anterior 9 vertebrae.

USNM 17097 (Part and counterpart) Nearly complete specimen (type).

Sillierpeton permianum

Fissure fill deposit in Arbuckle Limestone, Dolese Brothers Limestone Quarry, Fort Sill (Richard's Spur), Oklahoma.

UCMP 62580 Braincase.

SYSTEMATIC PALEONTOLOGY

Tetrapoda Goodrich, 1933

Lepospondyli Zittel, 1888

Aïstopoda Mial, 1875

Phlegethontiidae Cope, 1875

Revised diagnosis: Aïstopods with pointed snouts. Frontals fused and encompass the parietal foramen. Braincase ossified as a single unit, presumably incorporating the parietal, postparietal, tabular, exoccipital, basioccipital, and parasphenoid. Lower temporal bar formed by squamosal and jugal. Sixty-four precaudal vertebrae, ribs present to at least the 85th vertebra. Tail extremely long (100-190 vertebrae). Dorsal osteroderms absent, ventral gastralia thin, elongate and widely spaced.

Phlegethontia Cope, 1871

Revised Diagnosis: Phlegethontiids that have lost a separate foramen for cranial nerve III in the braincase wall.

Phlegethontia linearis Cope, 1871

Revised diagnosis: Phlegethontiid with high neural spines on at least anterior four vertebrae. Centrum length of anterior four vertebrae 6-7% the length of the skull.

Approximately 230-250 vertebrae in length.

Holotype: AMNH 6966, only known specimen.

Phlegethontia longissima Fritsch, 1875

Revised Diagnosis: Phlegethontiid with low neural spines throughout the column.

Anterior vertebrae approximately 12% the length of the jaw. 200-210 vertebrae present in the column.

Holotype: CGH 129.

Synonymy: *Phlegethontia serpens* (Cope, 1871)

Dolichosoma longissimum (Fritsch, 1875)

Dolichosoma angustatum (Fritsch, 1875)

Phlegethontia mazonensis (Gregory, 1948)

Aornerpeton mazonense (Gregory, 1948)

Phlegethontiidae incertae sedis

Sillerpeton permianum Lund, 1978

Revised Diagnosis: Phlegethontiid with a fossa for articulation of the dorsal end of the epipterygoid; a narrow vertical articular tubera basispheniodales; cultriform process not projecting beyond the edges of the braincase midorbitally; single foramen for cranial nerves V and VII, separate foramina for II and III.

Holotype: UCMP 62480

Synonymy: Aistopod (Gregory, Peabody and Price, 1956)

"Phlegethontia cf. longissima" (McGinnis, 1967)

Phlegethontiidae nomen dubium

Phlegethontia phanerhalpha Thayer, 1985

DESCRIPTION

Skull-Dermal

The description of the phlegethontiid skull is based primarily on AMNH 2564 (Fig. 1), MCZ 2204 (Figs. 5-7), NMW 1896 II 34 (Figs.3-4), and USNM 17097 (Fig. 12), with others noted where applicable. The skull of phlegethontiids is highly fenestrate. The endochondral portions are hyperossified, while the dermal bones are reduced for the most part to narrow, strut-like structures, giving it a superficially snake-like appearance. This light construction of the phlegethontiid skull makes breakage and disarticulation common. Additionally, the dermal bones only achieve tight articulation in larger specimens, making interpretation difficult. Skulls are usually found with the rostrum either displaced posteriorly or absent due to a zone of dissolution common at the margins of Mazon Creek nodules (Figs. 4 and 8). However the lower jaws usually remain in place, providing an estimate of skull size. Dermal ornamentation is limited to thin lines (Gregory, 1948) and nutrient foramina. Lateral line canal grooves are absent. There are no diagnostic differences between *Phlegethontia linearis* and *P. longissima* in cranial

anatomy, so they are considered together in the following description. *Sillerpeton* is only known from the braincase and will be considered below.

The nasal ramus of the premaxilla is equal in length to the maxillary ramus, and is longer medially than laterally, so that the portion along the suture is the most posterior part of the bone. Although McGinnis (1967) did not recognise a nasal ramus on the premaxilla, it is clearly present in specimens from Nýřany (UMMP 22278, NMW 1896 II 34; Fig. 4), Linton (AMNH 2564; Fig. 1) and Mazon Creek (FMNH PR 1358). The rostrum is narrowly rounded, and rapidly flares laterally in dorsal view, giving the premaxillae a V-shaped appearance. At the junction of the nasal and maxillary rami the postero-medial surface is concave, forming most of the margin of the external naris (the posterior border is established by the prefrontal). No ossified septomaxilla is present. Nutrient foramina pierce the lateral walls of the maxillary ramus dorsal to the “alveoli” in larger specimens. There is space for 7 teeth.

The maxillary ramus of the premaxilla abuts the maxilla with an oblique suture. The maxilla is a long, rectangular bone that could house up to 14 teeth. Like the premaxilla, nutrient foramina are developed above tooth “alveoli” on the lateral wall. It forms most of the ventral margin of the orbit, and extends from just posterior of the external naris to just beyond the orbit. It maintains a constant depth throughout its length, unlike the maxilla in *Oestocephalus*, which gradually tapers posteriorly (Carroll, 1998a).

The prefrontal is a roughly triangular bone (Figs. 1 and 4). It has a wide dorsal articulation with the nasal and frontal, and it articulated with the maxilla at a narrow point. The “hypotenuse” of the triangle is concave, and forms the anterior margin of the

orbit. The identification of this bone as the prefrontal is not certain; its shape, orientation, and the absence a lacrimal duct suggest it is the prefrontal, but it might represent the lacrimal or a fusion of lacrimal and prefrontal.

The nasal is the least well preserved bones of the skull (Fig. 4). It is inferred by the shape of the premaxilla and frontals to be a small, diamond-shaped bone, which runs along the side of the premaxilla and fits into the anterior prongs of the frontal.

The frontals are fused into a large single ossification, similar to sauropleurine and some diplocaulid nectrideans (Bossy and Milner, 1998). In dorsal view, the anterior margin is deeply W-shaped, forming three anteriorly oriented points, in between which lies the posterior half of the nasals (Fig. 1). The frontal is narrow between the orbits and laterally expanded just posterior to the orbit. The fused structure forms the entire dorsal margin of the orbit. Posterior to the widest point, the frontal comes to a point on the midline that is deeply cleft at its apex to accommodate the sagittal crest. This notch is relatively deeper in larger individuals. At its rostral end the notch expands laterally, mirroring an expansion in the dorsoanterior portion of the braincase, forming the parietal foramen. This morphology is similar to the parietal of *Amphisbaena alba* (Montaro and Gans 1999; Fig. 10). The sagittal crest extends into the area of the foramen, and articulates with the deepest anterior portion of the frontal notch. A ledge that forms on the highly ossified braincase further supports the frontals from the underside.

On the ventral surface of the frontals, two parallel medial ridges arise anterior of the braincase (MCZ 2334, MCZ 2204; Fig. 6), and run anteriorly at least to the orbit. They accommodate the dorsal point of the anterior keel of the braincase.

McGinnis identified the frontals as a fusion of the frontals and parietals. However, in all known aïstopods the parietal foramen is located well within the parietals; in no lepospondyl is the parietal foramen found on the parietal-postparietal suture as would be required following McGinnis' hypothesis. Conversely, the parietal foramen is found at or near the frontal-parietal suture in other lepospondyls such as microsaurs (e.g., *Odonterpeton*; Carroll and Gaskill, 1978) and nectrideans (e.g., *Ptyonius*; Bossy and Milner, 1998), so this interpretation is preferred. Furthermore, most aïstopods have a posterior projection into the parietal by the frontal lateral to the midline that approaches the parietal foramen in a probable phylogenetic sequence (Chapters 3 and 4). The phlegethontiid condition is the end point of this series.

Of the remainder of the skull roof and occiput, no separate bones may be identified; all were presumably incorporated into the massively ossified braincase. Lund (1978) described the presence of parietals, tabulars and a supraoccipital which distinguished *Phlegethontia* from "*Aornerpeton*" (the Mazon Creek phlegethontiids), which lacks these elements. However, I could find no separate bones in the areas indicated in his description in any specimen. Consideration of a two-dimensional representation of AMNH 2564 (Fig. 1) might give the appearance of separate parietals, but examination of the specimen shows the relevant areas to be the flattened shelf-like facet for the frontal articulation, and a ventro-lateral distortion due to crushing.

In lateral view, the postfrontal and the jugal form the posterior border of the orbit (Figs. 1 and 4). The postfrontal is a roughly triangular bone with its widest surface oriented dorsally, articulating with the frontal. There is no anterior contact with the prefrontal; the dorsal margin of the orbit is formed by the frontal. In AMNH 2564 (Fig. 1),

the descending arm of the postfrontal appears to be surrounded laterally, posteriorly, and medially by the jugal, forming a tongue-in-groove joint, although this does not seem to be the condition in the Mazon Creek specimens (e.g., MCZ 2204) and may be a taphonomic artefact. The jugal is an irregular triradiate bone. Anteriorly it articulates on the dorsal surface of the maxilla for a short distance, then it becomes dorsally inflected and rises into the main body of the bone, giving this process a small distal “foot.” A short, robust process extends posteriorly. Its ventral surface is concave for reception of the anterior process of the squamosal.

The squamosal is another triradiate bone. Its longest process is directed anteriorly, subhorizontally, where it articulates on the underside of the posterior process of the jugal. Its dorsal process narrows substantially before fusing with the braincase near the junction of the sagittal and nuchal crests. The ventral process covers the quadrate portion of the palatoquadrate laterally. Study of the Turnbull aïstopod (FMNH PR 281; Chapter 4) may suggest that the phlegethontiid squamosal incorporates the quadratojugal; however, there is no evidence that it existed as a separate ossification even early in the ontogeny of *Phlegethontia*. Additionally, there is no evidence of a suture on the anterior process, as suggested by Lund (1978). In fact, with the exception of UMMP 22278, there is no crack or ridge in that position in any specimen preserving that area.

No vomers or palatines are preserved in any phlegethontiid. The pterygoid is fused to the quadrate, forming a palatoquadrate (Figs. 1, 4-6). Lund (1978) identified this element as the “pterygoquadrate” since he thought he had identified the palatine as a separate element. Gallup (1983) followed this identification in his description of the ophiderpetontid *Coloraderpeton* because they retain a distinct palatine. My specification

of this element as the palatoquadrate follows its resemblance to the similarly named bone in nontetrapod sarcopterygians (Carroll, 1998a), and does not stipulate that the palatine is a part of its structure. Separate palatines and ectopterygoids are present on the palate of *Eustenopteron* as well (Jarvik, 1996). The palatoquadrate has three regions: the palatal ramus, the “quadrate,” and the epipterygoid. The palatal ramus lacks teeth. It runs closely parallel to the cultriform process leaving slit-like interpterygoid vacuities. The lateral edge begins anteriorly at a point, flares laterally to achieve its greatest span at about its mid length, and narrows again as it approaches the region of the quadrate ramus. There is no descending process or flange. The loose articulation with the basipterygoid process is at the junction of the quadrate and palatal rami. The quadrate ramus extends laterally from the basipterygoid process a short distance to the quadrate condyle. The anterior face of the quadrate ramus is deeply concave as seen in NMW 1896 II 34, possibly for the origin of jaw adductor muscles. The condyle itself is semicylindrical and is directed at nearly a right angle to the main axis of the skull.

The epipterygoid rises from the dorsal surface of the palatal ramus of the palatoquadrate and is tightly pressed to the lateral wall of the braincase. It is a thin, roughly rectangular sheet of bone that rises dorsally from the quadrate ramus and continues forward to just anterior to the foramen for cranial nerve II (optic foramen). On the posterior margin it surrounds the proötic foramen on all but its posterior margins. It continues horizontally to the optic foramen above the proötic foramen. The epipterygoid descends below the optic foramen, leaving its upper margin free from confinement. Just anterior to the optic foramen, the epipterygoid puts out an anteriodorsal process (called the anterior process by McGinnis, 1967).

In smaller specimens (e.g., USNM 17097), the epipterygoid is incompletely ossified; it does not maintain a horizontal upper border. Rather, it descends as it moves anteriorly, but ultimately fails to reach the foramen for the optic nerve.

Skull-Endochondral

The endochondral bones of the phlegethontiid braincase are indistinguishably co-ossified at an early stage, forming a mammal-like calvarium. It is best revealed in MCZ 2204, a large specimen from Mazon Creek (Figs 5-7). Further preparation of this specimen has revealed many significant new features. Throughout this paper the term braincase is used to refer to the entire structure, although elements of the dermocranium (e.g. parasphenoid, and presumably the parietals) are incorporated. For convenience's sake, the areas where a separate element would have existed are referred to by their standard names, but it should be noted that none of these bones show sutures at any stage of ontogeny. The only exception is the specimen described by Thayer (1985) that may show a suture between the basi- and exoccipital.

The braincase dominates the posterior half of the skull. In the largest individuals it is ossified from occiput to orbit. It is a high-sided structure, and is keeled anteriorly (Fig. 7), rising from the cultriform process dorsoanteriorly to meet the frontal just in front of the orbits, where it slots into the frontal's posterior recess above, and the paired longitudinal flanges below (also seen in MCZ 2334). Gregory (1948) and Carroll (1998a) suggested that the ventral descending flanges on the frontal protects the olfactory tracts; however, there are no foramina on the anterior sphenethmoid keel that would permit passage of the tracts. The olfactory bulbs probably passed from the braincase from

two anteriorly facing foramina located on the ventral keel just above the base of the cultriform process. The braincase is widest just below the skull table; the walls converge ventrally to the parasphenoid and dorsally to the sagittal crest.

Two large foramina are located within the lower half of the braincase (Figs. 6 and 7). The posterior foramen, located just anterior to the otic capsule, is the larger. It is the proötic foramen for the passage of the trigeminal nerve (V), and, according to McGinnis (1967), the hyomandibular branch of the facial (VII), and probably the abducens (VI). The anterior foramen is the optic foramen, for the passage of the optic nerve (II). *Sillerpeton*'s lateral wall ends at this foramen. Anterior and ventral to the optic foramen in MCZ 2204, lateral to the base of the cultriform process, is a small foramen. McGinnis tentatively suggested that it was for the passage of the oculomotor nerve (III), while cautioning that III usually exits posterior to the optic foramen (as is the case in *Sillerpeton*). Another possibility is that it is for the exit of the pituitary vein. This interpretation would require that III exits through either the proötic foramen or the foramina dorsal to the cultriform process. Regardless, the absence of a distinct foramen for III distinguishes the braincase of *Phlegethontia* from *Sillerpeton*. Just above the cultriform process, on the midline, is a large anteriorly directed foramen subdivided by a median septum (or possibly, two closely associated foramina), that McGinnis suggested passed the optic or basilar arteries, or the pituitary vein. However, since the anterior keel of the braincase tightly articulates with the frontal, it is more likely that this foramen was for the passage of the olfactory tract. There is also a ridge that runs on the lateral surface of the braincase about mid height, dorsal to the foramina for II and V (Fig. 6).

A sagittal crest is developed on larger individuals of *Phlegethontia* (e.g. MCZ 2204; Figs. 1 and 5). Although *Sillerpeton* possesses an incipient crest (McGinnis, 1967), smaller specimens of *Phlegethontia* (USNM 17077, FMNH PR 831) do not, despite being much larger than *Sillerpeton*. The crest begins anteriorly within the notch of the fused frontals, extending into the parietal foramen, and ends posteriorly behind the otic capsules, where it splits into two ridges that continue laterally along the posterior margin of the capsules, forming a nuchal crest for insertion of epaxial musculature. There is a swelling on the sagittal crest just posterior to the parietal foramen (AMNH 2564, MCZ 2204; Fig. 1).

The occiput of phlegethontiids is high and oval. The foramen magnum is large and round. Its border is thinnest dorsally, which suggests that a supraoccipital ossification is not incorporated into the co-ossified structure. It is recessed from the most posterior portions of the otic capsules, but incorporates nearly the entire space between the otic capsules, even in the largest individuals. The otic capsules establish the lateral extent of the skull. In the smallest specimens of *Phlegethontia* (USNM 17097, FMNH PR 831) and in *Sillerpeton*, the bony ridges surrounding the semicircular canals are visible on the exterior surface of the capsules. Assuming that there is a lower size limit for the proper functioning of the semicircular canal (Jones and Spells, 1963), these animals have among the smallest sizes possible for the vertebrate skull (Hanken, 1984; Carroll, 1997). There is no indication of a site of articulation with the proatlas. The jugular foramen pierces the exoccipital (the position of which is determined from the location of the suture in "*P. phanerhalpha*") lateral to the center of the foramen magnum in *Sillerpeton*, and the opisthotic lateral to the centre of the foramen magnum in *Phlegethontia longissima*

(revealed after further preparation of MCZ 2204). It pierces the opisthotic lateral to the base of the foramen magnum in "*P. phanerhalpha*" (Thayer, 1985), which might be a size related difference. The occipital condyle (actually a cotyle) is characteristic of all aïstopods. It is round and concave, and has a notochordal pit in its center, which suggests that, while *Phlegethontia* had an odontoid process on its atlas, at least part of the articulation with the skull was in soft tissue. Unlike osteolepiforms, which have a superficially similar occipital articulation, the notochord does not penetrate into the braincase.

In ventral view (Fig. 6), the dominant features are the large, pear shaped fenestrae ovals. They are located on the posteroventral surface of the otic capsules, and have their long axes oriented anteriomedially. Internally they have deep walls, and are narrower proximally. In USNM 17097 and MCZ 2204 the fenestrae ovals are tightly infilled by the stapes. The stapes is a broad plate of identical dimensions to the fenestra ovalis. The only other tetrapod groups that have similarly large plate-like stapes are caecilians and amphisbaenids. The stapes has neither a columella nor a stapedia foramen, but a crescentric ridge that is convex anterior and bevelled posteriorly runs laterally across its surface. It is highly suggestive of a muscle origin scar. If one reconstructs this hypothetical muscle one sees it is directed posteriorly and somewhat laterally, towards the remnants of the pectoral girdle. In modern frogs and salamanders, there is an ossicle accessory to the footplate of the stapes (sometimes fused to it) called the operculum. In salamandrids the operculum fills the entire fenestra ovalis. It serves as the origin of a muscle, the opercularis, which inserts on the pectoral girdle, and serves to transmit low frequency vibrations to the middle ear (Duellman and Trueb, 1986). No

phlegethontiid shows evidence of an accessory ossicle. However, it would benefit a limbless creature to be able to detect low frequency vibrations through the ground, such as the approach of a predator, and this may help explain the persistence of remnants of the pectoral girdle throughout the duration of aïstopods. This hypothesis is perhaps supported by the observation that caecilians, which lack any trace of the pectoral girdle, are the only group of modern amphibian that does not have an opercularis (Duellman and Trueb, 1986).

The parasphenoid is indistinguishably fused with the ventral braincase (Fig. 6). It has been further altered by the very large size of the stapes; most of the basal plate has been eliminated to accommodate the increased size of the fenestra ovalis. It is so altered that McGinnis (1967) described it as absent in *Sillierpeton*. Because *Sillierpeton* is at an early stage in ontogeny, she argued, the parasphenoid had not yet sutured to the braincase and had become disarticulated and lost. I contend it is already fused in *Sillierpeton*. The general outline is present and raised, the cultriform process is present between the foramina for the carotid arteries, and the basiptyergoid processes are beginning to become evident. In the largest phlegethontiid preserving the braincase (MCZ 2204), the general configuration is the same, but more detailed; the cultriform process is distinct and extends anteriorly from the braincase, the basiptyergoid processes are large and directed ventrolaterally, but the basal plate region is no more distinct than in *Sillierpeton*. It has fused to the braincase at such an early stage as to be indistinguishable from it.

MCZ 2204 (Fig. 6) shows a more ventrally pronounced cultriform process. The carotid artery foramina have developed into long grooves that run parallel to the midline a little less than half the length of the process from the basiptyergoid processes until their

entrance into the braincase. They may exit again further anteriorly where the cultriform process meets the ventral base of the sphenethmoid keel. In *Sillierpeton* the proötic foramen is ventral, and the basiptyergoid process is located on its posterior margin. In *Phlegethontia*, the proötic foramen is more dorsal and lateral, and the base of the basiptyergoid process is positioned further posterior to it. From a strong base, the basiptyergoid process descends ventrally and somewhat posteriolaterally. It ends in a roughened head that was capped in soft tissue in life. The anteromedial surface of the processes is slightly concave.

Skull-Lower jaw and dentition

Phlegethontiids have reduced the number of ossifications in the lower jaw to two. The anterior ossification is the dentary (McGinnis, 1967). All teeth are born on the dentary, and like the maxilla and premaxilla it is pierced by nutrient foramina below the base of the teeth (MCZ 2204). The posterior ossification, named the “posterior element” by McGinnis (but more descriptively called the posteromedial element), includes the areas occupied by the articular, angular, surangular and splenial in more primitive tetrapods (Fig. 4). On the lateral surface it extends from the articulation to the position occupied by the articular, about one third of the length of the jaw. Medially it extends below the tooth row to near the symphysis, which is occupied by the dentary only.

The more primitive ophiderpetontid genus *Oestocephalus* (Chapter 3) has a lateral depression below the “coronoid” process on the lateral surface of the jaw, analogous with the masseteric fossa of mammals, for the insertion of jaw adductor muscles.

Phlegethontia, in contrast, has neither such a depression nor a coronoid process.

Interestingly, the jaw is wider than it is high. The jaw is slightly inflected dorsally at the articular cotyle, which is a simple saddle-shaped structure. It is not as elevated above the tooth row as *Oestocephalus*. The articular cotyle is the posterior termination of the jaw; there is no retroarticular process. Because the jaw is so highly coossified it tends not to disarticulate, making it a good indication of overall skull length, better than skull length proper because the premaxillae tend to become lost or posteriorly displaced.

The teeth are simple, pointed cones. There are spaces for a total of 20-23 teeth. In larger specimens they are slightly recurved towards the tip. The first few teeth at the symphysis and the most posterior maxillary teeth are smallest, but no specimen shows “caniform” teeth except FMNH PR 1358. All teeth are ankylosed at their bases. As observed by McGinnis teeth, when laterally crushed, teeth split along their long axis. She also described a pattern of tooth replacement where alternate alveoli are occupied, and that, where replacement teeth are coming in, the bases are poorly ankylosed. This was assumed by McGinnis to be the result of resorption as the replacement pushed into the bases of the older teeth. This pattern was also noted in *Oestocephalus* by Carroll (1998a). In the new specimens from Nýrány (e.g. NMW 1896 II 34) teeth seem to occupy all alveoli. In other specimens, where there seem to be isolated tooth crowns there is no new cusp growing into the empty space. In some cases it is uncertain whether the isolated crowns are in fact from the toothed bone in question, or whether they belong to another just below of the surface of the matrix. No phlegethontiid has toothed palatines, vomers or coronoids; all teeth are concentrated on the dentary, maxilla and premaxilla.

Skull-Accessory orbital ossifications

Within the posterior portion of the orbits in phlegethontiids from Nýrány, Linton and Mazon Creek are several (more than six) elongate rectangular ossifications (Fig. 4). Each overlaps the next dorsal bone, and is overlapped ventrally. Most previous authors (Gregory, 1948; McGinnis, 1967) have referred to these as sclerotics. However, it seems impossible to articulate such long ossicles into a functional ring given the size of the orbit. Also, they are not arranged in an overlapping fashion as would be expected of a disarticulated sclerotic ring, but rather they are aligned as a continuous sheet-like surface. Lund (1978) referred to these as “cranial osteoderms” or “orbital osteoderms.” Among other lepospondyls, many microsaurians have palpebral ossifications (Carroll and Gaskill, 1978). In some the palpebral cups consist of a single longitudinal ossification (*Llistrofus*) while others have multiple ossifications arranged into either an elongate cup (*Hapsidopareion*, *Rhynchonkos*) or as a mass of small granules (*Asaphestera*, *Crinodon*). Given that in *Phlegethontia* these structures are always arranged horizontally in the posterior of the orbit rather than in a disassociated ring, and considering the range of variation possible in other lepospondyls, it suggests that they were a type of palpebral cup unique among vertebrates and not sclerotic ossifications.

Postcrania-Vertebrae and ribs

Phlegethontiid vertebrae (Figs 1-3, 5, 9-10) are similar to aistopod vertebrae in general. They are holospondylous and deeply amphicoelous, with the neural arches indistinguishably fused to the centra at an extraordinarily small size. They are cylindrical, although dorsoventral crushing expands the neural arches and sometimes gives the

vertebrae a square shape in dorsal or lateral view. The centra are narrowly waisted, constricting the notochord. In the smallest individuals, the neural arches dominate the vertebrae, which have relatively tiny centra, superficially resembling the condition seen in caecilians and small salamanders (Wake, 1966; Duellman and Trueb, 1986). The posterior articular surface of the centrum is slightly larger than the anterior centrum of the posterior vertebra, and when in close articulation the succeeding centrum fits inside, producing what Gallup (1983) has called “functional opistocoely.”

Most phlegethontiid specimens have very low neural spines. However, *Phlegethontia linearis* is distinguished from *P. longissima* by having neural spines as high as the neural arch on at least the anterior most four vertebrae (Fig. 2). Zygapophyses are horizontal to slightly ventrally inflected. There is a gap between the prezygapophyses, producing a v-shaped notch in the anterior margin of the neural arch. There is sometimes a similar notch between the postzygapophyses, but it is not usually as well developed. McGinnis (1967) described a longitudinal ridge running from the pre- to the postzygapophysis in vertebrae from Ft. Sill, but it is not present in the material from other localities. The precaudal centra are slightly keeled (Fig. 12). No intercentra or haemal arches are known in any aïstopod.

Transverse processes extend laterally from the base of the neural arch pedicle to a distance twice that of the zygapophyses, although this varies allometrically; in small individuals the transverse process extends only a little beyond the span of the zygapophysis. Diapophyses are borne on the transverse process; *Phlegethontia* does not have distinct parapophyses. Just posterior to the transverse process a foramen for passage of the spinal nerves opens on the lateral wall of the neural arch pedicle on all vertebrae

except the atlas, where it is anterior of the transverse process. Distribution of spinal nerve foramina is the same in *Oestocephalus*. *Lethiscus* seems to restrict spinal nerve foramina to more posterior trunk vertebrae (Wellstead, 1982), but it is a poorly preserved specimen. The nectrideans *Crossotelos* and *Sauroplorea bairdi* also have spinal nerve foramina (Bossy and Milner, 1998; Carlson, 1999). In *Crossotelos*, the spinal nerve foramina in the presacral vertebrae are positioned posterior to the transverse processes, as in aïstopods. The foramina are more anteriorly placed in the caudal vertebrae, which mostly lack transverse processes, unlike the 20+ rib bearing caudals in *Phlegethontia*. Most salamanders also possess intravertebral foramina for spinal nerves (Duellman and Trueb, 1986).

Vertebrae in *Phlegethontia longissima* gradually increase in overall dimensions for the first 20 vertebrae, where they achieve their largest size. This size is maintained for the subsequent 30-40 vertebrae. After this point, size begins to gradually taper until the end of the tail. *Phlegethontia linearis* has a greater degree of regional differentiation in vertebral size: the ratio of length of atlas centrum to longest dorsal centrum is 0.38, compared with 0.60 for *P. longissima*. However, the largest vertebra is the same proportion of the lower jaw size in each species: 0.19 in *P. linearis* and 0.20 in *P. longissima*, so the difference between the two species comes from small “cervical” vertebrae in *P. linearis*. It is unknown where the transition occurs between the shorter centra of *P. linearis* and the centra of equal length in both species. *Phlegethontia longissima* has 64 precaudal vertebrae (USNM 17097; the first preserved caudal in FMNH is the 66th). It cannot be determined where the first caudal vertebra is located in *P. linearis*; it is assumed to be similarly positioned. *P. longissima* has 177 vertebrae present

in the most complete specimen (NMW 1896 II 34) but it is missing the distal portion of the tail, giving an estimated total length of 200-210 vertebrae using the pattern of terminal central reduction in *P. linearis* as a model. *P. linearis* (AMNH 6966) has 220 vertebrae present, but it is missing a couple of body loops of undetermined length, giving it an estimated total length of 230-250. If the Mazon Creek phlegethontiids are as long as the Nýrány specimens and assuming that *P. linearis* has a similar number of precaudal vertebrae, it makes the tail of *Phlegethontia* amongst the longest known of all limbless tetrapods with approximately 135 caudal vertebrae in *P. longissima* and 190 in *P. linearis*.

Phlegethontiids lack the accessory vertebral articulations present in nectrideans and some ophiderpetontids, although FMNH PR 831 seems to have a secondary set of articulations below the prezygopophyses on the third and fifth vertebrae. If these are accessory articulations, they articulate upon a flat surface of the posterior centrum. This pattern is opposite the nectrideans, which have accessory articulations above the zygapophyses, as do snakes (Bossy and Milner, 1998). Phlegethontiids also do not possess basipophyses.

A proatlas can be seen in FMNH PR 831 (Fig. 8) and MCZ 2204 (Fig. 5). Previously, the only aistopod known to have a proatlas was the Mazon Creek ophiderpetontid *Oestocephalus* sp. (MCP 323; Carroll, 1998b). In common with the proatlas in *Oestocephalus*, *Phlegethontia*'s proatlas is a single median element and is convex dorsally, bridging the space between the occiput and atlas. There are no remnants of sutures on the midline, although it was presumably derived from paired elements, common to Paleozoic "labyrinthodonts" and some microsaurs. Unlike the *Oestocephalus*

proatlas, which is a short but wide strap-shaped bone, *Phlegethontia*'s is longer than it is wide, but this may be due to the extremely small size of the specimen. It is over twice as long as the odontoid process of the atlas. Assuming the proatlas is in natural articulation, there would be a short gap between the occiput and atlas. Gregory (1948) noted this gap in the larger USNM 17097. The gap presumably results from incomplete ossification of the adjacent bones. In *Oestocephalus*, the atlas is disarticulated from its natural position, but the relatively shorter proatlas would permit a tighter fit. The proatlas would have provided dorsal protection for the nerve cord between the occiput and atlas.

The anterior margin of the centrum of the atlas of *Phlegethontia* tapers to a rounded point ventrally, producing an odontoid process (USNM 17097, FM PR 831; Fig. 8). An odontoid process on the atlas is also present in microsaur, adelospondylids, lysorophids, and nectrideans (where it is progressively lost in derived keraterpetontids), and is a synapomorphy of Lepospondyli (Chapter 1). The odontoid process of *Phlegethontia* is a tapered anterior continuation of the centrum, giving the centrum a "procoelous" appearance. It is a smaller structure than what is seen in microsaur, but relatively larger than what is seen in the nectridean *Diploceraspis* (Beerbower, 1963). Unlike microsaur and nectrideans, the anterior centrum is not laterally expanded to articulate with exoccipital condyles.

The atlas centrum is slightly shorter than the second vertebra. The transverse processes are located posterior to the mid point of the centrum, and are directed caudally about 10° from lateral. Neither the atlas nor the second vertebra bears ribs. Transverse processes on vertebrae two through four are also caudally directed; the fifth has laterally directed transverse processes. A web of bone connects the distal end of the transverse

process to the posterior the rim of the centrum. The atlas is ventrally keeled from the anterior margin to near mid centrum. There are no prezygopophyses for articulation with the proatlas.

The second vertebra is not morphologically distinct from those subsequent to it. The transverse processes are just caudal to the mid point of the centrum, but more cranial than those of the atlas.

On the fourth centrum, the transverse processes are located at the mid point of the centrum length, and they angle caudally slightly. Beginning on the 8th (USNM 17097) to 12th (MCZ 2204) vertebra, the distal end of the transverse process rotates forward so that it angle cranially. In the very diminutive FMNH PR 831, however, the transverse processes are laterally directed until the 38th vertebra. When anteriorly directed, as in most of the dorsal vertebrae and the anterior most caudals, the transverse processes are inclined 30° from the transverse plane. Like the posteriorly directed atlantal processes, the inclined transverse processes are joined to the anterior centrum by a web of bone.

Changes can also be noted in the position of the base of the transverse process along the longitudinal axis of the vertebra. In USNM 17097, the bases of the transverse processes migrate to a more cranial position beginning at the 4th vertebra. In other specimens (FMNH PR 831) this does not occur until the anterior caudal vertebrae. Posterior to the last rib-bearing vertebra, the transverse processes lose the anterior inflection and are again laterally directed, as seen in the posterior caudal vertebrae of USNM 17097. Also posterior to the last rib-bearing vertebrae the transverse processes are gradually diminished until only a swelling remains.

The first caudal vertebra is identified as the first vertebra with haemal flanges running along the ventral surface of the centrum (Gregory, 1948; Zidek and Baird, 1978; Fig.12). In other tetrapods, haemal arches do not begin for several vertebrae posterior to the sacrum (Carroll, 1988), so if the haemal flanges are strictly homologous with the haemal arches the appearance of the flanges would be posterior to the actual beginning of the caudal series. However, although there is no true sacral vertebra since there is no pelvis, the first caudal vertebra has a rib with a unique morphology (see below). This suggests that the vertebra is modified from a sacral vertebra and thus the true count of caudal vertebrae is captured by the appearance of the haemal flanges. Terminal vertebrae are only known in AMNH 6966.

Ribs begin on the third vertebra. Aïstopods resemble modern apodous squamates in two respects. One, all apodous squamates have ribs starting on or before the fourth vertebra, and some species have ribs on the atlas. Two, most modern limbless squamates have accessory processes anterior and posterior to the rib-vertebra articulation (Hoffstetter and Gasc, 1969). Also, all ribs in aïstopods are functionally single headed, as do modern limbless squamates except scincids. The aïstopod rib has a short, robust anterior costal process (the “capitulum”), a tuberculum, and a longer posterior process (the short upright of the “k,” called the posteriomedial process by Baird, 1964, McGinnis, 1967, and Lund, 1978) that overlaps successive ribs (Figs. 1 and 5). In modern limbless squamates the area I call the tuberculum in aïstopods is the conjoined tuberculum and capitulum. The posterior process is present in the six anterior most ribs in AMNH 2564, seven in MCZ 2204, and eight in USNM 17097 (although it is much smaller on the eighth). On the 10th (AMNH 2204) or 13th (USNM 17097) vertebra the ribs change

orientation from a ventrolateral shaft to a more posteriorly directed shaft, which persists for the remainder of the column. In USNM 17097, thin, short posterior processes are present about a third of the length down the shaft on posterior precaudal vertebrae beginning on the 36th vertebra and continuing through the anterior caudals.

Rib shafts are generally slender in *Phlegethontia*. The anterior ribs are the most robust, but by the 30th vertebrae the shafts become very thin. In the posterior precaudals and anterior caudals. Rib shafts become hairlike, wispy structures. The posterior extent of rib bearing vertebrae is difficult to determine. AMNH 6966 does not show ribs well, so a count from *P. linearis* is lacking. The only specimen of *P. longissima* that shows ribs clearly along the length of the column is USNM 17097. It has ribs to the 82nd vertebra. This would leave over 100 caudal vertebrae without ribs, making the phlegethontiid tail a long whiplash like structure, very different than is known in ophiderpetontids (Zidek and Baird, 1978; Chapter 3). AMNH 6966 definitely has no ribs on its terminal 61 vertebrae before more anterior overlying vertebrae obscure the articulated series.

The first caudal vertebra's ribs have an unusual kink that orients their head at a 70° angle to the shaft (Fig. 12). This angle is much more acute than is seen anywhere else in the column, and it may indicate that this vertebra is modified from an ancestral sacral vertebra. If so, then the first occurrence of the haemal flanges gives an accurate count of the total number of caudal vertebrae.

USNM 4484 (Fig. 9) is anomalous because it has robust ribs, which led McGinnis (1967) to suspect it represented a new species. However, the patterns of rib shape and proportions are the same in this specimen as in all others. The ratio of jaw length to anterior vertebrae is the same as in *Phlegethontia longissima*. Further, other bones,

namely the pectoral elements and some vertebrae, are similarly swollen, and the skull is highly disarticulated, almost as if the constituents exploded outward from their actual positions. These features are what are seen in fossils in which the bones have been infilled with anhydrous minerals such as gypsum that are subsequently exposed to water. Therefore I think USNM 4484 has robust ribs due to taphonomic factors rather than any specific difference.

Postcrania-Pectoral Girdle

Located in the area of vertebrae three to six is an elongate sigmoidal bone of contentious identity. It has been previously described as “sickle shaped,” however, the “handle” is also curved, but much less so. In lateral view (Fig. 13, based on USNM 17097) it is inclined anteroventrally. The dorsal “handle” is shorter than the ventral “blade” and is directed posteriorly towards the neural arches. Its curve overlies the ribs near the level of the transverse processes. The “blade” is concave ventrally, and the point is directed towards the skull. A similarly shaped and positioned bone is also present in ophiderpetontids (Baird, 1964; Milner, 1994; Carroll, 1998a).

This element has been previously identified as the hyoid. However, this seems unlikely. In modern amphibians and reptiles the hyoids occupy the space between the lower jaws and, in salamanders, beneath the occiput (Duelman and Trueb, 1986). In adelospondylids (Andrews and Carroll, 1991) and lysorophids (Wellstead, 1991) the main hyoid apparatus is more posterior but, like salamanders, is associated with the occiput, not far back on the vertebral column. In *Dvinosaurus* (Bystrow, 1939), a temnospondyl, there are hyoid elements posterior of the occiput, but they are closely

articulated with other branchials that are at and anterior to the occiput. In all of these examples, the hyoid elements are stout and rather short bones. In contrast, the phlegethontiid element is well posterior of the occiput and is more gracile in construction. Its position relative to the ribs is the same as would be expected for the pectoral girdle. In most microsaur and in the nectridean *Scincosaurus* the pectoral girdle is positioned at the third vertebra, and in almost all other lepospondyls the pectoral girdle is located at the fifth vertebra, the same region in which the aïstopod element is found (Figs. 1, 2, 5, 9). The long narrow element found in microsaur and other lepospondyls that corresponds most closely with the phlegethontiid bone in position and orientation is the cleithrum, although it tends to be a shorter bone in microsaur. The length and sinusoidal shape is best matched if the phlegethontiid element is formed from a fusion of the cleithrum and clavicles of microsaur. If correct, the “blade” of the sickle corresponds with the curve of the clavicle. This hypothesis is supported by the presence of a swelling at the point where the two elements would contact and fuse in AMNH 2564 and USNM 4484. A break occurs at this point in USNM 4484 (Fig. 9), suggesting a possible weakness or incomplete fusion in this specimen.

Some might question why the cleithrum would be preserved vestigially over other pectoral constituents (Hook, 2000). The answer is twofold. First, there seems to be a phylogenetic predisposition towards preferential reduction and loss of the scapula and coracoids within lepospondyls. According to a recent phylogenetic analysis (Chapter 1) *Lepospondyli* is a monophyletic group. One of the most basal members of the lepospondyls is *Adelospondyli*, another group of elongate, limbless animals. Like aïstopods, they lack all traces of limbs and the pelvic girdle, and of the pectoral girdle

they are missing the endochondral bones (scapula and coracoids) but retain the dermal girdle (interclavicle, clavicle, and cleithrum) in seemingly unmodified states. Although they reduced their limbs independently, the fact that two so closely related groups follow the same rather unusual pattern suggests that there is a common underlying developmental pathway that is stable and available for selection to modify (see Chapter 4 for a further discussion of the underlying developmental mechanisms of aïstopods).

The second reason is the inferred presence of an “operculum-opercularis” type complex. While it is not possible to establish the presence of this or a similar structure directly, the circumstantial evidence is highly suggestive. In frogs and salamanders the operculum is linked to the anterior pectoral girdle by a thin muscle that transmits low frequency sound waves from the ground to the middle ear (Duelman and Trueb, 1986). The stapes of *Phlegethontia* has a lateral ridge that looks very much like a muscle scar. It is directed towards the area occupied by the remnant of the anterior pectoral girdle. Given this indirect evidence for a beneficial adaptation, and given the common phylogenetic predisposition for losing the endochondral pectoral girdle, the persistence of elements of the dermal pectoral girdle in *Phlegethontia* (and other aïstopods) seems less difficult to accept, despite the absence of all traces of limbs and pelvic girdle.

Postcrania-Dermal Ossifications

All aïstopods have extensive dermal scalation (Baird, 1964; Carroll, 1998b). Ophiderpetontids have short, stout “wheat-shaped” ventral gastralial and diamond-shaped dorsal osteoderms that covered the dorsal body and the adductor chamber of the skull. Phlegethontiids do not have dorsal osteoderms and the ventral gastralial are fine and

elongate. Like ophiderpetontids, the ventral gastralialia are arranged in a chevron pattern, with the apex of the chevron lying on the ventral mid line and pointing cranially.

Soft Tissue

Due to the fine preservation common to Mazon Creek, a few specimens of *Phlegethontia* show the impression of the body around the skeletal material (Fig. 14). The dorsal body extends from just above the posterior margin of the skull posteriorly just dorsal to the vertebrae, within one half the height of the neural arch. Ventrally the soft body begins below the lower jaw and continues well below the ribs by almost another full rib length. The gastralialia always closely correspond to the soft body impression, as would be expected of ossicles within the dermis.

FMNH PR 624 shows an elongate mass within the ventral portion of the body cavity (Fig. 14). This mass is 9.6 mm long, and is associated with vertebrae 21-30. It is an elongate, cylindrical object that appears somewhat jumbled and broken, but does not appear spiral or otherwise wrapped. Due to the rather anterior placement it is perhaps more appropriately interpreted as a stomach in-filling rather than an intestinal cast.

Lund (1978) described the presence of dark pigments in the anterior body and head of FMNH PR 1358. Dark patches are present in the areas indicated by Lund but are not present in any other specimens. In other amphibians from Mazon Creek, such as *Saurerpeton* (Godfrey, 1997; Figure 19.1) the dark pigments of the retina are preserved. This phenomenon is known from other localities as well, but is not present in phlegethontiids themselves. No such body coloration is present in any other aïstopod specimen.

DISCUSSION

Species Resolution

The question of species resolution in phlegethontiids remains difficult to answer, but details are becoming clearer based on new specimens. *Phlegethontia linearis*, known from only a single specimen (AMNH 6966 and its counterpart 6886; Turnbull, 1958), is distinguished from *P. longissima* by having high neural spines on at least the first four vertebrae, at least the first four centra reduced in size, and possession of a much longer vertebral column.

Vertebral counts in modern amniotes (Arnold, 1987) amphibians (Jockusch, 1997) and fish (Lindsey and Amson, 1981) can vary due to environment, and can change with growth. This may also pertain to *Phlegethontia* since there are no completely articulated vertebral columns currently known. However, two complete ophiderpetontid specimens are known from Nýřany (Chapter 3), which show that during growth from a basal skull length of 5 mm to 8 mm (an increase of 38%) no vertebrae were added to the column. This suggests that differences in vertebral count could have systematic importance in ařstopods.

It may further be argued that it makes no ecological sense for two so similar species to cohabit. Modern ponds show that, to the contrary, several different species of salamanders and frogs may coexist in the same area. Specific distinction for *Phlegethontia linearis* would only mean that three species of ařstopod were present at Linton, unless they were separated by time, but the relative placements of the species

within the stratigraphic column are unknown. Three distinctly different aïstopods are unquestioningly present at Mazon Creek (Chapter 4) so it is not an unrealistic number.

Sillerpeton is still maintained as a separate genus while “*Aornerpeton*” is reduced to subjective junior synonym of *Phlegethontia*. *Sillerpeton*, despite its younger age, is more basal due to the maintenance of a separate foramen for cranial nerve III posterior to the foramen for II. The foramen for III in *Phlegethontia* has either migrated anterior to the foramen for II or it has been lost (McGinnis, 1967). *Sillerpeton* is further distinguished by having the jugular foramen pierce the area usually occupied by the exoccipital while in *Phlegethontia* (including “*P. phanerhalpa*” which may show a suture demarking the exoccipital-opisthotic border) it pierces the opisthotic. Other features are more likely associated with small size.

The difficulties with determining species in aïstopods should now be apparent. Unique derived characters are present throughout the body; however, different portions of the body are preserved in the different localities. The most complete (in numbers of vertebrae preserved) are from the coal shales of Nýřany and Linton (NMW 1896 II 32 and AMNH 6966). Unfortunately, these are crushed onto two dimensions so details of important features of structure are lost or obscured. For example, the haemapophyseal flanges of the caudal vertebrae that might clarify whether the Mazon Creek specimens are shorter (the longest series of preserved vertebrae is 130) than the coal shale fossils (177 and 220 vertebrae are preserved respectively) are not visible in the flattened specimens.

Growth

Sufficient specimens of different size are now known from Mazon Creek that they may be arranged into a plausible growth series. Table 1 lists Mazon Creek specimens in order of size. There are a few anatomical trends worth noting. First, at an extremely small size, vertebrae (<1 mm in length) are fully ossified. This fact led Baird (1965) to conclude that aïstopods were direct developers, not passing through a larval stage. Supporting this hypothesis is the observation that no specimen has been found that shows the presence of gills or gill supports. Such structures are preserved in other taxa at Mazon Creek (Godfrey, 1997) so their absence is telling.

The smallest specimen (FMNH PR 831) lacks ribs, gastralia, cleithra and teeth. All of these are delicate structures, so their size may be below the resolution of the matrix in this particular nodule. The braincase is completely ossified posteriorly; ossification of the more anterior portion lags behind during development, and only fully ossifies in larger individuals. FMNH PR 831 shows a similar pattern to *Sillerpeton*. The appearance of the anterior keel in the largest specimens appears to coincide with the cessation of additional anterior ossification.

Endochondral ossifications appear before dermal ossifications. Dermal skull bones are highly incomplete in FMNH PR 831. Dermal bones, including the frontal, prefrontal, maxilla and both jaws, and possibly the palatal ramus of the palatoquadrate are present. In USNM 17097 the jugal is also present, the postfrontal is beginning to ossify, but the squamosal is still absent. The frontal is better defined, but the posterior prongs are still relatively short. No bones are present anterior to the prefrontal, but this is probably due to a zone of dissolution common at the edges of Mazon Creek nodules,

where the snout unfortunately lies. The epipterygoid has grown around the lateral walls of the braincase, but has not reached its full height. In the largest Mazon phlegethontid, MCZ 2204, the full suite of dermal bones is achieved, the epipterygoid is fully formed, and the sagittal crest is developed.

This trend of earlier ossification of endochondral bone and delayed ossification of dermal bone seems to be a phyletic character of phlegethontiids. According to preliminary phylogenetic analysis (Chapter 5) ophiderpetontids and *Lethiscus* are the most basal aïstopods, followed by the Turnbull specimen (Turnbull and Turnbull, 1955), and finally a monophyletic Phlegethontiidae. Ophiderpetontids have fully roofed skulls, but open temples. They have extensive dermal osteoderms that thickly cover the body early in growth. Their braincase anatomy is less well known because of the cover of the parasphenoid basal plate, but the otic capsules seem incompletely ossified (Figures 3c and d in Carroll, 1998a). The Turnbull aïstopod still has a full skull roof, but it has become narrower than the ophiderpetontid condition (Chapter 4). Dermal osteoderms are absent, and the gastralia has achieved a phlegethontiid state. However, the otic capsules appear to be incompletely ossified. It seems as if there has been a decoupling of commencement of ossification of endochondral versus dermal bones that is magnified phylogenetically, leading towards the phlegethontiid state. Hanken (1983) has discussed how growth can be terminated at an extremely small size by accelerating the completion of epiphyseal ossification in long bones, which can lead to gross changes in the morphology of other systems because they were unable to complete ossification. Hanken also discussed how hyperossification in one system (in this case the endochondral skull and vertebral column) is usually accompanied by a reduction in ossification in another

(here, dermal skull bones and dorsal ossicles). More specimens are required to ensure this observational trend is not a statistical anomaly.

Functional Morphology

Lund (1978) proposed an elaborate mechanism of cranial kinesis for the skull of *Phlegethontia*. In his model, the braincase formed a fixed bar in a four-bar kinematic chain. The palatoquadrate and “palatine” served as struts for force transfer to the mobile premaxilla. The cheek (comprised by the lacrimal, maxilla, postfrontal and “orbital segment of the braincase”) formed a dependent chain, linked to the principle chain (i.e., the premaxilla and frontals) by the premaxillary-maxillary joint and “possibly the palatine, and probably by connective tissue associated with the adductor mandibularis complex to the pterygoquadrate.” (Lund, 1978: 70) He also hypothesized a ligamentous connection between the posterior margin of the maxilla and the mandible. The result was that, when the palatoquadrate was protracted, the premaxilla would rise and rotate the maxilla about its articulation with the “lacrimal” while the jugal would slide ventrally on its articulation with the postfrontal (he also recognized the tongue-in-groove nature of this articulation). He also thought there was a potential laterodorsal rotation of the cheek reinforced by the “postorbital osteoderms” (my palpebral ossifications) and the squamosal-“postorbital”-“quadratojugal” complex.

I cannot concur with this functional interpretation. The contact between the dorsal process of the squamosal and braincase is here interpreted as fixed rather than as a potential pivot point. Lund’s “quadratojugal” is part of the posterior palatoquadrate. His “postorbital” is the anterior process of the squamosal, and I have not been able to find

even a crack in any specimen in the right position to suggest the presence of a suture, except perhaps in UMMP 22278. Lund identifies palatines and incorporates them as an important component of his kinetic chain, yet I have been unable to confirm the presence of these elements in any specimen.

There is evidence to suggest that there might be some kinetic mechanism at work. The maxillae do not have definite sutural articulations with its surrounding bones. The premaxillae are often posteriorly displaced, and the skull is usually disarticulated, suggesting at least the potential for relative movement of elements.

Unfortunately, correct homologies aside, Lund's kinetic model fails because the palatoquadrate *cannot move*. As described above, the palatoquadrate is the main force-transmitting bar of the model. However, the eipterygoid is firmly fixed to the braincase. During ontogeny the eipterygoid grew around the proötic foramen, almost enveloping it. If the eipterygoid were to protract, it would rapidly close off the proötic foramen and place great pressure on the trigeminal nerve, if not severing it outright. And if the palatoquadrate did not move, then the squamosal did not pivot, and the premaxillae did not rise.

The jaws operated using a simple inertial mechanism. There is no retroarticular process, so the depressors manibulae were small or absent. The absence of a high coronoid process or an opiderpetontid-like masseteric fossa permits the jaw adductor muscles to insert along the whole posterior third of the mandible, where there are no teeth. The adductors have their origin along the sagittal crest, which is higher in larger individuals, and the open cheek provides unrestricted expansion. *Phlegethontia* had weak depressors but a relatively strong bite, and could hold prey tightly.

The curious rib morphology of aïstopods has provoked much functional speculation, from a possible lateral arrangement (Baird, 1964) to the hypothesized “rib-walking” in the ophiderpetontid *Coloraderpeton* (Gallup, 1983). K-shaped ribs are restricted to the anterior 6 rib bearing vertebrae in *Phlegethontia* so rectilinear locomotion (Gans, 1986)—Gallup’s rib-walking—is unlikely to have been a primary means of propulsion. Further, the elongate and rather thin body possessed by *Phlegethontia* is at odds with the pattern in modern limbless animals, where thick bodies characterize rectilinear locomotion.

The posterior process of the rib is properly positioned and oriented to provide a large area for the insertion of M. iliocostalis. Ribs where this process is prominent seem to be frequently displaced posteriorly and dorsally, in the direction of the origin of the M. iliocostalis, the lateral most member of the epaxial musculature, which may suggest that it is relatively important for aïstopod locomotion. In snakes (Moon, 1999) and amphisbaenians (Gasc, 1981) M. iliocostalis has its origin from either a tendon (most squamates) or a tendinous sheet (*Amphisbaena alba*) coming off of the anterioventral half of M. longissimus dorsi. It then spans many segments (>10) and inserts as a tendon on the posteriolateral surface of the rib, about one third of the length of the shaft from the head. In *Amphisbaena* the insertion of M. iliocostalis is joined by the insertion of M. supracostalis ventralis superior (Gasc, 1981). These muscles assist in the lateral flexure of the animal, which forms the basis for most types of lateral undulation (Gans, 1985; Moon and Gans, 1998). Caecilians have a unique form of locomotion termed “internal concertina” (Gans, 1973) where the vertebral axis moves within a muscular sheath, forming anchor points with the substrate (usually burrows) by pressing out with the

posterior body wall and using that anchor to propel itself forward. It then establishes a new anchor point with the anterior portion of the body and draws the rest of the body forward, sets a new anchor with the posterior body, and repeats the cycle. Some caecilians are now known to supplement this locomotive strategy with a hydrostatic mechanism (O'Reilly et al., 1997). Caecilian muscular anatomy is very different from squamates as a result. There is less muscular differentiation; *M. dorsalis trunci* and *M. subvertebralis* are the dominant internal trunk musculature (Naylor and Nussbaum, 1980). Resegmentation is limited to myosepta spanning 3 to 4 vertebrae. Muscle insertions on ribs are not an important factor in locomotion, since caecilian ribs seem to lie between different layers of the lateral muscle wall while the muscles attach to the myosepta or other fascia.

The costal process of the rib matches closely the anteroventral process on the rib of *Amphisbaena alba* (Gasc, 1981). In *Amphisbaena*, the anteroventral process is joined to the tuberculum of the preceding rib by *M. tuberculocostalis profundis*.

Although it is impossible to reconstruct accurately the musculature of fossil animals with no close modern relatives, the presence of the posterior process, which is evidence for a highly developed iliocostalis-like muscle, suggests that *Phlegethontia* was an accomplished terrestrial lateral undulator and did not locomote like caecilians. The large orbits and lightly built, fenestrate skull similarly speak against a fossorial habit. Gregory (1948) interpreted *Phlegethontia* as fossorial, based upon the highly ossified braincase, forward position of the jaws, large round stapedial footplate, and low neural spines, which it has in common with amphisbaenids, which are unquestionably burrowers. Alternatively, limbless animals may frequently have solidly ossified because

a solid attachment is needed for the extra epaxial musculature needed to move the head. Limbed animals can lift their heads using their forelimbs, but the heads of limbless animals are limited in the amount of excursion possible vertically, unless compensated for by another system. All of this head motion must be executed by epaxial musculature if the pectoral girdle is reduced or lost, which requires a strong anchor and lever for force transmission. This is accomplished by the solid braincase.

Biogeography

Phlegethontiids are now known from Nýřany, Czech Republic, Linton, Ohio, Mazon Creek, Illinois, Ft. Sill, Oklahoma, the Swisshelm Mountains, Arizona, Jarrow, Ireland (Baird, 1964; McGinnis, 1967; Thayer, 1985; Carroll, 1998b) and Five Points, Ohio (Baird, pers. comm.). Isolated vertebrae have also been reported from the Lower Permian Sangre del Christo Formation in New Mexico (Berman, 1993), and the Dunkard Formation of Pennsylvania (Hook and Baird, 1993).

A series of vertebrae recently described from the Stephanian Bassin de Montceau-les-Mines of the French Massif Central (Dutuit and Heyler, 1994) were identified as "*Dolichosoma*" *longissimum*. The authors reported not less than 100 vertebrae preserved, including the end of the tail, of which the anterior most 15 vertebrae bear ribs. Examination of the close-up photograph of the rib bearing vertebrae reveal the laterally projecting, anteriorly placed transverse processes characteristic of phlegethontiid caudal vertebrae, and the approximately 85 rib free posterior caudal vertebrae are consistent with this identification.

Phlegethontiids are present throughout the “Edaphosaur-Nectridean” fauna of (Milner, 1993), but are restricted to the area immediately surrounding the paleoequator of Euramerica, like all other amphibians. Their physical form differs little from the Westphalian B of the Swisshelm Mountains to the Lower Permian of Fort Sill, a span of approximately 75 million years. It is easy to hypothesise that this extreme bradytely was enabled by the consistent climate that gives rise to the great coal deposits of this time, however, they persist into the Red Bed faunas of the Lower Permian with little change. Assuming this change of facies reflects a change in climate, it suggests that phlegethontiids were probably more widely distributed in Euramerica than is preserved in the fossil record, since they show the ability to adapt to different climates.

The absence of lateral line canal grooves and the relative scarcity of aïstopods in the aquatic deposits of Linton and Nýřány compared with obligate aquatic vertebrates suggests that phlegethontiids were primarily terrestrial or lived on the margins of the water in which their bodies were preserved (Milner, 1980). However, none are known from the terrestrial deposits of Joggins, Nova Scotia, which suggests that they either were not present in that environment, or that they were not prone to being trapped in the upright stumps that accumulate the largest portion of the fauna. The large orbits and lightly built skulls are evidence against a sub-surface habitus. *Phlegethontia* probably lived in the leaf litter around bodies of water, eating invertebrates, and returning to the water during the breeding season.

Relationships

Relationships within the Aïstopoda will be presented with the consideration of *Lethiscus* (Chapter 5). Preliminary analyses place phlegethontiids as the most derived of aïstopods, with the Turnbull aïstopod, *Oestocephalus*, *Ophiderpeton* and *Lethiscus* forming successive plesions.

Outgroup relationships of aïstopods were presented in Chapter 1. While many more fossils remain to be found and the pattern will undoubtedly change, the available data suggests that aïstopods are sister taxon of nectrideans, supported by the common presence fused, unipartite vertebrae without separate intercentra and relatively long transverse processes. Aïstopods and nectrideans also share several characters that are not fully distributed within both taxa including accessory articulations of the vertebrae (which are absent for the most part from phlegethontiids and where they exist are of a different morphology suggesting they were independently acquired) and intravertebral foramina for the spinal nerves posterior to the transverse processes in precaudal vertebrae, present in all aïstopods and in the Lower Permian nectrideans *Crossotelos* (Carlson, 1999) and *Sauropleura bairdi* (Bossy and Milner, 1998). The caudal vertebrae differ; phlegethontiids have a posterior displacement of the foramina while in *Crossotelos* the foramina migrate anteriorly. Additionally, sauroplurine and diplocauline nectrideans have frontals fused at the midline.

In Chapter 1 I placed lysorophids as immediate sister taxa to aïstopods, but suggested that this is due to convergence to a similar elongate-limbleless morphotype. There are no convincing synapomorphies linking lysorophids with nectrideans. Further

fossils must be found to test this grouping more vigorously. It should be noted that this cluster breaks down with only one extra step.

CONCLUSIONS

Two species of *Phlegethontia* are recognized. *P. linearis* is distinguished by the rather short centra and high neural spines of its anterior most vertebrae. It is also a higher number of vertebrae than *P. longissima*. *P. linearis* is only known from Cope's type, and it coexisted with both *P. longissima* and *Oestocephalus* in the coal swamps of Linton.

Contrary to previous authors, the skull anatomy of *Phlegethontia*, while superficially snake like, was not a highly mobile mechanism. The squamosal is inserted into the braincase, and the jugal has a solid tongue-in-groove joint with the postfrontal. The epipterygoid, a fused constituent of the palatoquadrate, tightly adhered to the braincase and surrounded the trigeminal foramen, making its mobility highly unlikely. Any possible movement would have had to be restricted to the premaxilla and maxilla.

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TABLE 1. *Phlegethontia longissima* specimens representing growth series from very young to mature.

Specimen Number	Jaw Length (mm)	Total Skull Length (mm)	Number of Vertebrae
FMNH PR 831	1.6*	3.36*	116
FMNH PR 624	4.15	5.32	100
USNM 17097	7.65*	4.0*	105
FMNH PR 1358	8.75	10.85	62
MCZ 2204	12.1*	?	13
NMW 1896 II 34	14.8	15.66	170
AMNH 2564	18.15	16.24	30
USNM 4484	26.2*	19.8	14

FIGURE 1. AMNH 2564, *Phlegethontia longissima*, from Linton, Ohio. Scale bar equals 10 mm.

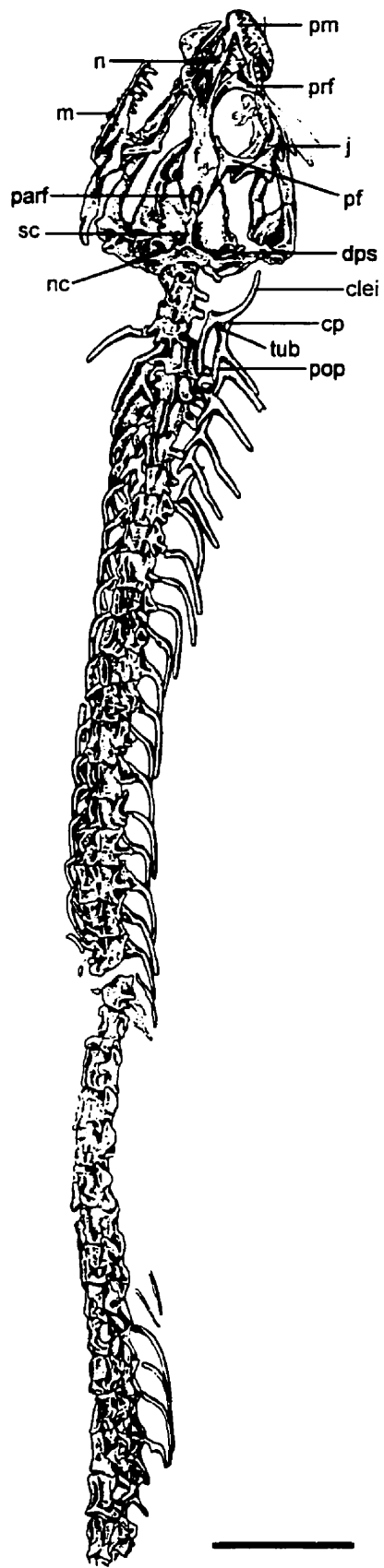


FIGURE 2. AMNH 6966, *Phlegethontia linearis*, from Linton, Ohio. Scale bar equals 5 mm.

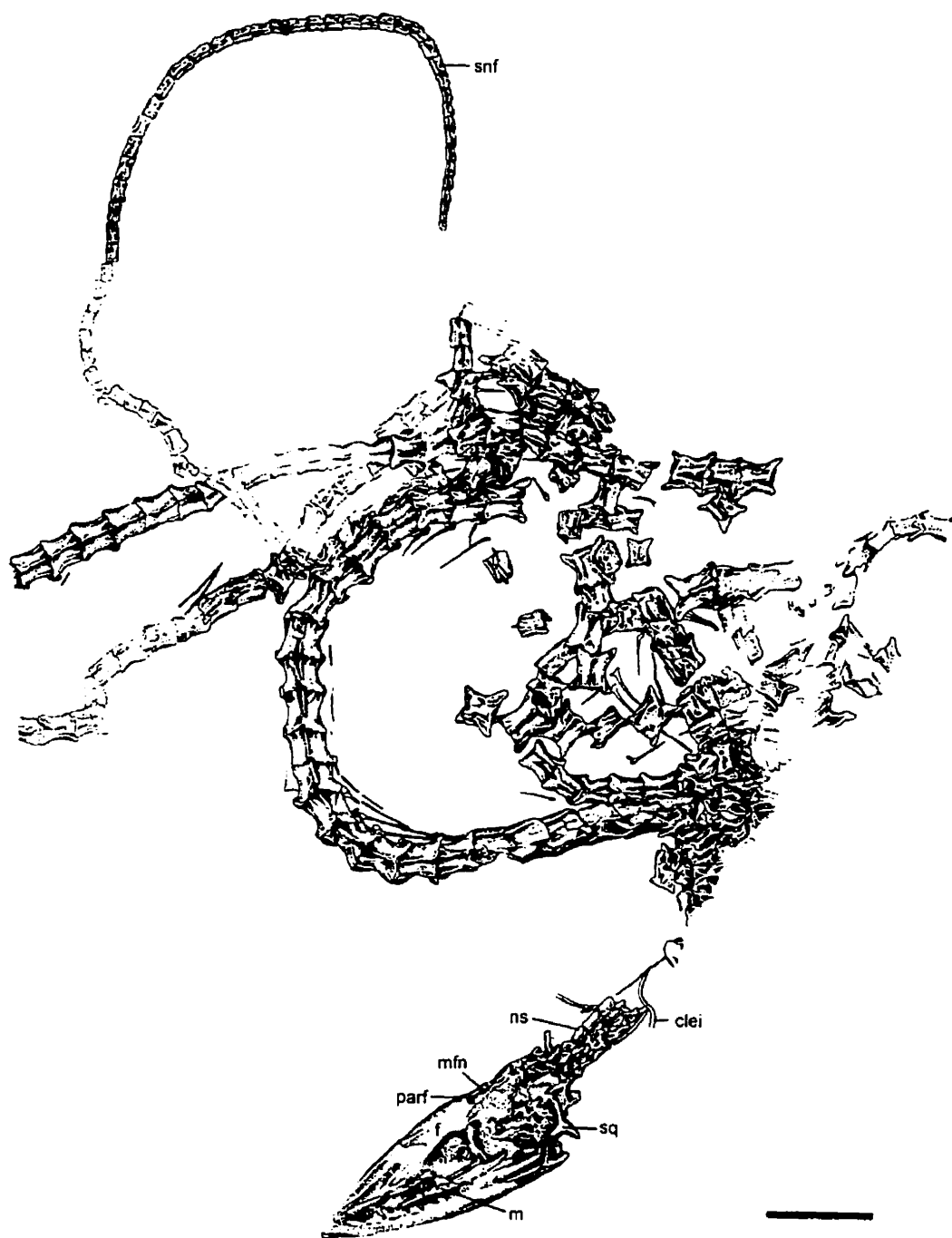


FIGURE 3. NMW 1896 II 34, *Phlegethontia longissima*, from Nyrany, Czech Republic.
Note the curvature on the anterior surface of the quadrate ramus of the palatoquadrate,
above the quadrate condyle. Scale bar equals 10 mm.



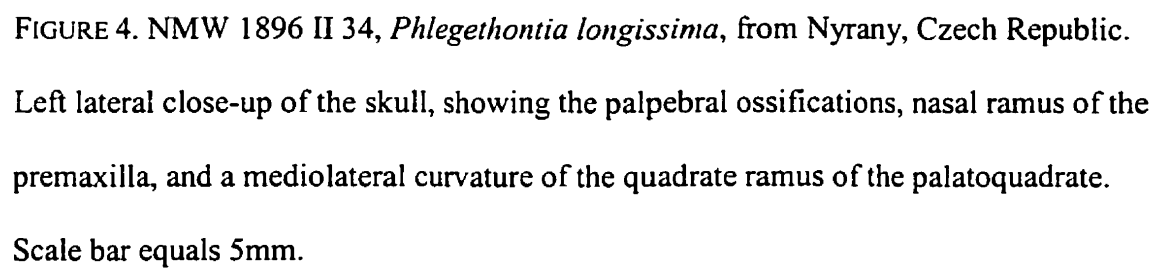


FIGURE 4. NMW 1896 II 34, *Phlegethontia longissima*, from Nyrany, Czech Republic. Left lateral close-up of the skull, showing the palpebral ossifications, nasal ramus of the premaxilla, and a mediolateral curvature of the quadrate ramus of the palatoquadrate. Scale bar equals 5mm.

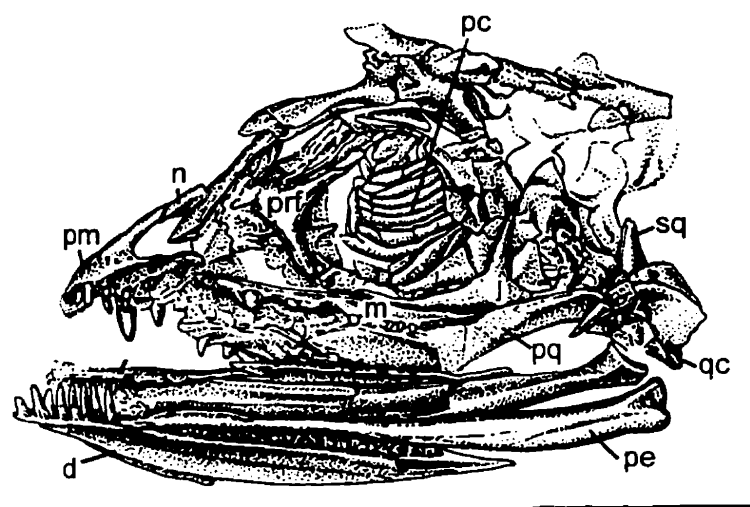


FIGURE 5. MCZ 2204, *Phlegethontia longissima*, from Mazon Creek, Illinois. Dorsal view. Scale bar equals 5 mm.

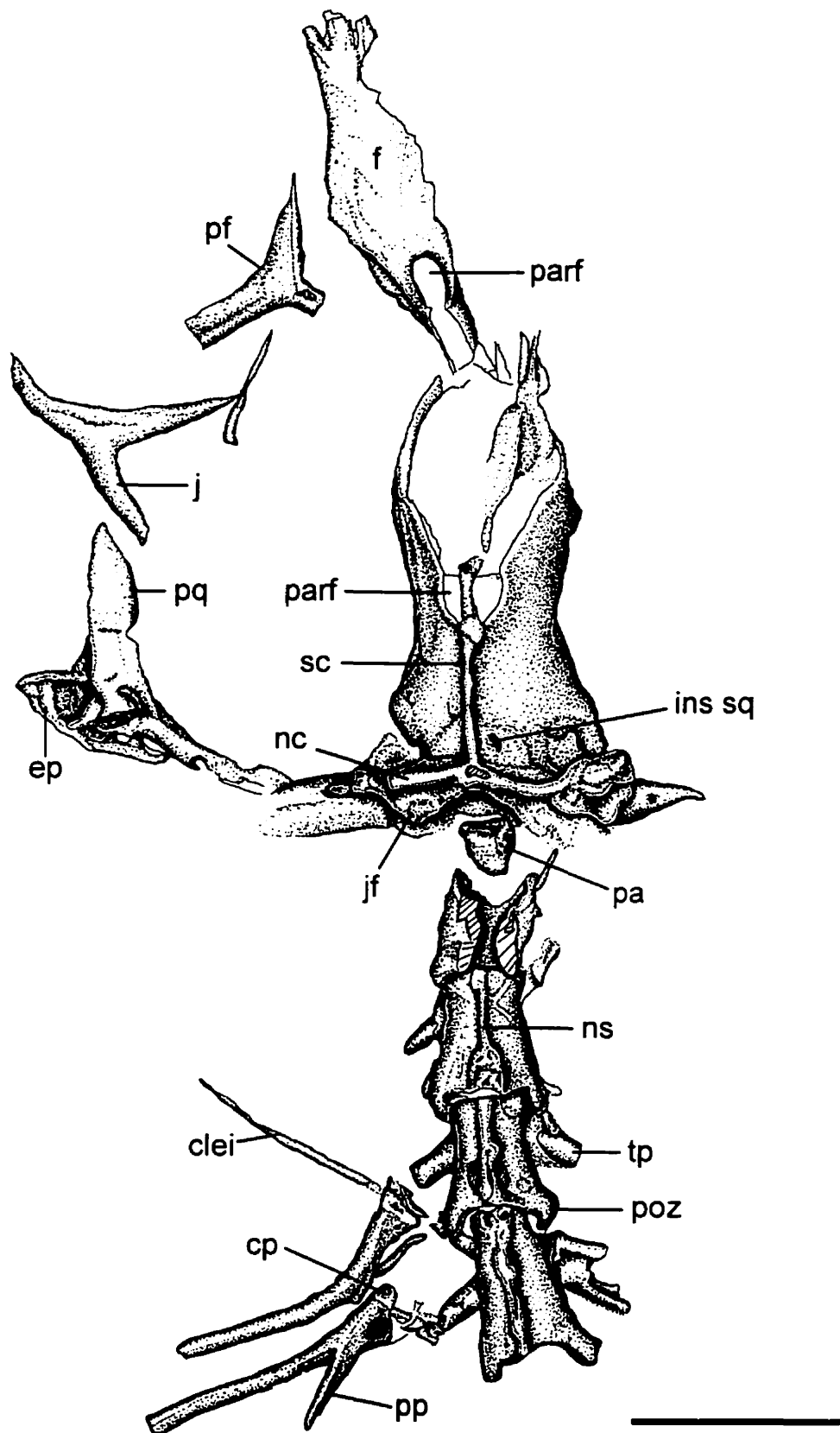


FIGURE 6. MCZ 2204, *Phlegethontia longissima*, from Mazon Creek, Illinois. Ventral view. Scale bar equals 5 mm.

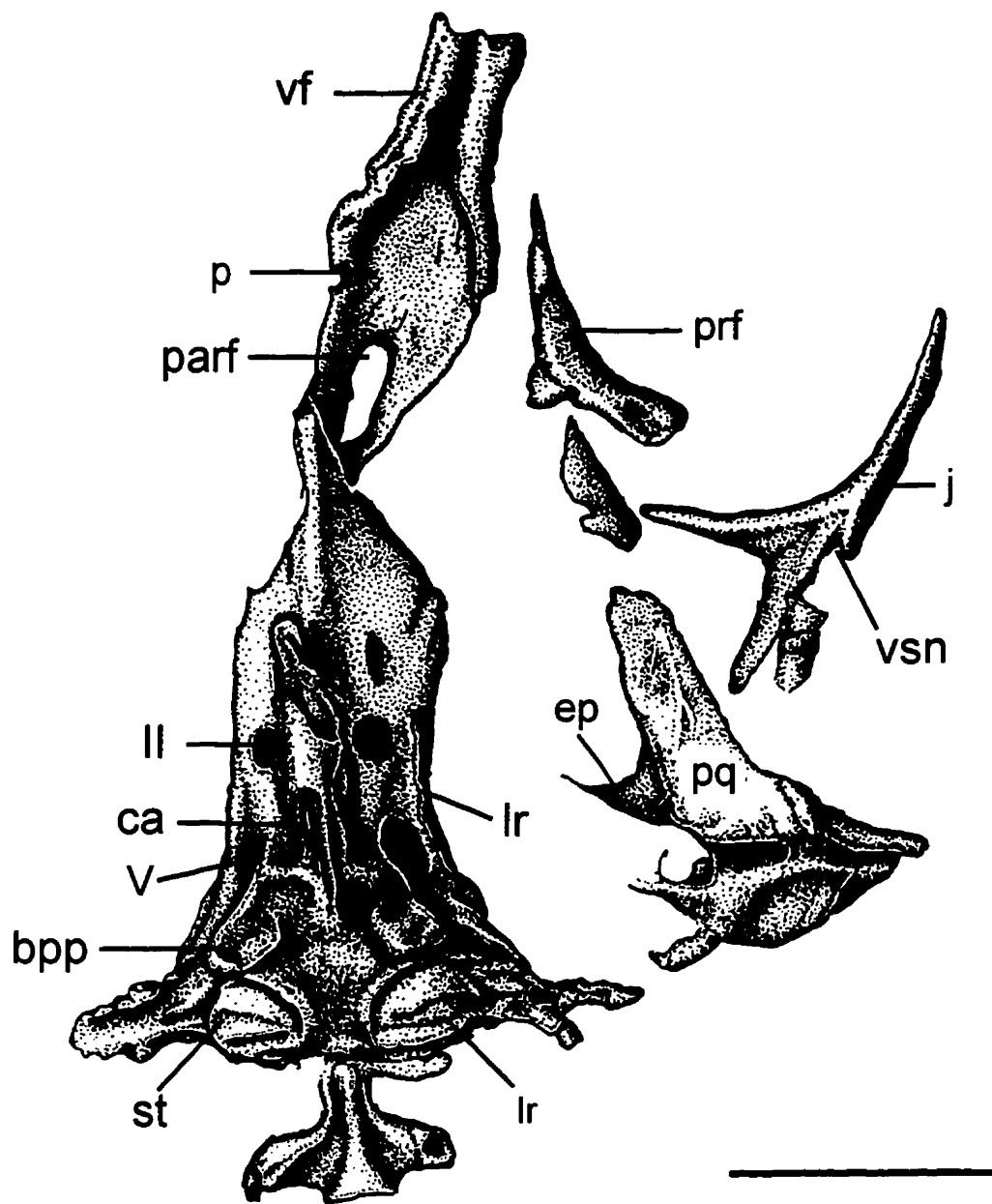


FIGURE 7. MCZ 2204, *Phlegethontia longissima*, from Mazon Creek, Illinois. Right lateral view of braincase, slightly off-set from horizontal. Scale bar equals 5 mm.

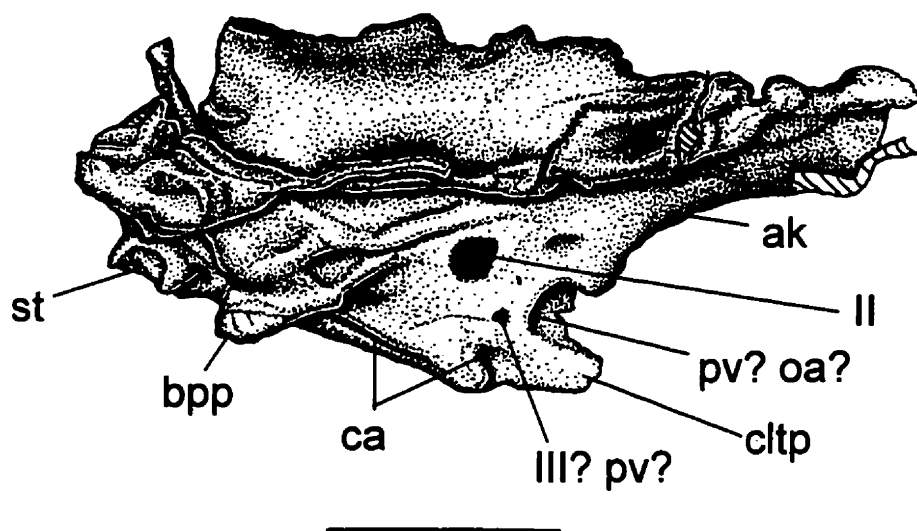


FIGURE 8. FMNH PR 831, *Phlegethontia longissima*, from Mazon Creek, Illinois. Left lateral view. Scale bar equals 1 mm.

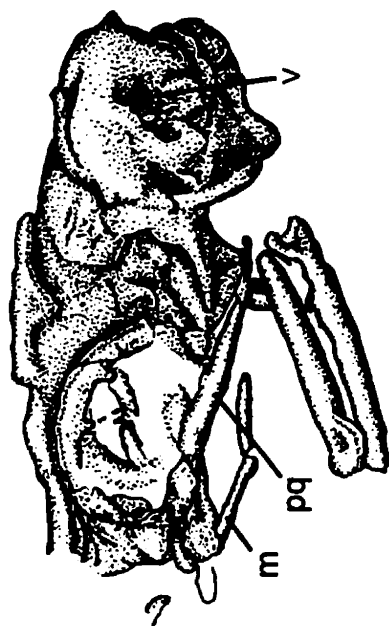
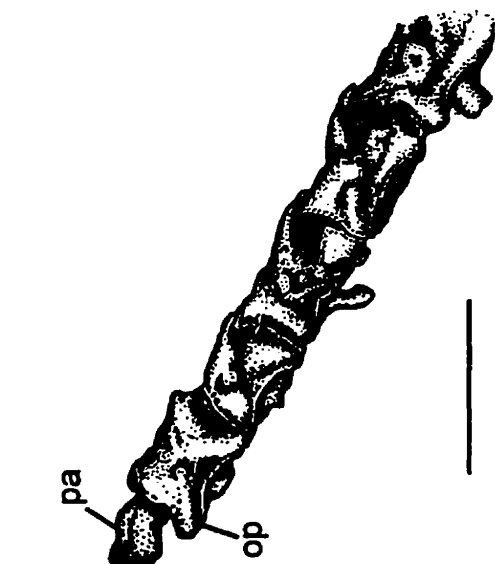


FIGURE 9. USNM 4484, *Phlegethontia longissima*, from Linton, Ohio. Scale bar equals 10 mm.

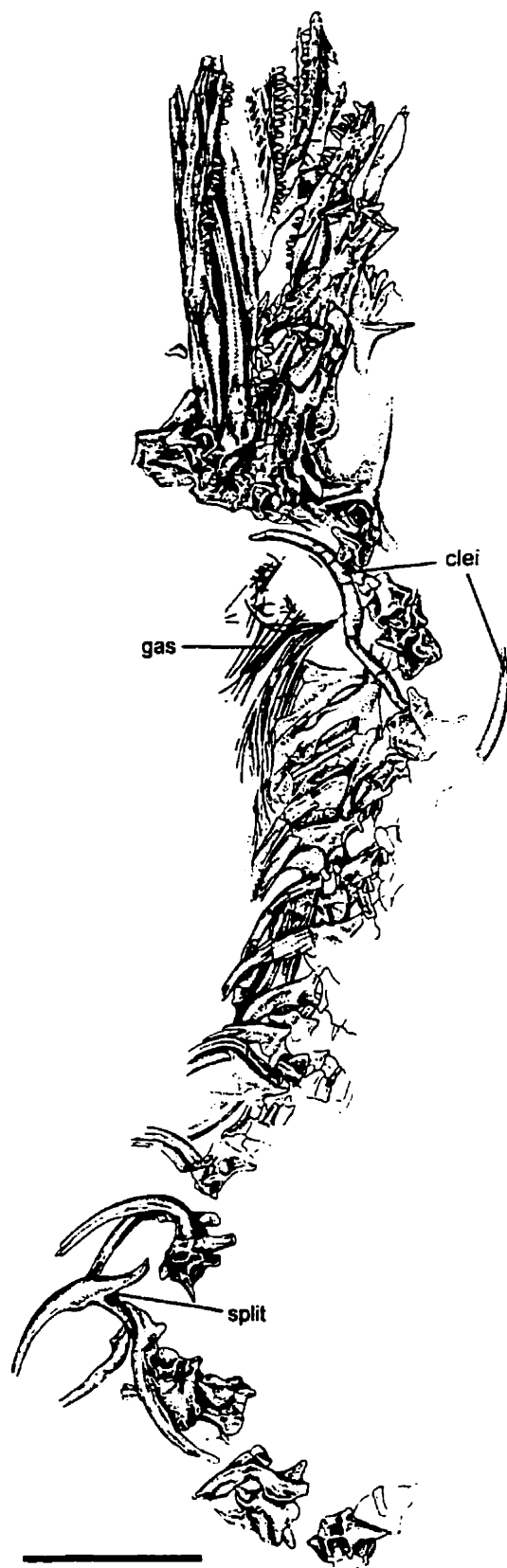


FIGURE 10. Dorsal view of the skull of *Amphisbaena alba*. The parietal receives the sagittal crest in a manner similar to the frontal of *Phlegethontia*. From Montaro and Gans, 1999.

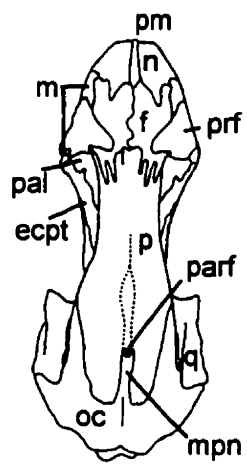
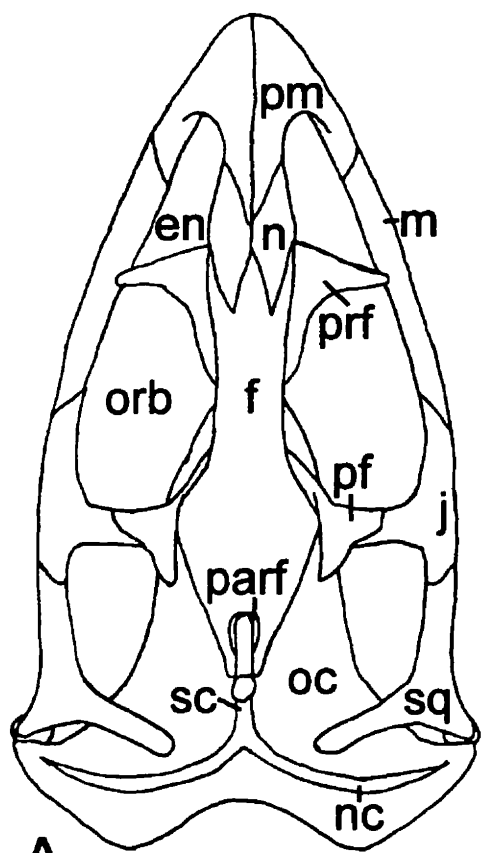
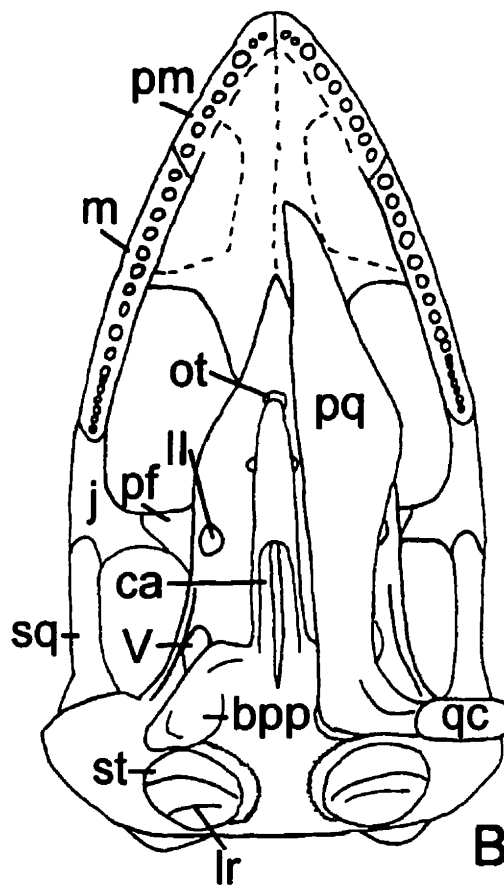


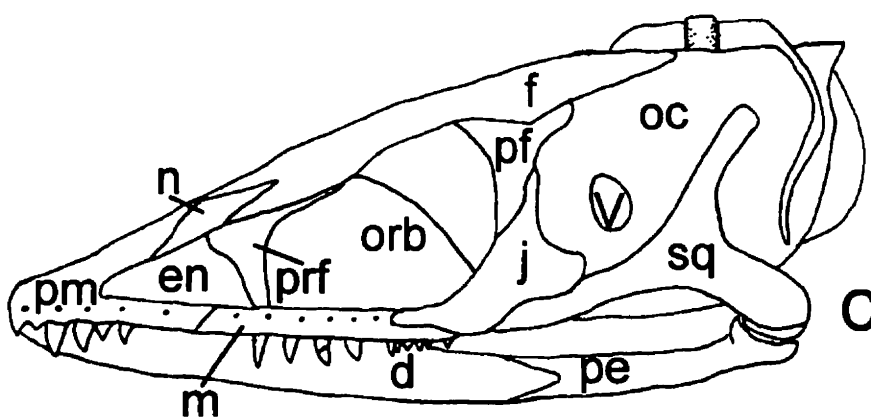
FIGURE 11. Reconstruction of cranial anatomy, genus *Phlegethontia*. A, dorsal view. B, ventral view. C, lateral view.



A



B



C

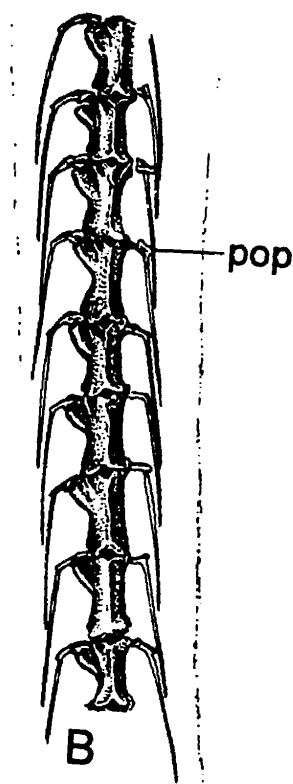
FIGURE 12. UMMP 17097, *Phlegethontia longissima*, from Mazon Creek, Illinois.

Transition from precaudal to caudal vertebrae, in ventral (A) and dorsal (B) views. Note the development of the median haemal groove on the first caudal vertebrae, and the greater angle the rib head makes to the rib shaft with that in more anterior and posterior vertebrae.



A

first
caudal



B

FIGURE 13. Reconstruction of the anterior postcranial skeleton of A) *Phlegethontia longissima* and B) *P. linearis*, showing the diagnostic difference between the length of the anterior vertebrae and height of the neural spines.

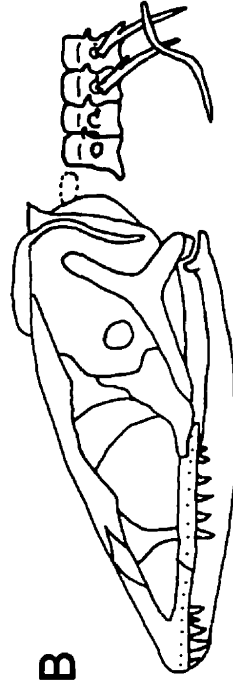
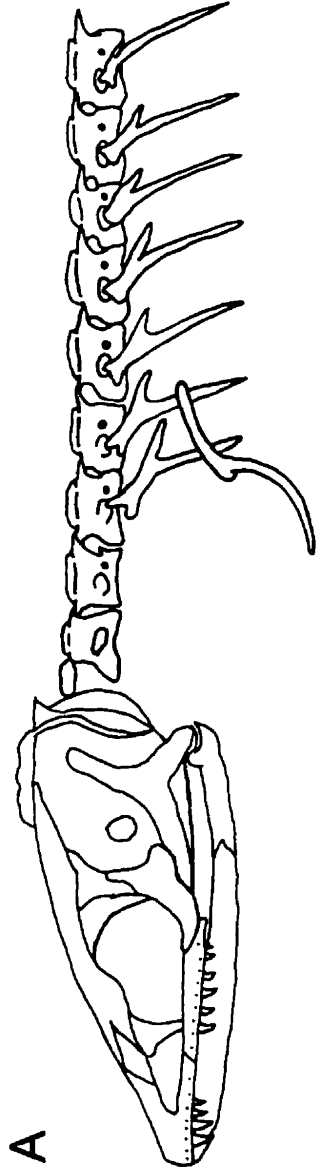
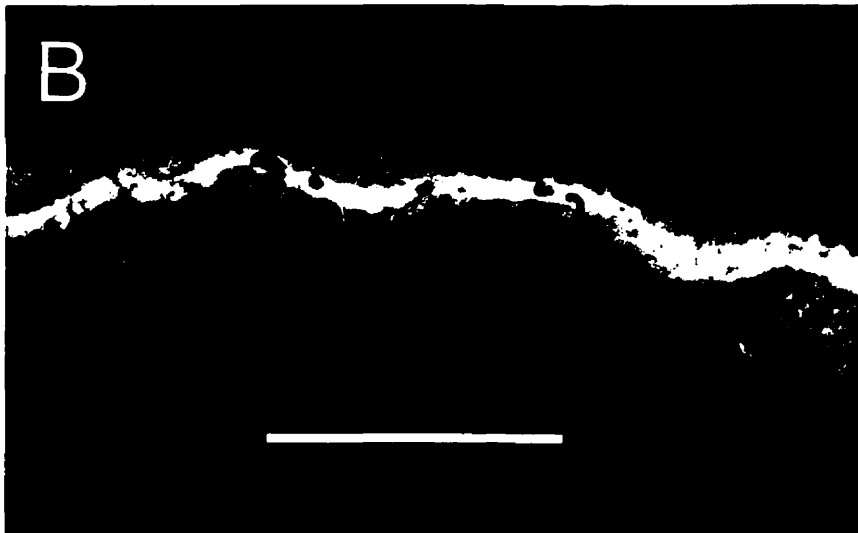


FIGURE 14. FMNH PR 624, *Phlegethontia longissima*, from Mazon Creek, Illinois.

Specimen shows a body impression (A), within which can be seen a cast of the intestinal tract (B), possibly the stomach. Scale bars equal 10 mm.



CHAPTER 3

REVISION OF OPHIDERPETONTIDAE

To be submitted as: Jason S. Anderson. The Cranial Anatomy of *Coloraderpeton brilli*, postcranial anatomy of *Oestocephalus amphiuminus*, and a reconsideration of the Ophiderpetontidae (Tetrapoda; Lepospondyli; Aistopoda). Prepared for the Journal of Vertebrate Paleontology.

PREAMBLE CHAPTER 3

Phlegethontiids are highly divergent, and it is difficult to homologize their massively coossified bones with the skull bones in most Paleozoic tetrapods. This is the reason most workers disagree so widely on exact bone identifications, which leads to vastly different functional interpretations. Ophiderpetontids are a step closer to primitive tetrapods in skull anatomy by retaining most dermal ossifications. Here I extend recent work by describing the skull of *Coloraderpeton brilli*, and considering the postcranial anatomy of ophiderpetontids in detail.

ABSTRACT

The cranial anatomy of *Coloraderpeton brilli* Vaughn is reconsidered in light of new ophiderpetontid material from Nýřany, Czech Republic. It is distinct from *Oestocephalus amphiuminus* in having a quadrate region extended further posterior of the occiput and a tabular restricted from the lateral temporal margin by the supratemporal. In contrast with the original description, *Coloraderpeton*, like all lepospondyls, lacks an intertemporal. *Coloraderpeton* has widely spaced teeth, which brings into question the utility if this character in separating *Ophiderpeton* from *Oestocephalus*. *Coloraderpeton* has additional rows of teeth on its palate, as opposed to the single row in *Oestocephalus*.

Oestocephalus has approximately 110 vertebrae in its complete column. Vertebrae are not added posteriorly with growth, making vertebral counts of systematic significance. Transverse processes remain laterally directed throughout the column, unlike *Phlegethontia*, which has an anterior migration of the bases of the transverse processes, and an anterior inflection that becomes more pronounced posteriorly. Ribs are present to about the 70th vertebra, leaving 40 rib free caudal vertebrae, which contrasts with the 100-160 rib free caudal vertebrae of *Phlegethontia*. Ribs are “K-shaped,” with an anterior costal process, and a long posterior process surrounding the tuberculum. No distinction can be made between any of the species in the genus *Oestocephalus*, except *O. nanum*, which has reduced dorsal osteoderms. Preliminary phylogenetic analysis indicated that the Ophiderpetontidae is paraphyletic, but taxonomic implications will be considered elsewhere.

INTRODUCTION

Aïstopods are elongate, limbless tetrapods with fenestrate skulls, no traces of limbs and only remnants of the pectoral girdle (Baird, 1964; Carroll, 1998b).

The later aïstopods possess ribs with a characteristic “k-shape.” With microsaur, adelospondylids, nectrideans and lysorophids they form a monophyletic assemblage of small tetrapods with unipartite centra called Lepospondyli (Carroll, 1995; Carroll et al., 1998; Chapter 1) that might include some (Chapter 1) if not all (Laurin and Reisz, 1997; Laurin, 1998) modern amphibians. Aïstopods first appear in the fossil record in the Viséan Wardie Shale (Wellstead, 1982) and are last known from the Lower Permian of Ft. Sill, Oklahoma (McGinnis, 1967). They are only found in deposits of equatorial Euramerica (Fig. 1). Traditionally they have been divided into three families: the Phlegethontiidae (Gregory, 1948; McGinnis, 1967; Lund, 1978; Chapter 2), Ophiderpetontidae (Boyd, 1982; Milner, 1994; Carroll, 1998a) and Lethiscidae (Wellstead, 1982). These families are distinct from each other morphologically but there is broad overlap in occurrence both in space and time. A comprehensive phylogenetic analysis of all aïstopods that will clarify the taxonomic status of the group is forthcoming (Chapter 5), but for the time being the current familial names will be used for ease of communication without stipulating their reality.

The Ophiderpetontidae has received some attention of late (Milner, 1994; Carroll, 1998a). The first named species, *Ophiderpeton brownriggi*, was described by (Huxley and Wright, 1867) from unprepared specimens from the Jarrow Colliery, Ireland. Hancock and Atthey (1868) named a second species, “*Ophiderpeton*” *nanum*, from the coals at Newsham, Northumberland, England. Subsequently, Cope (1868, 1875) and

Fritsch (1875, 1879) named several species (and a few genera) from the cannel coal deposits of Linton, Ohio and Nýřany and Kounova, Czech Republic. Schwartz (1908) added additional information to the descriptions of the Nýřany forms. Most of these species were reduced to a single representative per locality by the work of Romer (1930) and Steen (1930, 1938), who confessed to being unable to distinguish between the species from those localities. Baird (1964) reviewed the order, and further clarified some taxonomic and anatomical issues. He also published the occurrence of ophiderpetontids at Cannelton, Pennsylvania.

A new genus of ophiderpetontid, *Coloraderpeton brilli*, was named by Vaughn (1969) based primarily upon postcranial material from the Upper Permian Sangre del Christo Formation in Colorado. Zidek and Baird (1978) described the caudal vertebrae of ophiderpetontids from Linton, demonstrating that their caudal vertebrae are characterized by a pair of hypophyseal flanges, as Gregory (1948) did for phlegethontiids. Boyd (1982) prepared and redescribed *Ophiderpeton nanum* from Northumberland, demonstrating many anatomical similarities to the specimens from Ohio and the Czech Republic. Gallup (1983), in an unpublished Ph.D. thesis, presented a detailed description of *Coloraderpeton*, including for the first time cranial data. A new species from the Viséan of East Kirkton, England was described by Milner (1994). This is the second oldest specimen from the group, being slightly younger than *Lethiscus*. Milner also distinguished between the ophiderpetontids from East Kirkton and Jarrow, with single headed ribs, widely spaced teeth, broad snouts and a postorbital and those from Northumberland, Nýřany, and Linton, which have tightly packed, smaller teeth, lack a postorbital and have a narrower snout, resurrecting Cope's generic name *Oestocephalus*

for the latter group. Finally, Carroll (1998a) reviewed the cranial anatomy of *Oestocephalus*, describing, but not naming, an exquisitely preserved skull from Mazon Creek.

In the course of a revision of the Aïstopoda I reexamined the skull of *Coloraderpeton*, now in the collections of the Carnegie Museum. This paper presents new information on the cranial anatomy of ophiderpetontids, corrects errors in the description of Gallup (1983), and examines the postcranial anatomy of the group in light of new complete ophiderpetontid material from Nýřány discovered by Professor Robert Carroll in Vienna.

MATERIALS AND METHODS

Specimens from Linton and Mazon Creek, and galvanotypes of Fritsch's material from Nýřány were borrowed for comparison with peels from Vienna. Access to the material from Jarrow was limited; however, specimens from Jarrow held at the Museum of Comparative Zoology and a peel from a specimen in Dublin made by Katherine Bossy were examined. The skull of *Coloraderpeton* was removed from its plaster and polyethelene glycol base, and the ventral view was fully prepared using acetone and a fine needle. Specimens were drawn using a Wild dissecting microscope and a camera lucida.

Specimens Examined

Oestocephalus amphiuminum

Linton: AMNH 1734, AMNH 6857, AMNH 6908, ANMH 6912, AMNH 7000, BM R.2676, BM R.2673, BM R.2657a, CM 26455, CM 68340, CM 68352, CM 68353, CM 68354, FMNH PR 1690.

Nýřany: NMW 1895-2327, NMW 1899.IX.34, UMMP 22277 (galvanotype of CV 130), UMMP 22274 (galvanotype of CV 124).

Mazon Creek: MCP 323.

Coloraderpeton brilli

CM 47687.

Abbreviations

Institutional—AMNH, American Museum of Natural History; BM, British Museum (Natural History); CM, Carnegie Museum of Natural History; FM, Field Museum of Natural History; MCP, Mazon Creek Paleontological Collection, Northeastern Illinois University; MCZ, Museum of Comparative Zoology; NMW, Naturhistorisches Muesum Wien; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

Anatomical—alp, anterolateral process; ang, angular; art, articular; bo, basioccipital; clei, cleithrum; cp, costal process of rib; d, dentary; do, dorsal osteoderms; eo, exoccipital; exn, external naris; f, frontal; gas, gastralia 1, lacrimal; j, jugal; m, maxilla; n, nasal; ns, neural spine; p, parietal; parf, parietal foramen; pe, pectoral element; pf, postfrontal; pm, premaxilla; po, postorbital; pof, proötic foramen for passage of Vth cranial nerve; pp, postparietal; ppp, posterior process of postparietal; pq, palatoquadrate; prf, prefrontal; ps,

parasphenoid; psp, posterior spine; qc, quadrate condyle; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; t, tabular; tub, tuberculum; v, foramen for the trigeminal nerve; vii, foramen for facial nerve.

SYSTEMATIC PALEONTOLOGY

Tetrapoda Goodrich, 1930

Lepospondyli Zittel, 1888

Aistopoda Mial, 1875

Ophiderpetontidae Schwartz, 1908

Coloraderpeton brilli Vaughn, 1969

Holotype—UCLA VP 1689.

Type Locality—Interval 300 of Brill (1952), NE1/4, SW1/4 sec. 22, T 49 N, R 10 E, Fremont County, Colorado.

Horizon—About 1450 feet above the base of the Sangre de Christo Formation, Upper Pennsylvanian (Missourian). Red to greenish gray shale with a few thin beds of dark-gray limestone.

Diagnosis—Neural spine is high and does not run the length of the neural arch.

Tuberculum and anterior process of rib condylar, not cupped. Posterior process of rib short and rounded. (Vaughn, 1969)

Revised Diagnosis—Ophiderpetontid aistopod sharing with *Oestocephalus*: loss of the postorbital; posterior process of the frontal extending into the parietal; long posterior parietal process extending to the tabular. It shares with *Ophiderpeton*: long, widely

spaced teeth. It shares with *Oestocephalus*, and the Turnbull aïstopod: k-shaped ribs on all precaudal vertebrae (the posterior process of the rib is greatly reduced if not absent posterior to the 7th vertebra in *Phlegethontia*).

Description

The skull is exposed in three dimensions. It has undergone dorsoventral crushing, obscuring the braincase and occiput. The left side of the skull remains reasonably well articulated, but the right side is disarticulated and folded under, covering most of the palate. The right palatine has also been displaced so that it nearly abuts the left palatine and palatoquadrate. The rostrum has become quite disarticulated and broken, making interpretation difficult. The right mandible is posteroventrally displaced. Fractures are common over the entire surface. The surface has ornamentation of widely spaced circular pits on the premaxilla, prefrontal, lacrimal, postfrontal, jugal, anterior dentary, and, in much lesser density, on the parietal and postparietal. The dermal ornamentation is shallow and sparse compared to other lepospondyls such as *Pantylus* (Romer, 1969) and *Diploceraspis* (Beerbower, 1963).

The rostrum is severely disarticulated, which unfortunately seems to be normal for aïstopods (Fig. 1). The left side of the skull is missing the premaxilla, while the right premaxilla is only partially visible. It is overlain by the right prefrontal (Fig. 2). Its anterior shows little beyond its having an equal height to the prefrontal. Gallup (1983) seems to have misidentified the prefrontal as the premaxilla.

The nasal is not preserved in this specimen. Since the anterior margin of the frontal is broken, it has probably been lost. Another possibility is that it was fused with the prefrontal, which seems rather large for an ophiderpetontid.

The frontal was probably a diamond-shaped bone, although both bones end at an anterior break. The frontal comes to a long, tapering point posteriorly, where it is surrounded laterally and medially by the parietal. These posterior projections end far anterior to the parietal foramen as in other ophiderpetontids. The relationship between the posterior projection of the frontal and the location of the parietal forms a gradational transformation series within aïstopods, with a progressive shift toward the parietal foramen. In the Turnbull specimen (Chapter 4) the posterior projections extend to the level of the parietal foramen, and in *Phlegethontia* the posterior processes of the fused frontals surround the parietal foramen.

The parietal has the largest area of any bone in the skull; only the maxilla is longer (Fig. 1). It extends over three-quarters of the length of the skull. Between the orbits and supratemporal it spans the entire width of the skull table. The parietal foramen is located at the mid point of its length. The anterior border of the parietal has a w-shape caused by the posterior projections of the frontal, similar to the condition in other ophiderpetontids. This is superficially similar to the anterior margin of the phlegethontiid frontal and may have been why McGinnis (1967) identified that bone as a frontoparietal.

The posterior border of the parietal is complex. There is a posterior projection of the parietal into the postparietal along the midline, which is countered just laterally by an anterior projection of the postparietal into the parietal which extends nearly as far anterior as the supratemporal. The parietal then sends a long, narrow process posteriorly and

slightly laterally almost to the occiput. It contacts the tabular posteriorly. The process is roughly equal in width to the supratemporal. *Oestocephalus* also has this posterior process (BM 2673), but it is neither as long nor as wide as in *Coloraderpeton*. Carroll (1998a) reconstructed MCP 323 as lacking the posterior parietal process, but examination reveals it to be present, but reduced reflecting the smaller size of this skull (Fig. 3). The parietal-postparietal border in *Ophiderpeton brownriggi* is almost straight; however, there are two lateral projections of the posterior parietal directed towards the tabular that might represent an earlier stage in the development of these posterior parietal projections (Milner, 1994). An alternative interpretation is that the postparietals have put forward two anterior projections into the parietal. This interpretation is appealing because the median portion of the parietal is almost as far posterior as the lateral posterior process.

The postparietal is about half as long as the parietal (Fig. 1). It is roughly triangular in shape. It has a relatively straight lateral border with the parietal and tabular. This is in contrast with the laterally rounded postparietal-tabular border in *Oestocephalus* (BM 2673, MCP 323; Carroll, 1998a). The greater lateral extent makes the postparietals in *Oestocephalus* wider than the width of the postorbital skull table, while they are narrower in *Coloraderpeton*. Postparietals are also wider than the postorbital skull table in *Ophiderpeton brownriggi* (Milner, 1994) which suggests that the relatively narrow postparietals of *Coloraderpeton* is derived.

The tabular in *Coloraderpeton* is very much reduced in size compared to *Oestocephalus*. It is restricted to the lateral occiput and skull table. It makes contact with the posterior parietal projection which, because it almost reaches the occiput, limits the anterior extent of the tabular. *Ophiderpeton brownriggi* also has a short tabular, but the

postparietal is restricted posteriorly so the tabular is equal in length. The tabular of the Turnbull specimen (FM PR 281) is a very large bone which, like *Oestocephalus*, has a laterally rounded contact with a large postparietal, and it curls ventrally around the braincase. This is possible because of the far anterior location of the suspensorium in the Turnbull specimen.

The supratemporal is a long, narrow bone that forms the lateral margin of the posterior skull table. It extends from the occiput half way to the parietal foramen, about one quarter of the skull's total length. In contrast with other ophiderpetontids, the supratemporal reaches the posterolateral corner of the skull table; the tabular occupies this position in *Oestocephalus* (Carroll, 1998a) and *Ophiderpeton brownriggi* (Milner, 1994). The supratemporal is also prevented from reaching the occiput in the Turnbull aïstopod by the large tabular. Gallup (1983) identified an intertemporal at the anterior end of the supratemporal. Examination of the "sutures," however, reveals them to be fractures that pass through not only the supratemporal, but also the posterior process of the parietal and the postparietal. Furthermore, an intertemporal is absent in all other aïstopods and lepospondyls (Carroll et al., 1998; Chapter 1) so its presence in *Coloraderpeton* would be surprising.

The prefrontal is a relatively large bone. The right prefrontal is most informative (Fig. 2). It shows in its anterior surface the curved posterior margin of the external naris, and on its posterior surface the anterior orbital margin. Dorsally, it has a posterior supraorbital projection towards the postfrontal, but it does not seem as long as in *Oestocephalus* (Carroll, 1998a), although this area has suffered from breakage.

The lacrimal is seen just below the right prefrontal. As in *Oestocephalus*, it is a relatively small bone. The ventral portion of the anterior orbital margin is fully preserved. It has a posterior projection on its ventral surface that extends towards, but seemingly not reaching, the jugal, which means that the maxilla forms the ventral orbit. The exterior surface of the lacrimal is broken away, revealing the passage of the lacrimal duct. It bisects the lacrimal horizontally.

The maxilla of *Coloraderpeton*, as in other ophiderpetontids, is an extraordinarily long and narrow bone. It stretches from near the anterior rostrum to the level of the supratemporal. It bears about 15 teeth, which are equal in length throughout. A particularly striking feature of ophiderpetontids is the distance the posterior maxilla extends unsupported into the temporal opening, forming the anterior half of an incomplete lower temporal bar. In phlegethontiids, the lower temporal bar is completed by the squamosal and jugal, and the maxilla ends at the level of the jugal.

The postfrontal is best seen on the right side (Fig. 2). It is a roughly square shaped bone. The posterior orbital margin is well preserved. The postfrontal continues the orbital margin ventrally, limiting the participation of the jugal. There is no evidence of a postorbital.

The jugal is a triangular bone (Fig. 4). Its base sits upon a dorsal shelf of the maxilla. It has a sort, narrow anterior process that forms the posteroventral corner of the orbit, but probably does not reach the posterior process of the lacrimal. It also has a longer posterior process that continues along the maxilla. The posterior process is swollen and rounded distally. This posterior process doubles the length of the jugal. Gallup described this posterior process as a quadratojugal. In his reconstruction (Gallup,

1983: Fig. 2) it is shown to run the entire posterior length of the maxilla. No such elongate bone occurs in the specimen, except for one element that is dentigerous. It is part of the displaced right maxilla. The posterior process of the jugal is also elongate in *Oestocephalus* (Carroll, 1998a), but is not as long as in *Coloraderpeton*.

As observed by Gallup (1983), the squamosal runs along the elongate quadrate ramus of the palatoquadrate on the left side (Fig. 5). However, Gallup reconstructed the squamosal in a mediolateral position. In fact, it overlies the quadrate ramus of the palatoquadrate on its lateral to posterodorsal surface. It is also a much smaller element than portrayed by Gallup. As in *Oestocephalus* (Carroll, 1998a), the squamosal has a loose articulation with the supratemporal and tabular, but in *Coloraderpeton* the squamosal (and quadratojugal) seem almost recessed into the surface of the quadrate ramus of the palatoquadrate.

The quadratojugal is an oval bone, about twice as long as the squamosal, that lies between the squamosal and quadrate condyle. This bone is distinct on the left side of the skull (Fig. 5). Its suture with the squamosal is a smooth curve that is quite unlike the irregular cracks that cut across (and through) all bones. On the right side, however, the squamosal and quadratojugal are fused, leaving no sutures. This provides support for my hypothesis that the “squamosal” in *Phlegethontia* is actually a fusion of the squamosal and quadratojugal (Chapter 2). In the Turnbull aïstopod (Chapter 4), the quadratojugal is large and covers the whole lateral surface of the quadrate condyle while the squamosal is restricted to a dorsal position, between the supratemporal and tabular, with only a small portion descending towards the quadrate.

Aïstopods are distinguished among tetrapods for having a fused quadrate, pterygoid, and epipterygoid, forming a palatoquadrate similar to that found in non-tetrapod sarcopterygians such as *Eustenopteron* (Jarvik, 1996). Other authors (Lund, 1978; Gallup, 1983) have called this element the pterygoquadrate, to emphasize the retention of a separate palatine, also clearly present in *Coloraderpeton*. Separate palatines are also present in *Eustenopteron*, so this seems an unnecessary distinction to make. The palatal (or pterygoid) ramus of the palatoquadrate runs the entire visible length of the palate. It is narrow, sutures to the palatine laterally, and leaves a narrow slit-like interpterygoid opening, similar to that of *Oestocephalus* (Carroll, 1998a). The quadrate condyle seems to be slightly bicondylar. It is extended far posterior to the occiput at the end of an elongate quadrate ramus. In all ophiderpetontids, the quadrate condyles migrate posteriorly with growth. The smallest specimen of *Oestocephalus* (NMW 1899.IX.34), the total skull length (TSL) is 5.85 mm, while the basal skull length (BSL) is 5.05 mm, placing the quadrate condyle 8% of the TSL posterior the occiput. In the slightly larger specimen NMW 1895-2327 (TSL 7.95) the quadrate condyle is only 6% of the TSL posterior to the occiput, but this specimen has suffered some disarticulation. In MCP 323 (TSL 18.45 mm) the quadrate condyles are similarly located. In the largest specimen of *Oestocephalus* (AMNH 6857, TSL 48.23 mm) the quadrate condyles are located 22% of the TSL posterior to the occiput, but this is an overestimate since the anterior of the skull is not preserved. The quadrate condyle is much further posterior in *Coloraderpeton* than in *Oestocephalus*, being 31% the TSL posterior to the occiput, despite the skull of *Coloraderpeton* being smaller (TSL 34.65 mm) than the largest *Oestocephalus* skulls.

The epipterygoid rises dorsally from the posterior palatal ramus of the palatoquadrate. The epipterygoid runs along the entire lateral wall of the braincase. It is well ossified, in contrast to the rest of the braincase, which is not preserved in *Coloraderpeton*. Carroll (1998a) suggested that the braincase in MCP 323 was not ossified because of the juvenile nature of the skull; *Coloraderpeton* suggests that ophiderpetontids have poorly ossified braincases. This is in stark contrast to the almost mammal like calvarium of phlegethontiids (Chapter 2). Further, the new Nýrány specimens are much smaller than MCP 323 from Mazon Creek, so the latter might not be a particularly young individual.

Two foramina are visible on the medial surface of the epipterygoid near the mid point of the skull. The larger, more anterior and dorsal of the two is interpreted as the trigeminal foramen, for the passage of the trigeminal nerve. In *Phlegethontia* and the Turnbull aistopod (Chapters 2 and 4) the epipterygoid only partially surrounds the trigeminal foramen; at least the dorsal margin of the foramen is free. The posterior and more ventral foramen is possibly for passage of the facial branch of cranial nerve VII. Matrix or other bones may obscure additional foramina.

The palatine is a broad bone in *Coloraderpeton*. Both the left and right are visible, although the right is displaced far to the left. The left is fractured at the mid point and the anterior half is positioned more laterally than the posterior half. It had three or four tightly packed rows of small teeth running parallel to the marginal tooth row (Fig. 6). Its full extent is unknown, but as preserved it spans about one third of the length of the skull. The only other palatine known in an aistopod is MCP 323, which has only a single

row of teeth. Those teeth are relatively larger, being almost equal in size to the marginal teeth, and they are spaced further apart.

The left jaw is preserved in nearly the correct position (Fig. 6), while the right has been displaced posteriorly. Both show the lateral surface. It seems to lack the masseteric fossa present in *Oestocephalus*, although it has a large enough surface area to support large M. adductor mandibulae. When the tooth row is positioned horizontally, the jaw is wider than it is deep, similar to *Phlegethontia*. This orientation also removes the “hockey-stick” shape described by Gallup (1983). Instead of having a sharp dorsal posterior inflection as reconstructed by Gallup, the articular is directed dorsally and slightly laterally to the main body of the jaw.

The articular has a complex interdigitating suture with the angular and surangular just below the articular cotyle (Fig. 4). In *Oestocephalus* (BM R.2673) the articular can have a long ventral extension that forms the entire posterior margin of the jaw, but this character is variable. In MCP 323 the large ventral portion of the articular is restricted to the medial surface. BM R.2657a shows close correspondence to the articular of *Coloraderpeton*, although with a greater posteroventral extent. In the remainder of jaw anatomy *Coloraderpeton* closely resembles other ophiderpetontids. The surangular occupies most of the lateral surface of the posterior jaw. The surangular-angular suture is nearly obliterated, but it can still be traced as a thin crease. I have placed it in a more ventral position than Gallup (1983), who extrapolated a crack posteriorly through an otherwise featureless portion of the jaw. The angular extends anteriorly from the articular to nearly the midpoint of the jaw. The dentary is extremely long. It occupies three quarters of the length of the jaw. The medial surface is unavailable for study.

Milner (1994) used the pattern of dentition as a character to distinguish *Ophiderpeton* from *Oestocephalus*. She restricted *Ophiderpeton* to the ophiderpetontids from Jarrow and East Kirkton. They have a slightly shorter, and relatively stouter, skull, a broad, blunt snout, retain the postorbital, and have widely spaced, long teeth. *Oestocephalus*, from Nýřany, Northumberland, and Linton, have more elongate, narrower skulls with a more pointed snout, and shorter, very closely packed teeth. But there are exceptions. The smaller specimen of *Oestocephalus* from Mazon Creek has relatively widely spaced teeth (Carroll, 1998a).

Coloraderpeton also violates this rule. It has long slender marginal teeth that are widely spaced, similar to those of *Ophiderpeton*. These teeth are conical, and have a hollow pulp cavity that, when broken, makes the bases resemble sockets. McGinnis (1967) also noticed this trait in phlegethontiids. These pulp cavities, when the cusps are broken, resemble thecodont alveoli. Contra Gallup (1983), the teeth are not thecodont. They are instead ankylosed to the bone that bears them. *Coloraderpeton*'s teeth are slightly recurved at the tip. The largest even appear sinusoidal, similar to the teeth of juvenile rhizodont sarcopterygians.

Oestocephalus amphiuminus Cope, 1868

Holotype—AMNH 6857

Type Locality—Diamond Mine, Linton, Ohio

Horizon—Canneloid shale below Upper Freeport Coal, Allegheny Group, late Westphalian D.

Referred Species—*Oestocephalus remex* (partim) Cope, 1869; *Thyrsideum fasciculare* Cope, 1875; *Oestocephalus* (*Ophiderpeton*) *granulosum* Fritsch, 1879; *Oestocephalus* (*Ophiderpeton*) *vicinum*, Fritsch, 1879.

Revised Diagnosis—Ophiderpetontid with tabular at lateral margin of skull table; teeth tightly packed. Shares with *Coloraderpeton*: loss of the postorbital; posterior process of the frontal into the parietal; a long posterior parietal process permitting contact between the parietal and tabular; postparietal. It shares with *Coloraderpeton*, *Ophiderpeton*, and the Turnbull aistopod: k-shaped ribs that span all precaudal vertebrae (the posterior process of the rib is greatly reduced if not absent posterior to the 7 vertebra in *Phlegethontia*).

Description

Carroll (1998a) has recently described the cranial anatomy of *Oestocephalus*, and little can be added. The investigation of *Coloraderpeton* has revealed the importance of the posterior process of the parietal, and prompted reinvestigation of this region in MCP 323. A revised reconstruction of this skull is presented in Figure 14.

The first complete ophiderpetontids were found in the collection of Nýřany specimens at the Naturhistorisches Museum in Vienna (Wien). They are two juveniles, one 36% larger than the other is. The larger, (NMW 1895-2327, BSL 7.95 mm) is covered by dorsal osteoderms so thickly that it obscures much of the cranial morphology. The smaller (NMW 1899.IX.13, BSL 5.05 mm), however, is unobscured by osteoderms, and has a few cranial features worth noting.

The skull is crushed flat dorsoventrally except for the palatoquadrate, which maintains distinct three-dimensionality (Fig. 9). It seems as if the dermal bones comprising the skull table are paper-thin, the outlines of the underlying palatoquadrate are clear on the dorsal surface. Unfortunately, this obscures sutures. It also produces cracks that run along the length of the palatoquadrate, which appear superficially similar to sutures. The median suture is definitively present, as is the parietal foramen. The frontal has its characteristic posterior process into the parietal. The anterior margin of the frontal appears to resemble that of *Phlegethontia*. It has a long median process, and a smaller lateral process. Alternatively, the median process is a nasal, but there is no likely suture present. The parietal has a well-developed posterior, but no median, process. This contrasts with MCP 323, which has weakly developed posterior processes, although it is over a centimeter (70%) larger. Other than the postparietal and the maxilla, other skull table bones are indistinct, unfortunately including the relationship between the tabular, supratemporal, and lateral skull margin.

NMW 1899.IX.13 preserves the entire vertebral column (Fig. 11A). It has an estimated count of 110-112 vertebrae, of which the anterior 95 are well ossified. The remaining vertebrae are represented as faint impressions in the matrix. All vertebrae become completely ossified by the time the size represented by NMW 1895-2327 is reached (Fig. 10, 11B). It has 108 fully ossified vertebrae and no remaining impressions. This suggests that at least the caudal vertebrae ossify from anterior to posterior, similar to the pattern seen in some modern amphibians (Carroll, et al., 1999). It also suggests that no additional vertebrae are added with growth, contra (Baird, 1964), and that vertebral count has significance for aïstopod systematics. However, a sample of two complete

specimens is insufficient for making this determination with any degree of confidence. Populations of snakes (Arnold, 1987), fish (Lindsey and Arnason, 1981), and salamanders (Jockusch, 1997), among modern vertebrates, may undergo a change in the usual number of vertebrae in response to environmental factors during development. Vertebral number seems to remain about a mean in a particular locality (Arnold, 1987), which might be the case for the two specimens in question. Complete specimens from Linton and Mazon Creek, along with new complete Nýřany specimens, need to be identified to clarify this question.

The vertebrae of *Oestocephalus*, like all aĭstopods, have a simple, spool-shaped amphicoelous centrum fused indistinguishably to the neural arch at extremely small sizes. Centra are waisted, constricting the notochord. They have a narrow ventral keel precaudally, and two haemopophyseal flanges run longitudinally along either side of the midline on caudal centra (Gregory, 1948; Zidek and Baird, 1978). Neural arches run the whole length of the centrum (Fig. 12). The neural spine is low and runs the length of the neural arch. The zygopophyses form the lateral most portions of the neural arches other than the transverse processes. They are horizontal to slightly ventrolaterally inclined, but never more than a few degrees.

There is a notch between the postzygopophyses for the reception of the neural arch of the succeeding vertebra. This tight fit helps to integrate the zygosphene, present on the anterior neural arch (AMNH 6857; Fig. X), within the zygantra. Unfortunately, no other specimen shows this accessory articulation, so it cannot be discounted that the zygosphene is part of a broken neural arch. Baird (1964) offered this notch as a potential character for distinguishing between ophiderpetontid and phlegethontiid vertebrae. It is

deep, he argued, in *Oestocephalus*, but shallower in *Phlegethontia*. However, this character is highly affected by preservational factors; it can vary from distinct to absent in succeeding vertebrae. Furthermore, “shallow” and “deep” are extremely difficult to judge. The notch in the ninth vertebra of the type of *Oestocephalus* (AMNH 6857) seems to be absent, while some of the caudal vertebrae of *Phlegethontia longissima* (USNM 17097) seem relatively deep.

The transverse process extends from the neural arch pedicle just above the centrum. A foramen for the spinal nerve is located just posterior to the transverse process except for the atlas, where it is anterior to the transverse process. Anterior to the transverse process a web of bone extends anteroventrally to the edge of the centrum. Just anterior to the transverse process the web is notched (Fig. 12). Anterior to the notch the web comes to a lateral point, and then rapidly joins the centrum. This point is not swollen, but it is positioned in the same location as the anteroventral shaft of the double transverse process of the Turnbull aïstopod. Phlegethontiids have single transverse processes without a trace of a remnant of the parapophysis

Coloraderpeton was described as having a transverse process with two facets (Vaughn, 1969). Vaughn argued that the “capitulum” would fit nicely into the posterior facet while the costal process would simultaneously fit the anterior facet. If this interpretation were correct, and I am correct in suggesting that the rib only articulated with the posterodorsal shaft of the transverse process in the Turnbull aïstopod (Chapter 4), then the rib head that articulates with the transverse process in *Oestocephalus* and *Phlegethontia* is a tuberculum, contra Baird (1964) and subsequent authors. The parapophysis, with which the capitulum articulates, is located anteroventral to the

diapophysis in most tetrapods (Romer, 1956). Primitively, the tetrapod parapophysis is located on the intercentrum, which is anteroventral to the neural arch that bears the diapophysis. In microsaur, when the intercentrum is not present, there is a lateral expansion of the posterior rim of the preceding centrum to articulate with the capitulum (Carroll, 1998c). This interpretation would mean that the costal process of the rib may be a displaced capitulum (although the example provided by modern apodous squamates shows the single articular facet can be a fusion of the tuberculum and capitulum), and that the point on the web anterior to the transverse process is a remnant of the area that supported the parapophysis. This is bolstered by the presence double-headed ribs reported in *Lethiscus* (Wellstead, 1982; but see Chapter 5). However, other primitive ophiderpetontids have single-headed ribs (Milner 1994), so the costal process might also be interpreted as a neomorphic character.

A lateral, spike-like, process is present just posterior to the diapophysis. It originates on the shaft of the transverse process, although in some vertebrae it appears to arise from the base of the transverse process as a separate shaft. It may have developed to provide a lateral attachment for a muscle such as *M. tuberculocostalis profundis*, which would help to reduce torsional forces (see below). The lateral spike, diapophysis and the point on the anterior web of bone connecting the transverse process to the centrum together give the transverse process a triradiate shape in dorsal view.

Carroll (1998b) described the aïstopod proatlas in *Oestocephalus* (MCP 323), and that of *Phlegethontia* is described in Chapter 2. It is a single median ossification rather than the primitive paired structures. Reexamination of AMNH 6857 shows it to be possibly present as well. It is short and wide, while the proatlas in *Phlegethontia* is longer

than wide, which might be due to small size. It articulates with the occiput and anterior atlas neural arch; however, there is no atlas prezygopophysis or related structure on the occiput to receive the proatlas.

The atlas is seen in detail only in MCP 323 (Carroll, 1998a: Fig. 2). It has a more elongate centrum than immediately succeeding vertebra. This extension takes place anterior to the neural arch, which is the same length as the arches in succeeding vertebrae, and is suggestive of the odontoid process of the atlas present in *Phlegethontia* (Gregory, 1948; Chapter 2). It is especially reminiscent of the odontoid process of USNM 17097 described by Gregory which has a similar blunt anterior surface. This is probably a character that changes with growth, since the smallest specimens of *Phlegethontia* have a rounded odontoid. The odontoid process of the atlas is a synapomorphy of Lepospondyli (Chapter 1). Behind the second vertebra, the length of the centra increases, to match that of the atlas at vertebra five.

The transverse process of the atlas is a simple shaft, without the extra processes and webs of bone present for the rest of the trunk region. It arises posteriorly from the neural arch pedicle and is directed posteriorly at about 30° from lateral. The second vertebra is indistinguishable from subsequent vertebrae except for its lack of ribs. The transverse processes of the second, third and fourth vertebrae are relatively short; from the fifth on they are very long (over twice again the lateral distance spanned by the zygopophysis). In MCP 323 at least the first seven, and in AMNH 6857 the first ten, vertebrae have posteriorly directed transverse processes, with the posterior spike-like projection appearing on the posterior margin of the diapophysis by the eighth vertebra. NMW 1895-2327 from Nyírány has posteriorly directed transverse processes to the

eighth vertebra (Fig. 10), and lateral spike-like projections starting from at least the sixth. However, the very small Nýrány specimen (NMW1899.IX.13; Fig. 11A) has laterally directed transverse process throughout the column, although the lateral spikes still seem to appear at the sixth vertebra.

For the remainder of the column, the transverse processes are positioned on the mid point of the central length and are laterally directed. Lateral spikes are present until the ribs are lost, at about the 70th vertebra. After the ribs are lost, the transverse processes maintain their lateral extent for another seven vertebrae, and then are rapidly reduced to small bumps. Central length reaches its maximum at about the 10th vertebra, and is maintained until the suspected beginning of the caudal region, when they begin to gradually taper off until the end of the tail.

Caudal vertebrae in ophiderpetontids are defined by the presence of two ventrally directed haemal flanges that run longitudinally on either side of the midline (Zidek and Baird, 1978). This feature is also present in phlegethontiids (Gregory, 1948). Unfortunately, dorsolateral crushing has obscured this morphology in the Nýrány specimens of *Oestocephalus*. Haemal flanges seem to be present on approximately the 60th vertebra of NMW 1899.IX.13 (Fig. 11A). If this were correct, *Oestocephalus* would have 10 rib bearing, and 38 rib-less, caudal vertebrae. In comparison, *Phlegethontia* has 65 precaudal vertebrae and ribs on at least the anterior 85 vertebrae, leaving well over a hundred ribless caudal vertebrae. The appearance of haemapophyseal flanges cannot be identified in the Turnbull aistopod (Chapter 4), but it has at least 88 rib bearing vertebrae, like *Phlegethontia*, leaving 52 non rib-bearing vertebrae. If the location of the most posterior rib is properly identified, it means that the progression of elongation from the

108 vertebrae of *Oestocephalus* to the possibly 250 vertebrae of *Phlegethontia* is achieved by adding only 15-20 precaudal vertebrae. The Turnbull aïstopod is intermediate between *Oestocephalus* and *Phlegethontia* in counts of total and rib free caudal vertebrae, but has the same number of rib bearing vertebrae as *Phlegethontia*.

Ribs have a characteristic “k-shape” formed by the tuberculum, anterior or costal process, posterior process, and descending rib shaft (Fig. 12). The aïstopod rib head is similar to what is seen in modern limbless squamates (except skinks) in having a single articular facet with accessory processes to either side of it (although only one process may be present in some species; Hoffstetter and Gasc, 1969). It differs in the distal displacement and posterior orientation of the posterior process, which in squamates is short and directed towards the vertebra. The tuberculum of aïstopods is articulated with the transverse process (Fig. 13) in specimens from Linton (AMNH 6857; BM R.2673, Fig. 12) and Nýřany (NMW 1895-2327, NMW 1899.IX.34). The costal process is an anterior continuation of the rib shaft. It is likely that the costal (or anterior) process is a modified capitulum. This is bolstered by the similar medial cupped morphology, which was probably finished in cartilage in life. In *Coloraderpeton*, the tuberculum and costal process are condylar, not cupped (Vaughn, 1969; Gallup, 1983).

The posterior process has a web of bone between it and the rib shaft. It forms an angle of 35° with the rib shaft. The rib shaft has a ventral curve that directs it away from the posterior process. This curve gives the shaft a ventral inflection. The curvature of the shaft is unlike that of *Oestocephalus nanum* which has a kink at the base of the otherwise straight rib shaft that directs it parallel to the posterior process (Boyd, 1982). Baird (1964) and most subsequent authors described the posterior process as a

“posteriomedial” process. Gallup (1983), however, reconstructed the posterior process with an anterior orientation, necessitated by the articulation of both tuberculum and costal process with facets on the transverse process. Both of these interpretations are at odds with the fossil evidence. In most specimens of *Oestocephalus* (e.g. AMNH 6857, BM R.2673) and *Phlegethontia* (AMNH 2564, MCZ 2204) that show this area well, the posterior process overlaps the rib on the subsequent vertebra. For a “posteromedial” process to achieve this orientation it would require an anterior displacement to bring the process around the next posterior rib, and a subsequent posterior displacement to achieve the overlap. For Gallup’s orientation to achieve the preserved arrangement, each rib in each specimen would have to rotate about the costal process over 180°. Where ribs are clearly displaced in the fossils, however, they are flipped along their long axis away from the vertebra but maintain their relative position along the vertebral column. Therefore, it is a simpler explanation to accept that they are preserved in their proper position, especially considering how little displacement is present elsewhere in the skeleton. This orients the posterior process horizontally, the rib shaft posteroventrally, and the costal process anteriorly, towards the transverse process of the proceeding vertebra.

The remnant of the pectoral girdle is reduced in *Oestocephalus*. As in *Phlegethontia*, it is always positioned in the region of vertebrae three to five, lateral to the ribs (Fig. 10). However, it seems to be reduced in size relative to the length of the vertebrae. In AMNH 6857 it has a slight sickle shape, but is unlike the long, deeply curved bone in *Phlegethontia*. In MCP 323, it is straight. In Chapter 2 I argued that this bone represents either the cleithrum or a fusion of the cleithrum and clavicle, based upon length, position, and orientation. Also, some specimens of *Phlegethontia longissima*

(USNM 4484) seem to show a line of weakness between the lower sickle “blade” and the upper “handle” that might represent incomplete fusion between the clavicle (a rounded bone that is found in a corresponding position in limbed tetrapods) and cleithrum (a straight bone likewise found in the same position). My hypothesis of fusion is bolstered by the condition of the “hyoid” in *Coloraderpeton*. As reported by Gallup (1983), this bone is shorter and relatively wider than in *Phlegethontia*. It also ended in blunt, rough ends. Unfortunately, this bone was unfigured in Gallup (1983), and can no longer be located with assurance.

The pattern of ophiderpetontid osteoderms was discussed by Baird (1964), and Carroll (1998a, b). The small Nýřany specimens add important information about the relative timing of appearance of these osteoderms. The smaller specimen (NMW 1899.IX.34) has dorsal osteoderms concentrated in the terminal tail area, around the last 20 vertebrae (Fig. 11A). Interestingly, only dorsal osteoderms seem to be present; the elongate ventral gastralium are not evident anywhere in the specimen. There are a few osteoderms around the posterior skull, but much less than the adult condition. In larger but still very small NMW 1895-2327 (Fig. 10), all dorsal osteoderms are present throughout the column. They are so thick in the lateral fenestrae of the skull that they obscure much of its morphology. The tightly packed, elongate ventral gastralium are present, arranged en chevron, with the apex of the chevrons pointed anteriorly. While the vertebrae ossify from front to back, the dorsal osteoderms ossify from back to front. Further, the dorsal osteoderms seem to appear before the ventral gastralium, but this might be because they stand out against the surface of the cannel coal in which they are preserved at a smaller size.

DISCUSSION

Species Resolution

With no more than two complete specimens available from each of the localities, the question of species resolution is difficult to answer. The Ophiderpetontidae includes at least three member genera: *Ophiderpeton*, *Oestocephalus*, and *Coloraderpeton*. *Ophiderpeton* was restricted to the two older species by Milner (1994): *Ophiderpeton brownriggi* and *O. kirktonensis*. A third species, “*Ophiderpeton*” *swisshelmense*, is not a member of this genus (the nature of this rank aside) because the presence of a parapophysis suggests double headed ribs. The only ophiderpetontid with two facets for rib articulation is *Coloraderpeton*, but the Turnbull aïstopod also has a remnant of a parapophysis (Chapter 4), so “*O.*” *swisshelmense* is not even definitely a member of Ophiderpetontidae. *Ophiderpeton* is clearly distinct from *Oestocephalus* in many characters. *Ophiderpeton* retains a postorbital, which is lost in *Oestocephalus* and *Coloraderpeton*, but it is restricted from the orbital margin, which is derived relative to most other Paleozoic tetrapods. *Ophiderpeton* has single headed ribs while *Oestocephalus* and *Coloraderpeton* have k-shaped ribs, but they are functionally single headed since only the tuberculum articulates with the vertebra. Unfortunately, deposits from both Jarrow and East Kirkton preserve much less detail than at Nyírány, Linton and Mazon Creek. For example, Milner was unable to identify intravertebral spinal nerve foramina, which she attributed to quality of preservation.

Coloraderpeton brilli is clearly a distinct species. It is very similar to *Oestocephalus* in cranial anatomy (except for the greatly posteriorly extended quadrate condyles and the restriction of the tabular from the lateral skull margin) and the pattern of dermal ossicles. It differs substantially in its postcranial anatomy. *Coloraderpeton* has high neural spines that are longitudinally restricted, rather than having low blades that run the entire length of the neural arch (Vaughn, 1969; Gallup, 1983). They seem to have two facets on the transverse processes, sometimes borne on distinct shafts, that might suggest that the ribs, with their condylar rather than cupped heads, are double headed. Further, the ribs have a greatly reduced posterior process, which migrates proximally in the posteriormost portion of the rib bearing vertebral column (Gallup, 1983).

The question remains: how many species are valid within *Oestocephalus*? Previously, many species were recognized. The work of Romer (1930), Steen (1930, 1938) and Baird (1964) restricted the number or permitted species to one per locality. Currently there are four species recognized: *O. granulosum* from Nýřany, Czech Republic, *O. vicinum* from Kounova, Czech Republic, *O. nanum* from Newsham, Northumberland, England, and *O. amphiuminus*, from Linton, Ohio. MCP 323 has not been named as a species and is known as *Oestocephalus* sp. (Carroll, 1998a). Of these species, no distinguishing feature can be found, except possibly for *O. nanum*. *O. nanum* has the tightly packed ventral gastral plates common to other ophiderpetontids, but has only traces of dorsal osteoderms, despite being larger than NMW 1895-2327 which has a full covering of dermal ossifications. This might be significant because, as noted above, ventral gastral plates seem to appear slightly later than the dorsal osteoderms. Of aïstopods, only phlegethontiids and the Turnbull aïstopod have lost the dorsal osteoderms. Further,

the Turnbull aïstopod, similar to *O. nanum*, has “k-shaped” ribs far posteriorly along the vertebral column, which might suggest that *O. nanum* represents a step towards the pseudophlegethontian condition, which is itself a transition from the ophiderpetontid to phlegethontiid bauplan. *O. nanum* may also have an interclavicle resembling that of some microsaurs (Boyd, 1982). Respecting the tentative nature of any hypothesis based upon as small a sample as is available for aïstopods, the name will be provisionally retained, but *O. nanum* is reduced to Ophiderpetontidae incertae sedis. The remaining species, *Oestocephalus granulorum* and *O. vicinum*, are reduced to subjective junior synonyms of *Oestocephalus amphiuminus*, the name with priority.

A brief word regarding the current paradigm shift within systematics is necessary. I agree with many current systematists (Cantino et al., 1999) that the logical basis behind Linnean ranks, from the genus up, is untenable from the standpoint of evolutionary taxonomy. However, I also recognize the difficulties associated with the transition from a typological system of nomenclature dating back centuries to one based upon monophyly (sensu Hennig, 1966). I am therefore providing revised Linnean classifications of the Ophiderpetontidae and Phlegethontiidae (Chapter 2) for historical continuity. However, a new classification of aïstopods based upon the Phylogenetic System (de Queiroz and Gauthier, 1990, 1992; see <http://www.ohiou.edu/phylocode/> for an on-going discussion of a new code of taxonomy based upon phylogenetic systematics) will be presented elsewhere (Chapter 5).

Locomotion

Reconstruction of musculature present in fossil animals with no extant relatives is a difficult task. In Chapter 2 I described a few features of epaxial musculature that could explain the peculiar rib morphology of aïstopods. I suggested that the posterior process of the rib formed the insertion surface for a muscle similar to the *M. iliocostalis* of snakes and amphisbaenians (Gasc, 1981; Moon, 1999). This muscle facilitates bending, which is necessary for all types of limbless locomotion except rectilinear locomotion (Gans, 1962, 1986; Moon and Gans, 1998). The anterior costal process matches closely the anterioventral process on the rib of *Amphisbaena alba* (Gasc, 1981), which is joined to the tuberculum of the preceding rib by *M. tuberculocostalis profundis*. The lateral spike on the posterior transverse process is unique, and its function remains mysterious. One possibility is that it provided a lateral attachment for a *M. longissimus dorsi*-type muscle.

The differences in the patterns of vertebral and rib morphology in ophiderpetontids and phlegethontiids suggests that they had different locomotor mechanisms. If my muscular reconstruction is correct, the reduced posterior process of *Phlegethontia* might have made it less efficient at bending its body laterally compared to *Oestocephalus* or *Coloraderpeton*. On the other hand, *Phlegethontia* had more vertebrae along which to propagate a wave, so it may be that was less important for *Phlegethontia* to optimize the angle of excursion between successive vertebrae.

Gallup (1983) hypothesized that *Coloraderpeton* was a “rib-walker.” Modern snakes that employ rectilinear locomotion tend to be short and deep bodied, which ophiderpetontids are relative to phlegethontiids. Because I consider that Gallup’s reconstruction of the rib orientation requires too much unlikely post-mortem

disarticulation, I also view his functional interpretation of the rib-based locomotion as unlikely. It would be exceedingly difficult to “rib-walk” upon posteroventrally directed rib shafts. I think that ophiderpetontids were accomplished benders, and that their locomotive strategy utilized this trait. Unfortunately, most forms of limbless locomotion, except rectilinear locomotion, utilizes of lateral undulation (Gans, 1986), so exactly which type of limbless locomotion was its preferred mode of motion is unknown. Advanced lateral undulation, side-winding and slide pushing incorporate lateral undulation to the greatest degree, so they might be possibilities.

Habitat

Oestocephalus is found in aquatic environments with a frequency that some authors (Milner 1980, 1993) have taken as indicative that they are terrestrial components and not obligatorily aquatic in their habitus. This is supported by the absence of lateral line canal grooves, which are present in unquestioningly aquatic lepospondyls including diplocaulid nectrideans (Bossy and Milner, 1998) and the microsauro *Microbrachis* (Carroll and Gaskill, 1978; Carroll, 1998). The large orbits and long, open skull likewise speak against fossoriality, although the temporal osteoderms might represent an adaptation towards borrowing. *Oestocephalus* was probably a terrestrial leaf litter occupant, and limited arboriality might have been possible.

Relationship to Phlegethontiids

Progression towards the derived phlegethontiid condition added few precaudal, but greatly augmented the number of caudal, vertebrae. This stands in stark contrast to

the pattern of elongation in snakes, which have very few caudal, but many presacral, vertebrae. The presacral vertebrae of snakes also differ in having nearly an identical morphology, compared with the progressive differentiation of aïstopods. Cohn and Tickle (1999) suggested that this was due to the migration of regions of expression of genes that specify thoracic identity, which, because aïstopods follow a different morphologic pattern, suggests that another genetic mechanism responsible for aïstopod elongation (see Chapter 4 for further discussion).

CONCLUSIONS

Coloraderpeton is closely related to *Oestocephalus*, and both are derived relative to *Ophiderpeton*. *Coloraderpeton* can be distinguished from *Oestocephalus* by the more greatly posteriorly extended quadrate condyles, the restriction of the tabular from the lateral margin of the skull table, and the more substantial postcranial differences such as the transverse processes bearing two facets, the high, longitudinally restricted neural spines, and the reduced posterior processes of the ribs, highlighted by Vaughn (1969).

Ophiderpetontids are the shortest aïstopods, having only 110 vertebrae, compared with 140 in the Turnbull specimen and up to 230-250 in *Phlegethontia*. Vertebrae do not seem to be added during growth, with the proviso that this is based upon only two specimens from the same locality.

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FIGURE 1. CM 47687, *Coloraderpeton brilli*. Camera lucida drawing of the dorsal skull table.

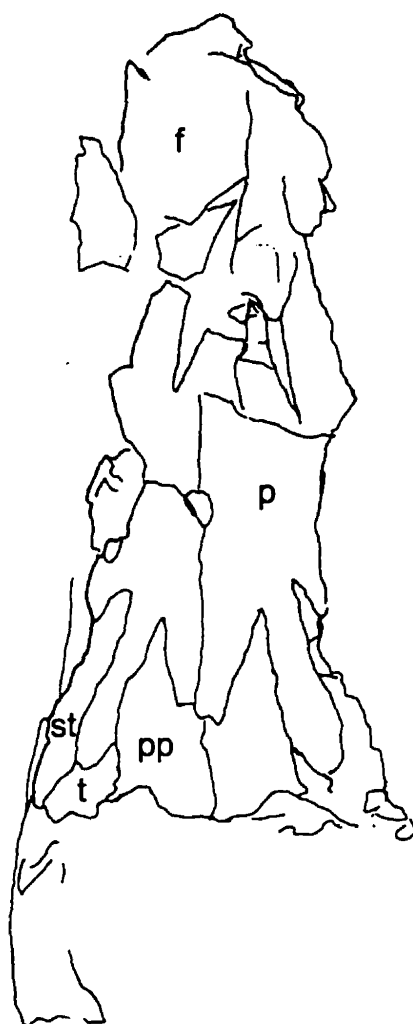


FIGURE 2. CM 47687, *Coloraderpeton brilli*. Anterolateral right skull of *Coloraderpeton brilli*.

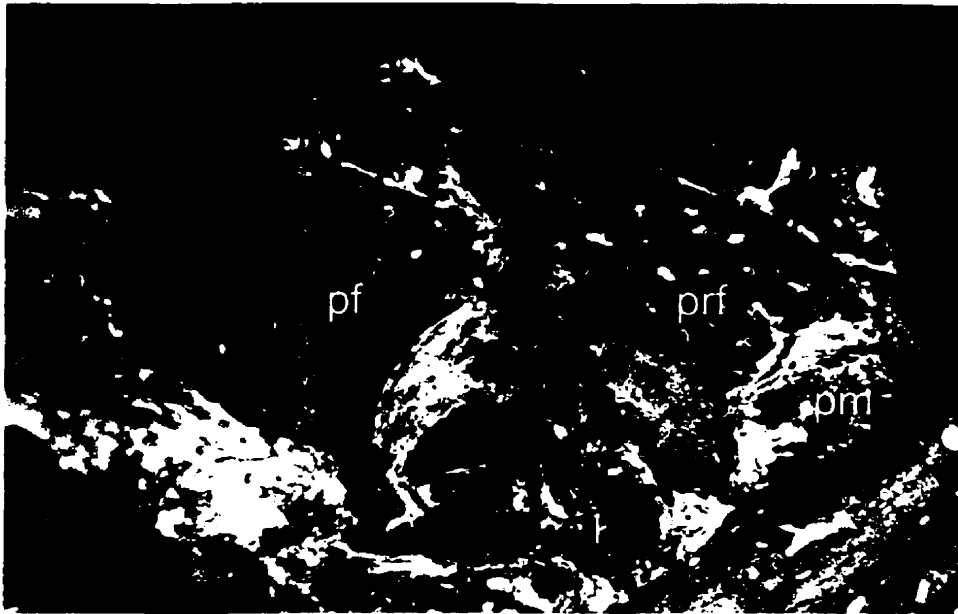


FIGURE 3. MCP 323, *Oestocephalus amphiuminus*, from Mazon Creek, Illinois. Scale bar equals 5 mm.

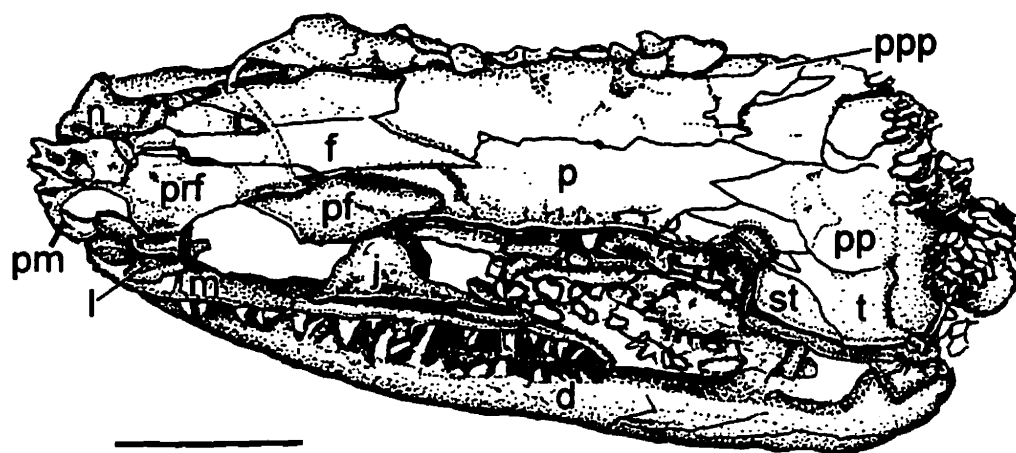


FIGURE 4. CM 47687, *Coloraderpeton brilli*. Right jugal and portion of maxilla.

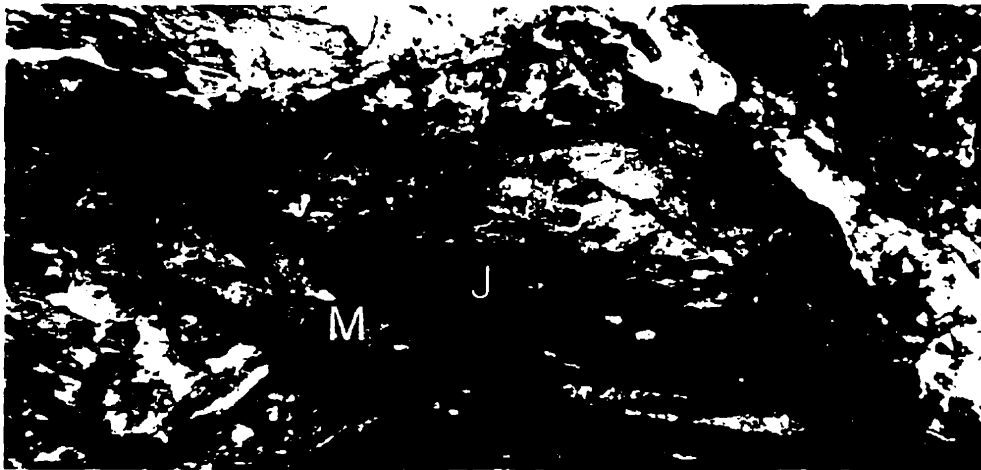


FIGURE 5. CM 47687, *Coloraderpeton brilli*. Posterior left lateral portion of the skull.

Scale bar equals 4 mm.

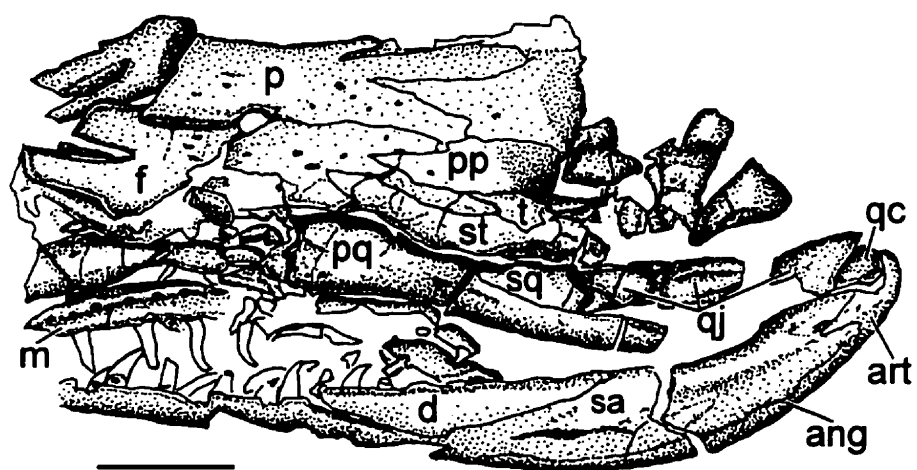


FIGURE 6. CM 47687, *Coloraderpeton brilli*. Left palatine, showing multiple rows of teeth. To the left may be seen part of the right maxilla. To the right is the left lower jaw.

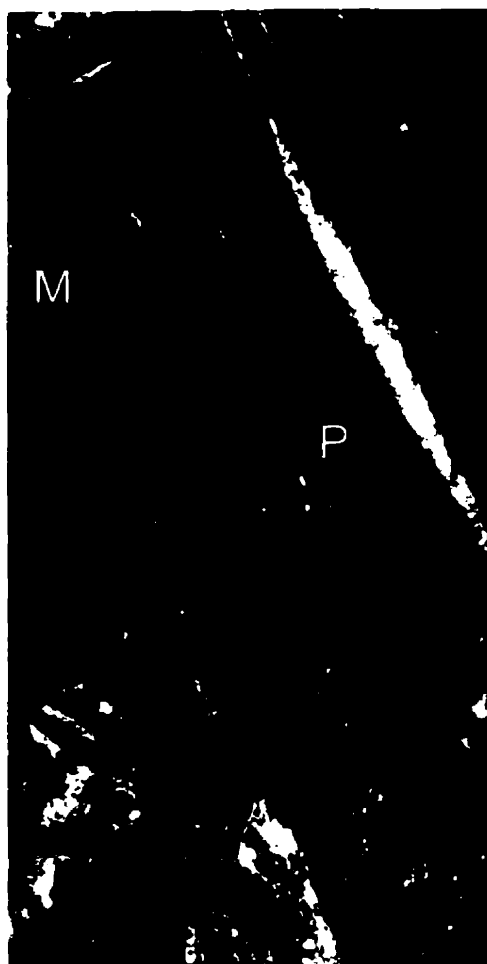


FIGURE 7. CM 47687, *Coloraderpeton brilli*. Dorsal skull reconstruction.

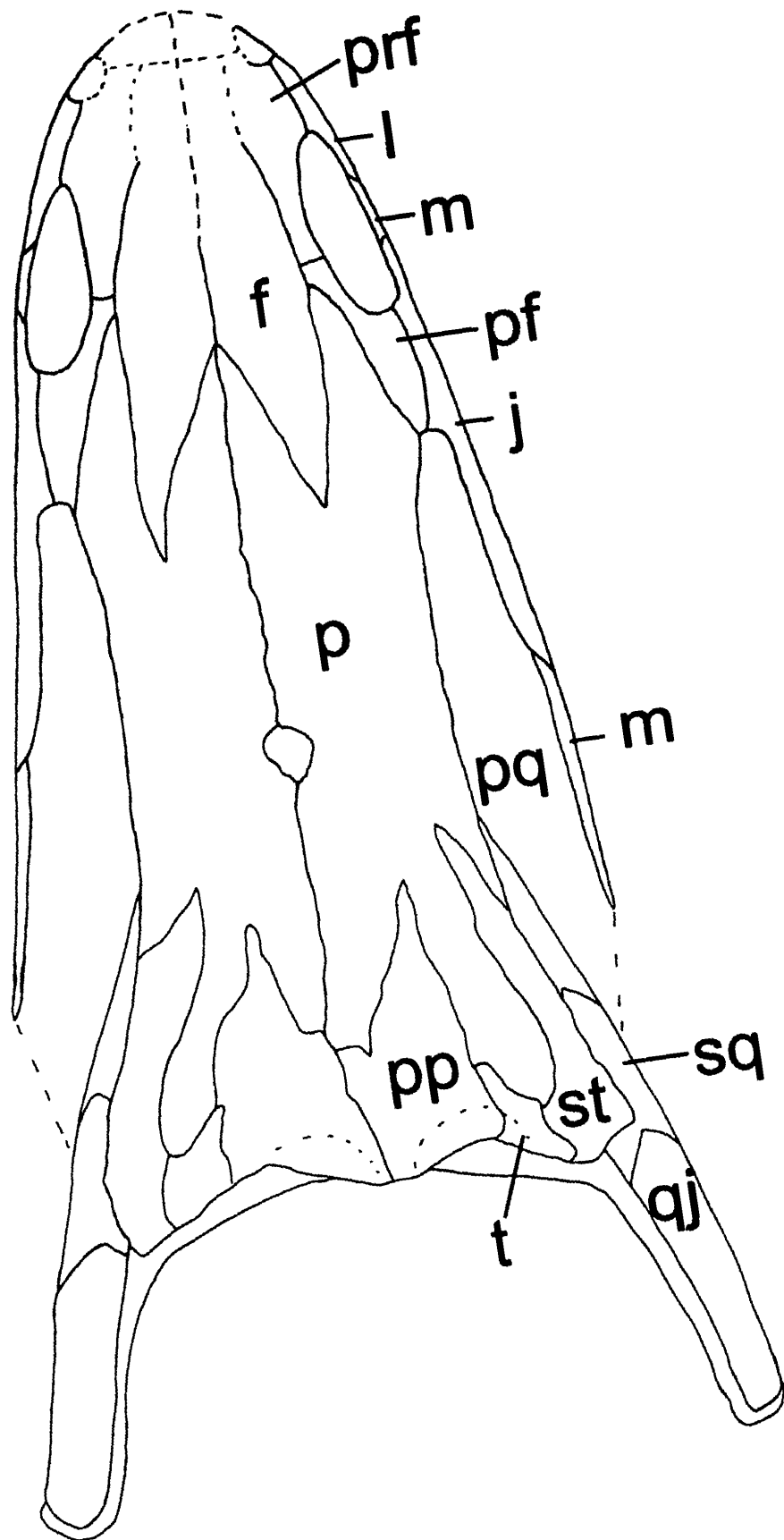


FIGURE 8. CM 47687, *Coloraderpeton brilli*. Left lateral skull reconstruction.

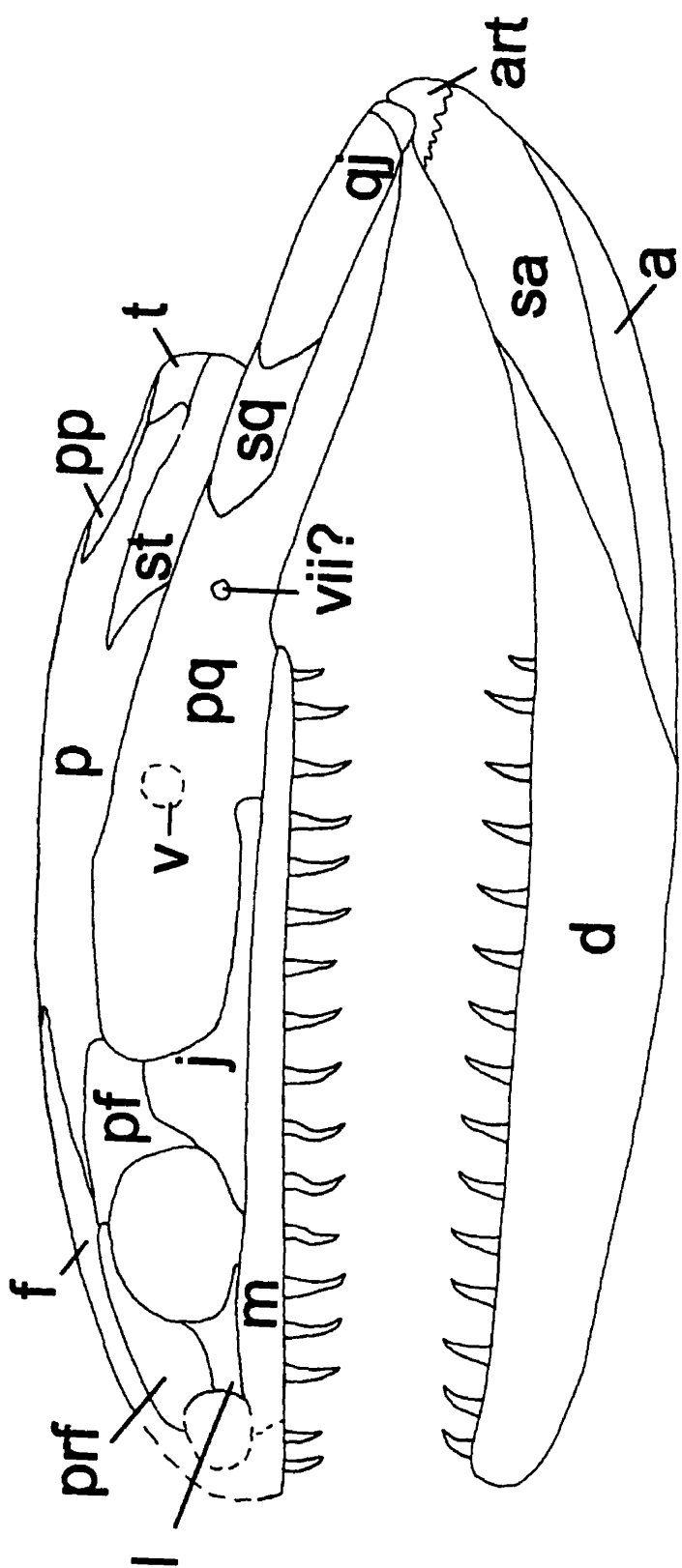


FIGURE 9. NMW 1899.IX.34, *Oestocephalus amphiuminus*, from Nýřany, Czech Republic. Dorsal skull table. Scale bar equals 1 mm.

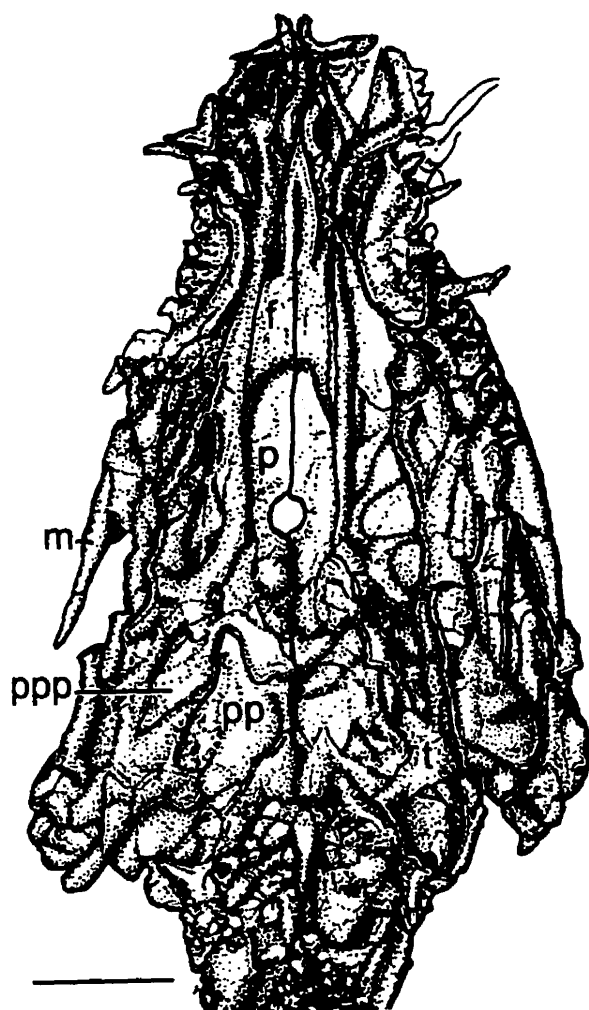


FIGURE 10. NMW 1895-2327, *Oestocephalus amphiuminus*, from Nýřany, Czech Republic. A) Dorsal view of anterior vertebral column and skull B) Ventral view. Scale bar equals 10 mm.

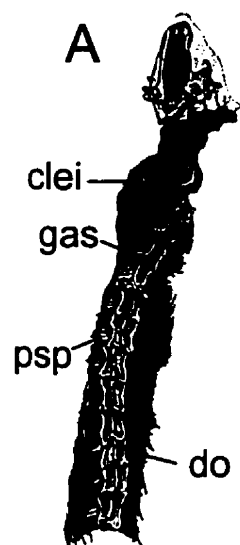


FIGURE 11. A) NMW 1899.IX.34, *Oestocephalus amphiuminus*, from Nýřany, Czech Republic, ventral view. B) NMW 1895-2327, terminal vertebrae. Not to scale. Note the fully ossified vertebrae to the end of the tail, in contrast with the loss of definition near the end of NMW 1899.IX.34. The first vertebrae possibly showing haemal flanges is indicated.



The image area is mostly blank, suggesting the photograph of the specimen was not rendered or is obscured. Two solid black circles are visible on the right margin of the page.

FIGURE 12. BM R.2673, *Oestocephalus amphiuminus*, from Linton, Ohio. Anterior vertebrae, possibly beginning at the 7-9th vertebra. Specimen shows ribs in articulation, and characteristic pattern of dermal osteoderms. Scale bar equals 10 mm.

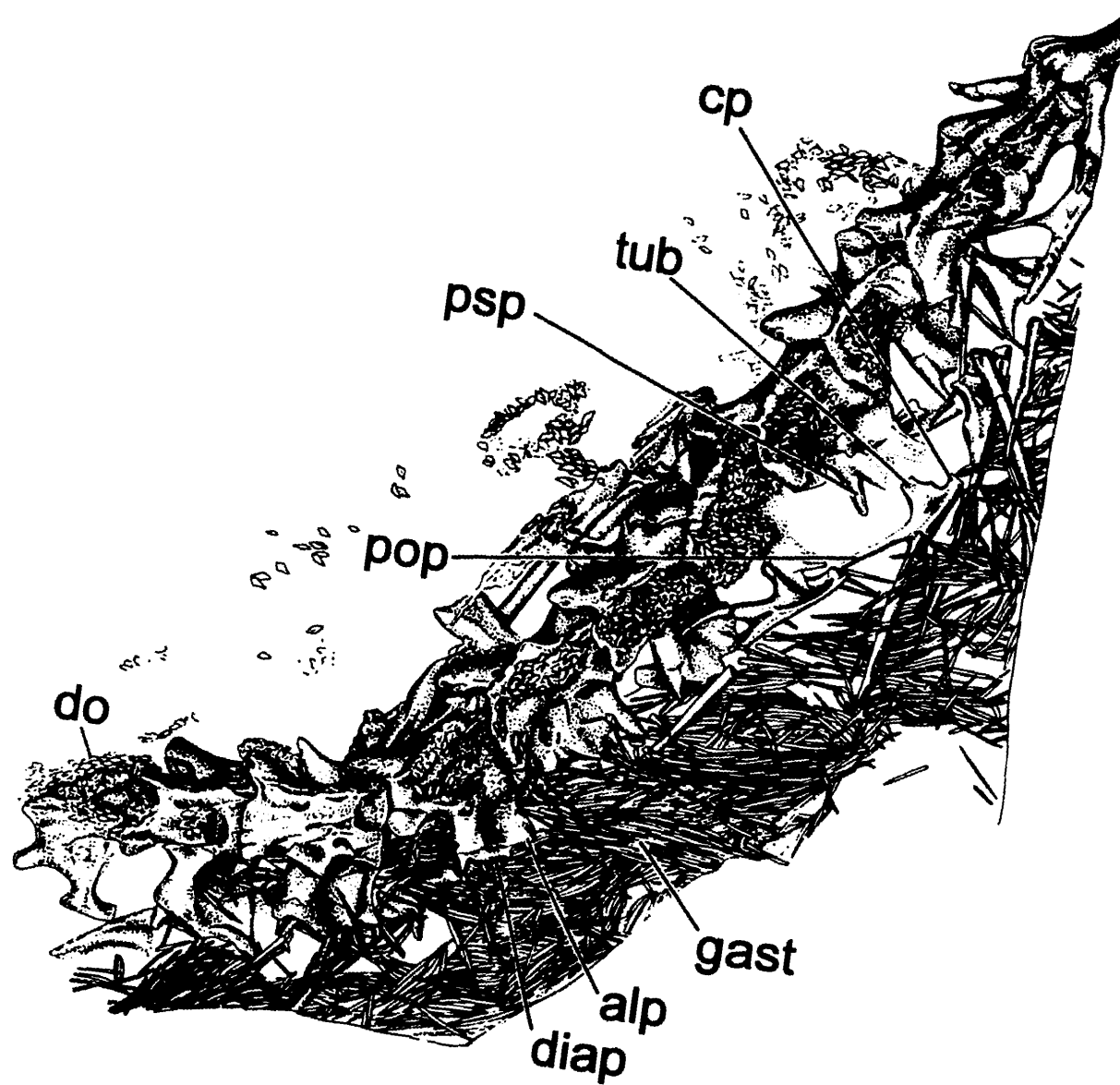


FIGURE 13. FMNH PR 1690, *Oestocephalus amphiuminus*, from Linton, Ohio. Close up dorsal view of a rib in articulation with the transverse process. Scale bar equals 4 mm.

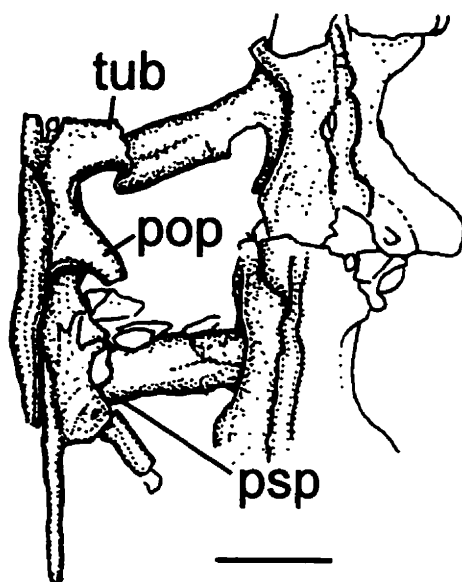
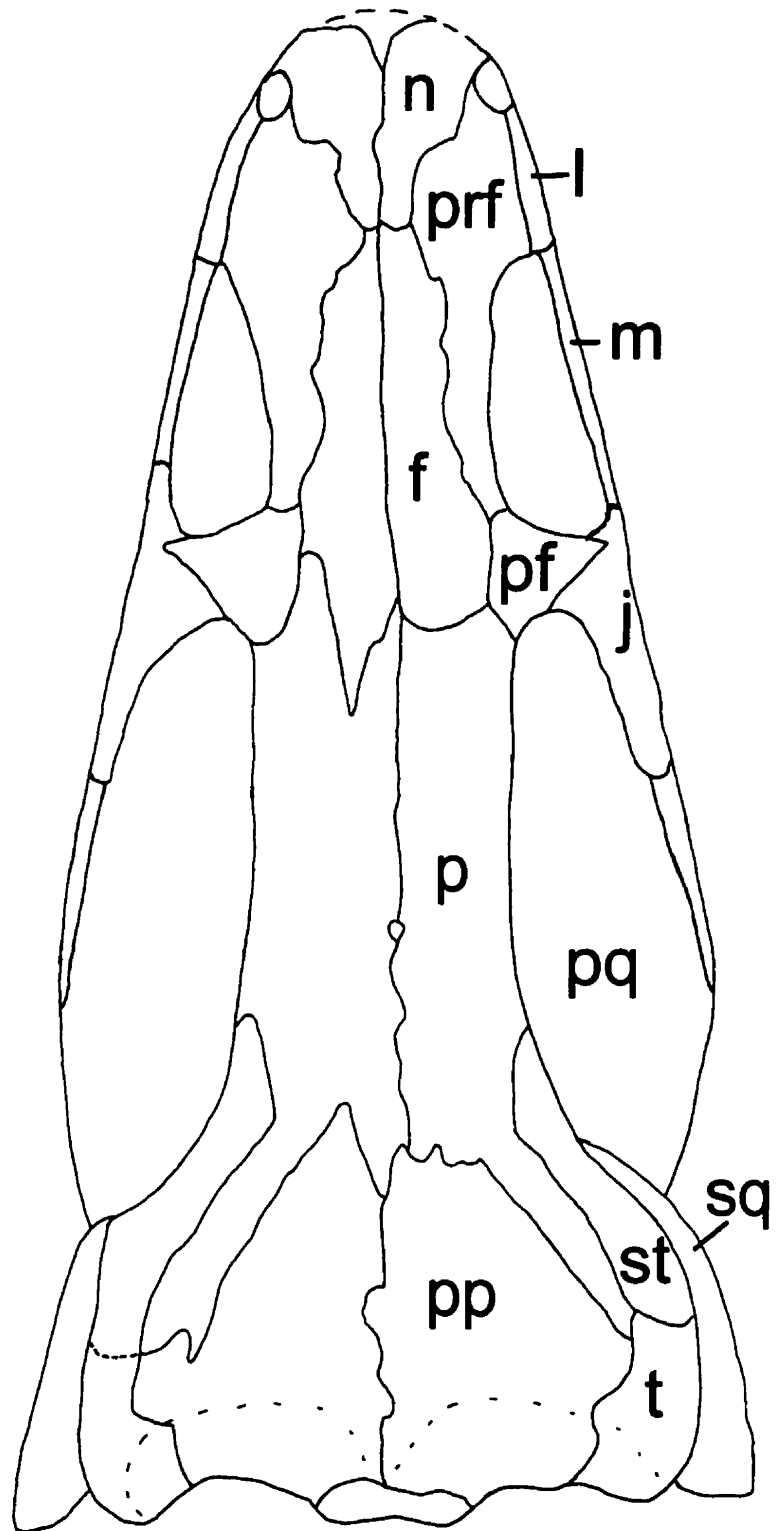


FIGURE 14. New reconstruction of *Oestocephalus amphiuminus*. Revised from Carroll (1998a).



CHAPTER 4

A NEW SPECIES OF AĪSTOPOD FROM MAZON CREEK, ILLINOIS

To be submitted as: Jason S. Anderson. A new aĭstopod (Tetrapoda; Lepospondyli) from Mazon Creek, Illinois. Prepared for the Journal of Vertebrate Paleontology.

PREAMBLE CHAPTER 4

With the characterization of the two most common aïstopod morphotypes, judgements may be made on new forms. This specimen was originally described as a phlegethontiid. Removal of kaolinite that was filling the braincase revealed a skull table with distinct sutures, quite in contrast with the massively coossified skull of *Phlegethontia*, present in individuals much smaller than the specimen in question. Comparison with known aïstopods revealed it to be a new form, following an entirely different pattern of the skull table. This new species is intermediate between the two families described in the previous chapters. The following chapter describes this new aïstopod, and proposes potential developmental mechanisms that might achieve the highly derived phlegethontian from the more primitive Paleozoic tetrapod condition.

ABSTRACT

Pseudophlegethontia turnbullorum, new genus and species, is the third distinct aïstopod known from the Pennsylvanian of Mazon Creek, Illinois. It is morphologically intermediate of the derived phlegethontiids and the more basal, but equally unusual, ophiderpetontids, making it crucial to understanding the anatomy of both groups and inferring possible developmental mechanisms leading to the phlegethontiid condition. Like ophiderpetontids, *Pseudophlegethontia* possesses a relatively short body (140 vertebrae), “k-shaped” ribs extending far back on the vertebral column, distinct skull roof bones, and a temporal opening without a lower temporal bar. However, it has a pointed snout, quadrate condyles well anterior to the occiput, an epipterygoid that rises high on the lateral braincase, thin gastralia, and lacks dorsal osteoderms, which are phlegethontiid characters. Uniquely, *Pseudophlegethontia* has an extremely anterioposteriorly elongate quadrate, and an extended postparietal region. Preliminary phylogenetic analysis places it as sister taxon to *Phlegethontia*, with *Oestocephalus*, *Ophiderpeton*, and *Lethiscus* forming successively further outgroups, suggesting that the Ophiderpetontidae is not a monophyletic family within Aïstopoda.

INTRODUCTION

The Lepospondyli is a diverse assemblage of Paleozoic tetrapods united by simple, spool-shaped vertebral centra, an odontoid process on the atlas, and absence of the following characters common to primitive “labyrinthodonts:” labyrinthine in-folding of tooth dentine, the intertemporal bone, independent atlas intercentra, and a squamosal notch (Carroll, et al. 1998; Chapter 1). They comprise the Aïstopoda, Nectridea, Microsauria, Adelospondyli and Lysorophia and were present from the Viséan to the Lower Permian throughout equatorial Euramerica and into the Upper Permian of North Africa (Milner, 1993). According to recent phylogenetic analyses, lepospondyls are monophyletic (Carroll, 1995; Laurin and Reisz, 1997, 1999; Laurin, 1998; Chapter 1), and may include some (Chapter 1), if not all (Laurin and Reisz, 1997, 1999; Laurin, 1998) modern amphibians. Complicating our ideas of lepospondyl origins and evolution is that they first appear in the fossil record as clearly distinct groups, already highly derived relative to all other early tetrapods. There are no plesiomorphic forms that provide convincing links to any known “labyrinthodont.” Further, most lepospondyls are small, and it has been argued that most of the characters that link the various groups may be convergences due to small size rather than homologies reflecting shared common ancestry (Carroll, 1986; Carroll, 1995; Carroll, 1999).

The Aïstopoda best exemplifies the difficulty of establishing relationships among lepospondyls. They are small, extremely elongate animals with fenestrate skulls, a palatoquadrate (as opposed to clearly distinct quadrate, epipterygoid and pterygoid), a unipartite amphicoelous centrum indistinguishably fused to the neural arch, spinal nerve

foramina posterior to the laterally extended transverse processes, no limbs or pelvis and retaining only remnants of the pectoral elements (Baird, 1964; Carroll, 1998b; Chapters 2, 3 and 5). They fall into two discrete morphological types: the slightly built, elongate Phlegethontiidae and the shorter, stouter, highly ossified Ophiderpetontidae (a third family, Lethiscidae, has also been recognized but ongoing study indicates a close affinity with ophiderpetontids; Chapter 5).

During the course of a revision of aïstopods from North America and the Czech Republic, the specimen described as *Phlegethontia* by Turnbull and Turnbull (1955) was reexamined. After removing kaolinite that filled the skull cavity and producing new latex peels (following the method of Baird, 1955), the specimen was discovered to possess a skull table of separate ossifications rather than the hyperossified braincase characteristic of *Phlegethontia*. The individual elements of the skull table follow a very different pattern than *Oestocephalus*, known from the same locality (Carroll, 1998a; Chapter 3). This specimen provides the first evidence of a possible intermediate between the phlegethontiid and ophiderpetontid morphotypes. It may also serve as a basis for hypothesizing potential mechanisms to explain the evolution of the phlegethontiid condition from more basal aïstopods.

Locality Information and Geologic Context

Mazon Creek, from the Westphalian C-D boundary (Peppers, 1996), is one of the richest and most extensively studied fossil localities of the Paleozoic. Fossils are preserved in nodules found within the beds of the Mazon and surrounding creeks and in

the spoil heaps of coal mines in the area. A recent review of the locality and history of fossil collection may be found in Shabica and Hay (1997).

The fossil bearing stratum is the Francis Creek Shale within the Lower Carbondale Formation. Nodules are only found in the 3-5 meters overlying the Colchester No. 2 coal seam (Baird, 1997 a). The facies is interpreted as estuarine and coastal coal swamps grading into marine (Baird, 1997 c). Two distinct faunae are recognized: the nearshore (with terrestrial erratics) Braidwood Fauna and the deeper marine Essex fauna (Richardson and Johnson, 1971; Baird, et al. 1985, 1986; Baird, 1997 b).

The specimen in question was found in March, 1953, by the late Mrs. Priscilla Turnbull, while collecting with her husband, Dr. William Turnbull of the Field Museum of Natural History, on the spoil heaps around Pit 11. It was found weathered apart, but remained reasonably well preserved.

MATERIALS AND METHODS

Abbreviations

Institutional—AMNH, American Museum of Natural History; BM, The Natural History Museum (formerly the British Museum (Natural History)); CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; NMW, Naturhistorisches Museum Wien; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

Anatomical—ap, anterior process of the rib; ang, angular; art, articular; bo, basioccipital; cp, costal process of rib; d, dentary; eo, exoccipital; ep, epipterygoid portion of palatoquadrate; exn, external naris; j, jugal; m, maxilla; n, nasal; ns, neural spine; op, odontoid process of the atlas; orb, orbit; p, parietal; parf, parietal foramen; pe, pectoral element; pf, postfrontal; pm, premaxilla; po, postorbital; pop, posterior process of rib; pof, proötic foramen for passage of Vth cranial nerve; pp, postparietal; pq, palatoquadrate; ps, parasphenoid; q, quadrate condyle; qj, quadratojugal; rp, retroarticular process; sa, surangular; sq, squamosal; st, supratemporal; t, tabular; tub, tuberculum; v, vomer.

SYSTEMATIC PALEONTOLOGY

Tetrapoda Goodrich, 1930

Lepospondyli Zittel, 1888

Aïstopoda Mial, 1875

Pseudophlegethontia gen. nov.

Diagnosis—Aïstopod with pointed snout; no lower temporal bar; skull table consisting of postorbital, frontal, parietal, postparietal, tabular, supratemporal, squamosal found as suturally attached units; quadrates well anterior of the occiput; elongate postorbital and frontal; zone of mobility between squamosal and quadratojugal; large postparietals and tabulars, odontoid process on atlas reduced to a small nubbin within anterior central rim; dorsal osteoderms absent; thin elongate gastralria; 140 vertebrae.

Pseudophlegethontia turnbullorum sp. nov.

Holotype—FMNH PR 281; only known specimen.

Etymology—"The Turnbills' False *Phlegethontia*;" in honor of the co-discoverers and original describers, and the nomenclatural history of the specimen.

Type Locality—Spoil heaps at Pit 11, Wilmington Township, Will County, Illinois

Horizon—Francis Creek member, Lower Carbondale Formation, directly above Colchester (No. 2) Coal, lower Westphalian D.

Diagnosis—As for genus.

Description—Skull

FMNH PR 281 consists of part and counterpart of a nodule. One hundred forty vertebrae are preserved in articulation, representing the entire column (Fig. 1).

Weathering has destroyed much of the palate and fine details of the first 30 vertebrae.

The anterior portion of the dorsal skull is still within the matrix; further preparation was impossible without risking damage. There seems to be very little displacement of elements in the specimen, suggesting that the specimen was rapidly buried.

The skull is diamond shaped in dorsal view (Fig. 1 B). The mandibles come together at a point, as in phlegethontids (Chapter 2), rather than forming a blunt snout, characteristic of ophiderpetontids (Carroll, 1998a). The right side is displaced ventrally and somewhat anteriorly. The postorbital skull roof, cheek, palatoquadrate, and lower jaw were accessible for study from latex peels. The remainder of the skull is hidden by matrix except for what can be seen with x-ray photographs.

Frontals, postorbitals, parietals, supratemporals, postparietals, tabulars, squamosals, and quadratojugals are present. There is no dermal ornamentation. Sutures are well defined, simple and deep, suggesting that they are still open. The skull roof maintains its height above the epipterygoids but has collapsed to the level of the vertebrae posterior to the quadrates, which suggests that the rest of the braincase was poorly ossified. This supposition is substantiated by the lack of solidly ossified otic capsules. The condition of the skull is consistent with immaturity.

Only the posterior portion of what must have been a very long frontal remains. It ends in a point lateral to the parietal foramen. The frontal is bounded laterally by the postorbital, which is also a long element. Although the anterior extent of the postorbital is unknown, it reaches posteriorly beyond the parietal foramen to the suspensorium. It forms much of the lateral margin of the preserved skull table, and extends posteriorly about three-quarters the length of the parietal, where it meets the squamosal. The squamosal is supported anteriorly and ventrally by a slight ventral flange of the postorbital, which, along with the attached squamosal, has been displaced medially and rotated laterally (Fig. 1 B). The parietal is paired, comes to a point on the midline anteriorly and posteriorly, and is waisted posterior to the parietal foramen. The supratemporal spans the distance from the tabular posteriorly to the lateralmost portion of the parietal where it contacts the frontal. This contact prevented an articulation between the postorbital and parietal. The postparietal is large, nearly as long as the parietal, and with its counterpart are as wide as the more anterior skull table. It receives the posterior median apex of the parietals anteriorly, and comes to a point on the posterior midline that projects posteriorly over the occiput. The tabular is almost as long as the postparietal. It

curves laterally to surround the braincase, and overlaps the postparietal. An anterior recess receives the rounded posterior border of the supratemporal.

The narrow anterodorsal process of the squamosal inserts into the postorbital. Dorsally, the squamosal articulates with the supratemporal and, less certainly, the tabular. It descends to meet the quadratojugal in a simple butt joint, which is disarticulated (Fig. 2). It is uncertain whether this articulation was part of a kinetic system, or if it is due to immaturity. The quadratojugal is triangular. The base lies ventrally along, but not participating in, the articular surface of the quadrate. It fits within a depression on the quadrate's lateral surface. The ascending process articulates with the squamosal obliquely, but its precise nature is obscured by disarticulation.

Additional information comes from the X-ray photographs taken by Turnbull and Turnbull (1955; Plate 9 reproduced as Fig. 3). The general outline of the missing anterior skull roof is shown, revealing the location of the external nares. The anteriormost bones, the premaxilla or nasal, show a median suture. The postfrontal and dorsal portion of the jugal are also visible, defining the position and size of the orbit, which closely resembles that of *Phlegethontia* in being large and only slightly anterior of the mid portion of the skull, rather than far anterior and somewhat smaller as in ophiderpetontids. The "sclerotic ring" of Turnbull and Turnbull is probably the product of photo retouching (W. Turnbull, pers. comm.).

The palatoquadrate is a well-ossified bone. Lund (1978) and Gallup (1983) have called this bone in other aïstopods the "pterygoquadrate" because the palatine is not incorporated. Carroll (1998a) identified it as a palatoquadrate due to its similarity to the structure of that name in *Eustenopteron*. As in other aïstopods, it has three regions that

will be considered separately for ease of communication: the quadrate condyle, epipterygoid, and palatal ramus of the pterygoid. The palatal ramus runs parallel to the braincase and the cultriform process of the parasphenoid (Fig. 1 B) forming the lateral border of an elongate, slit-like interpterygoid vacuity, which are preserved as far anteriorly as the orbits. More posteriorly, the lateral edge of the palatal ramus flares laterally up to the level of the parietal foramen, where it achieves its widest dimension, and then it rapidly returns medially and rises as the epipterygoid. The epipterygoid (Fig. 2) does not show its entire lateral surface, probably due to weathering. Its anterior edge, where it descends onto the palatal ramus without a suture, and the posterior edge where it extends into the quadrate ramus are all that are clearly shown. A large, faint depression that might be the foramen for the trigeminal nerve (V). If so the epipterygoid does not fully enclose it; at least the dorsal margin is not bordered by the epipterygoid, as it is in *Phlegethontia*.

The quadrate ramus extends laterally to the quadrate condyle slightly further than in *Phlegethontia*. The condyle is broken from the quadrate ramus on both sides, but the breaks are not in the same position and do not seem to be loose sutures. The quadrate condyles are placed anterior to the otic capsules, similar to its position in *Phlegethontia*.

Resolution in the area of the braincase is poor; nonetheless some features may be seen. The lateral, high-sided walls seem to be approaching an anteriorly keeled sphenethmoid above the cultriform process as in *Phlegethontia*, although it is insufficiently preserved to be certain. Other than the possible trigeminal foramen, no other foramina are preserved. The occiput is obscured by the postparietals and tabulars dorsally, the parasphenoid ventrally, and the atlas posteriorly.

Ventrally, the basal plate of the parasphenoid is incompletely ossified; there are no basipterygoid processes, and it has not coossified with the basioccipital (Fig. 4). The otic capsules are incompletely ossified, and the stapes is not preserved. Exoccipitals are present lateral to the atlas odontoid process but are too fragmentary to discuss in detail. The parasphenoid plunges into the matrix so that the concave cultriform process is visible only in dorsal view. It is broken anteriorly so its full extent is unknown, but it probably continued some distance since it is still relatively wide at the break. Of the remainder of the palate nothing is preserved except two tooth-bearing bones visible near the jaw's symphysis in dorsal view. They are disarticulated and flipped horizontally so their tooth cusps are pointed dorsally. These may be the vomers or premaxillae. If they are vomers, they form the entire anterior margin of the choana.

The lower jaw is comprised of multiple ossifications posteriorly as in ophiderpetontids (Carroll, 1998) but a single large anterior ossification resembling that of phlegethontiids (McGinnis, 1967; Chapter 2). The articular is grooved transversely and slightly obliquely to receive the widened quadrate. The articular is set at a 15° angle to the long axis of the jaw. Beneath the articular lie the surangular and angular, although the lateral surface is not well exposed. The surangular contacts the entire ventral border of the articular, and extends anteriorly a little less than one-third the length of the mandible. The angular forms the ventral margin of the posterior jaw. It extends about half the length of the jaw. Posteriorly, it forms a short triangular retroarticular process (Fig. 1 B). The remainder of the jaw is composed of the dentary. Near the symphysis, three nutrient foramina can be seen in ventral view on the lateral surface of the dentary. The dentary bears about 30 short, tightly packed, conical teeth. They are equal in length throughout

the series except for the occasional replacement tooth, and are present along nearly the entire length of the dentary. Teeth are ankylosed to the dentary, and where broken show the remnant of the pulp cavity that gives a superficial resemblance to a tooth socket.

Postcranial Skeleton

One hundred forty vertebrae are in articulation, representing the entire vertebral column (Fig. 1 A). The nodule was found split, leaving the fossil exposed to weathering. The anterior most 30 vertebrae have suffered the most degradation. Fine details, including rib head morphology, is likewise obscured.

The vertebral configuration is typical of aïstopods. They have elongate, cylindrical centra indistinguishably fused with the neural arches. Centra are deeply amphicoelous and hourglass shaped due to waisting that constricts the notochord (Fig. 4). The ventral surface of the centrum is slightly keeled, although this is lost in some due to weathering. The anterior central articulation is slightly smaller in diameter than the posterior articulation of the preceding vertebra, which the anterior fits into when they are closely articulated. Transverse processes are prominent but not as laterally extended as in *Phlegethontia*. They have two robust cylindrical axes except on the first seven to nine vertebrae (Fig. 6). The diapophysis on the bipartite transverse process is dorsal and posterior to the ventral portion of the transverse process, which presumably used to bear a parapophysis (which usually occupies this area), although ribs are single headed. The diapophysis is also more laterally directed, but this is relative since both portions of the transverse process are directed anteriorly in most vertebrae. Neural spines are low along the length of the arch, and there is an indentation between the postzygopophyses that

forms a notch in the posterior margin of the neural arch, as in *Phlegethontia*. The zygopophysis forms the lateralmost portion of the neural arch, excepting the transverse process. No neural arches bear clear articulations accessory to the zygopophyses. At least 86 vertebrae bear ribs, and the 54 terminal vertebrae are ribless, which is a shorter region than the approximately 100 ribless caudal vertebrae of *Phlegethontia* (Chapter 2).

The atlas is found tightly wedged between the exocipitals (Fig. 4). It has a narrow, keeled centrum. It is longer than the succeeding several vertebrae. On its anterior surface it bears an odontoid process. Unlike the odontoid process found in *Phlegethontia* or *Oestocephalus* (Chapters 2 and 3), it does not form as a narrowed anterior continuation of the centrum. Instead, it is a small, median structure that lies above the rim of the anterior centrum, in a position similar to what might be expected of a displaced atlas intercentrum. Transverse processes are attached on the mid portion of the vertebra, and project laterally.

The second vertebra is similar to the succeeding three except for its lack of ribs. Its centrum is about 15% shorter than the length of the atlas centrum, but is equal in length to the third. It is ventrally keeled and its single transverse process is placed medially and projects laterally.

Several bone fragments lateral to the atlas and second vertebrae on the left side of the specimen (Fig. 4) may be seen in ventral view. These are taken to be fragments from the skull and parts of the remainder of the pectoral girdle; however, part could represent a proatlas.

The third, fourth and fifth vertebrae are very similar. They all bear ribs, and have simple laterally projecting transverse processes that are placed midway on the length of

on the neural arch pedicle. The transverse process on the sixth vertebra maintains a lateral projection, but the base of the transverse process begins to shift anteriorly. The transverse processes on the seventh and eighth show a slight (about 13°) anterior inclination (Fig. 6). By the 11th vertebra the inclination has reached 20°, and the transverse process gains its doubled appearance. This configuration is maintained until ribs are lost.

The half of the nodule showing the ventral surface preserves 58 vertebrae. The whole column is preserved in dorsal view. The half showing the dorsal column had undergone previous preparation with a grinder to reveal the vertebrae that descended below the surface of the nodule, destroying the ventral view of the newly exposed vertebrae in the process. Aistopod caudal vertebrae are distinguished by having parallel ventral haemal flanges (Gregory, 1948; Zidek and Baird, 1978; Chapter 2) which are not present in any of the vertebrae retaining the a ventral surface, meaning all are precaudal vertebrae. *Phlegethontia* has 64 precaudal vertebrae, and *Pseudophlegethontia* may have a comparable number.

Vertebral size is roughly the same (1.1-1.2 mm central length) from the atlas to the 20th vertebra. Dimensions then increase to about the 57th, where the largest size is achieved (1.5 mm). This size is maintained for the next ten vertebrae. There is a slight size decrease after the 70th vertebra, but size remains constant until the region of the last preserved rib, around the 88th-94th vertebra, after which size begins gradual tapering until the final centrum, which is only 0.5mm in length. Transverse processes maintain their full lateral span until the 94th vertebra, and then are rapidly reduced. Ribs may have been present until this point.

Ribs are not well preserved. They have the characteristic “k-shape” formed by the tuberculum, anterior (costal) process, and posterior process (posteriomedial process of Baird, 1964 and McGinnis, 1967; Fig. 7). Modern apodous squamates also have accessory rib processes, which serve as insertion points for muscles and ligaments that attach the rib to the vertebrae, and via differentiated medial muscles, to other ribs (Hoffstetter and Gasc, 1969), although the posterior processes in squamates tends to be at the rib head, rather than down the shaft as in aïstopods. What is troubling is the presence of the bipartite transverse process. Where clearly shown, the ribs are associated with the dorsal of the two columns (the diapophysis), at the tuberculum. If the rib is oriented so that both the tuberculum and anterior process are in contact with the transverse process, the posterior process would project dorsally and the main rib shaft laterally. The interpretation of the rib head as singular produces a more natural configuration, resembling the posteriorly directed vertebrae of caecilians (pers. obs. of *Typhlonectes natans*), and is consistent with the rib head morphology seen in modern apodous terrestrial vertebrates (Hoffstetter and Gasc, 1969).

Long posterior processes are present to at least the 57th vertebra, where the ventral surface of the column is lost. Unfortunately the dorsal view of the specimen does not clearly display the ribs. However, long posterior processes are present equally far posteriorly in ophiderpetontids (Chapter 3), while in phlegethontiids they are limited to the first 6 bearing vertebrae (McGinnis, 1967; Chapter 2). *Pseudophlegethontia* follows the ophiderpetontid body plan in this regard.

Pectoral remnants are not preserved in their entirety, but a portion of one seems to be present lateral to the third vertebra. The identification of the sinusoidal elements in

aïstopods as pectoral is somewhat controversial (Hook, 2000). Gregory (1948), Baird (1964), and McGinnis (1967) identified them as hyoid elements. However, as argued Chapter 1, they are always found in the region of vertebrae 3-6, lateral to the ribs; in no modern amphibian are the hyoids found that far posteriorly (Duellman and Trueb, 1986). In size, shape, and orientation, these elements resemble the cleithra or a fusion of the cleithra and clavicles of other lepospondyls (Carroll, 1998a, b; Chapters 2, 3).

Aïstopods have two types of dermal ossifications: elongate ventral gastralialia and diamond shaped to circular dorsal osteoderms. Ophiderpetontids are the most highly ossified, with thick ventral armor arranged in a chevron pattern with the apex pointed cranially, and closely packed dorsal osteoderms that extend into the cheek region of the skull (Chapter 3). Phlegethontiids, on the other hand, are much more lightly ossified (Chapter 2). They retain no dorsal osteoderms, and their ventral scalation is reduced to thin, fine bones that are less densely packed. *Pseudophlegethontia* has phlegethontioid style gastralialia and no osteoderms (Fig. 8). Bones at the apex meet either end to end or with one side comprising the whole apex and the other butting against it, but there is no noticeable pattern of one side or the other being more likely to occupy the apex.

DISCUSSION

Pseudophlegethontia displays many of the derived characters found in *Phlegethontia* but less fully expressed. The skull roof is less well ossified than the ophiderpetontid condition, but has not lost all of the bones absent in *Phlegethontia*. The frontals are elongate, although seemingly not fused as in *Phlegethontia*, and two posterior projections approach the parietal foramen presaging the enwrapped foramen of the

phlegethontiid skull roof (Chapter 2). Ophiderpetontids also have frontals with posterior projections into the parietals, but the frontals remain quite distant from the parietal foramen, as is the primitive condition (Carroll, 1998a; Chapter 3). The jaw has reduced the number of ossifications compared with *Oestocephalus*, since *Pseudophlegethontia* seems to lack a splenial. A large dentary occupying the anterior portion of the jaw is a derived character shared with *Phlegethontia*, but the retention of several postdentary bones is plesiomorphic. However, the area once occupied by the splenial is now filled by the dentary, while in *Phlegethontia* it is incorporated into the posterior element (McGinnis, 1967; Chapter 2) so the large anterior dentary might be convergent.

The transitional nature of *Pseudophlegethontia* is more evident in the postcrania. Preliminary phylogenetic analysis places *Pseudophlegethontia* between *Oestocephalus* and *Phlegethontia*. This implies an increase in vertebral counts within the Aïstopoda. The precaudal count increases slightly within the group, from fewer than 60 in *Oestocephalus*, to 64 in *Phlegethontia* (no count is available for *Pseudophlegethontia*). The total number of rib bearing vertebrae increases a bit more substantially, from 70 in *Oestocephalus* to 85-88 in *Phlegethontia* and *Pseudophlegethontia*. This means that 10-20 caudal vertebrae bear ribs, which contrasts with the number of rib bearing vertebrae in other lepospondyls of 5 or fewer (Chapter 1). Extant snakes do not bear free ribs on their caudal vertebrae, although some fossil forms do (Hoffstetter and Gasc, 1969). More strikingly, the number of rib free caudal vertebrae increase from 38 in *Osetocephalus*, to 52 in *Pseudophlegethontia*, to 100-160 in *Phlegethontia*. Elongation in aïstopods is primarily driven by an increase in numbers of caudal vertebrae, mostly posterior of the rib-bearing region.

This phyletic increase in the number of caudal vertebrae stands in contrast with the pattern of elongation in serpents. Cohn and Tickle (1999) examined the pattern of expression of HoxB5, HoxC6, and HoxC8, all previously identified as important for axial patterning, in the developing python. They found that the expression domains of these genes had migrated from the thoracic region cranially to the atlas and caudally to the pelvis, effectively converting the body into an elongate thorax. The authors hypothesized that this is the reason for the loss of the forelimb, because the chemical signal to specify the location for the formation of the limb bud is not delivered due to the region's new "identity" as a flank. The specification of hind limb seems unaffected since the expression domains terminate at or above the location of the hindlimb, but development of the apical ectodermal ridge never occurs, leaving a severely truncated limb.

Aïstopods have elongated their body in a different manner. The vertebral column retains regionalization that is absent in snakes. The anterior two vertebrae are ribless, contrasting with the single rib free atlas of snakes. The transverse processes gradually shift position and orientation along the column. There is first a gradual increase in the length of the centrum and a subsequent decrease of size, while snakes have a vertebral column with repeated identity of morphology. The snake tail is always shorter than the trunk, although some groups have relatively high numbers of caudal vertebrae (Hoffstetter and Gasc, 1969). Finally, aïstopods retain portions of the pectoral girdle (as do other elongate limbless lepospondyls such as adelospondylids, and the amphisbaenid *Bipes*). This suggests repeated somitomere subdivision throughout the column, but primarily focused in the caudal region, without a change in the expression domains of regulatory genes specifying flank identity. Serpents, with their shorter tails, seem to

restrict the areas where vertebrae may be added to the precaudal region. Amphisbaenids (Hoffstetter and Gasc, 1969) and caecilians (Taylor, 1964) have extremely short tails. Of extant limbless taxa, aïstopods are most closely resembled by the limbless anguid lizard *Ophisaurus*, which has 54 presacral and 90-100 caudal vertebrae (Hoffstetter and Gasc, 1969). Further insight into possible developmental mechanisms underlying aïstopod elongation awaits the genetic characterization of this squamate.

The pattern that emerges within the aïstopod lineage, incorporating the new information from *Pseudophlegethontia*, is consistent with ontogenetic trends within phlegethontiids proper and suggests that heterochrony played a role in the origin of the derived phlegethontiids, if not aïstopods as a whole. Gould (1977) observed that changes in the timing of different developmental features is a system specific event, with respect to a reference point provided by phylogeny, so different systems may have different patterns of heterochrony. In a single organism, one system may be neotenic, for example, while another may display hypermorphosis.

In Chapter 2, I described a pattern in phlegethontiids in which endochondral ossification is accelerated while dermal components of the skeleton are delayed until later in ontogeny. At extremely small sizes, the braincase is fully ossified, but the full complement of dermal skull bones is not ossified until much larger size is achieved. The extent of skull ossification is reduced; the jaw already has only a single anterior ossification, in common with *Phlegethontia*. *Oestocephalus* itself, although it possesses a complete skull roof (like all lepospondyls it lacks an intertemporal), has a reduced number of ossifications (only one splenial), the extent of those ossifications (e.g., the open cheek) but more fully ossified vertebrae than any possible “labyrinthodont”

precursor. *Phlegethontia*, in contrast, has apparently incorporated most of the posterior dermal skull (parietal, postparietal, tabular, supratemporal, parasphenoid, etc.) into its unitary, co-ossified braincase. Ophiderpetontids have extensive dorsal and ventral dermal armor similar to many “labyrinthodonts” (e.g. *Greererpeton*; Godfrey, 1989), while *Pseudophlegethontia* and phlegethontiids lack the dorsal osteroderms, and the ventral gastralia are reduced to very slender bony rods. Although a juvenile, *Pseudophlegethontia* is already twice the size at which ophiderpetontids fully ossify their dorsal dermal ossicles, so they are not missing because of immaturity.

What seems to be occurring within aïstopods is a delay in the ossification of dermal bone, and a hyperossification of bones of endochondral origin. Hanken (1983) has observed in modern taxa that hyperossification is often accompanied by reduced ossification elsewhere in the body, which aptly describes the pattern seen within aïstopods.

Pseudophlegethontia also provides evidence for a double headed origin of the single headed aïstopod rib. It retains remnants of a parapophysis despite its having a single headed rib articulation with the transverse process. This means that the anterior process may be a displaced capitulum (contra Baird, 1964 and subsequent authors) that has been co-opted for another function (see Chapters 2 and 3 for further discussion). In the ophiderpetontid *Coloraderpeton*, a single transverse process bears two distinct facets (Vaughn, 1969); however, the ribs probably articulate with a single head, as in all other aïstopods (Chapter 3). *Lethiscus* has been described as having double headed ribs (Wellstead, 1982), but a rib found in articulation with the transverse process suggests that it too has an anterior costal process (Chapter 5). Despite the atavistic appearance of a

parapophysis in *Pseudophlegethontia*, the actual presence of double headed ribs predates any known aïstopod.

Phylogeny

The in group relationships of aïstopods will be specifically addressed in Chapter 5. Preliminary phylogenetic analysis places *Pseudophlegethontia* as out group to *Phlegethontia*, with *Oestocephalus*, *Ophiderpeton* and *Lethiscus* as successively more distant plesions. If this topology is correct, then the Ophiderpetontidae is not a monophyletic group, however the taxonomic implications will not be considered further at present. It is clear that there is a close association between *Phlegethontia* and *Pseudophlegethontia*. Furthermore, *Pseudophlegethontia* bridges the morphologic gap that existed between the two main morphotypes of aïstopods.

Most localities where aïstopods are found (Nýřany, Linton and Five Points, Mazon, Jarrow, Swisshelm Mountains) have two genera present: an ophiderpetontid and a phlegethontiid. Linton has three species with *Oestocephalus* and two phlegethontiids, *Phlegethontia longissima* and *P. linearis*, but these are morphologically very similar species. Mazon Creek is unique in having three clearly distinct forms, but each is a rare occurrence (amphibians represent 0.004% of total fossils from the Essex fauna which predominates the locality where this specimen was found; Baird and Anderson, 1997), suggesting that they are being washed into the Essex fauna from land (Baird et al., 1985, 1986). (Milner, 1980) has suggested that aïstopods are terrestrial erratics based upon their low prevalence in the preserved fauna at Nýřany. They do not have lateral line canal grooves which are present in many undoubtedly aquatic lepospondyls like diplocaulid

nectrideans (Bossy and Milner, 1998) and the microsauro *Microbrachis* (Carroll and Gaskill, 1978). They do not seem particularly well adapted for a fossorial habitus with their large orbits and high-sided tropibasic skulls. However, they do share a massively ossified braincase and large, plate like stapes with modern fossorial vertebrates like caecilians and amphisbaenids. Aïstopods probably spent their time rooting about for invertebrates in the lush leaf litter within the Carboniferous coal swamps surrounding the oxbow lakes (Hook and Baird, 1986, 1988) and estuaries (Baird et al, 1985a, b, 1986) of the Pennsylvanian.

CONCLUSIONS

Pseudophlegethontia turnbullorum is a distinct new taxon of aïstopod that shares characters with both ophiderpetontids and phlegethontiids. It has a pointed snout, reduced dermal scalation, and open temple without a lower temporal bar. It bridges the morphological gap between two very different, although clearly related, elongate limbless tetrapods. This is especially important because of the phylogenetic problems posed by the elongate, limbless morphotype (Chapter 1). Because of functional convergence and strong character correlation, limbless tetrapods tend to cluster in phylogenetic analyses with strong bootstrap and Bremer support values, seemingly forming well supported clades. These instances of “long branch attraction” are only broken down by adding the relevant plesiomorphic taxa; differential weighting schemes do not seem to be effective (Lee, 1998). Fortunately, *Pseudophlegethontia* is such a plesiomorphic taxon, providing insight into the relationships among aïstopod groups.

ACKNOWLEDGEMENTS

I would like to thank John Bolt for kindly providing desk space and a microscope during my visit to the Field Museum of Natural History to review the collection of Mazon Creek nodules. I thank William Simpson and the late Steve McCarroll for filling my loan request during the hectic period surrounding the SVP meetings of October, 1997. Access to additional specimens was provided by Don Baird, David Berman, and Mary Dawson of the Carnegie Museum of Natural History; Gene Gaffney and Charlotte Hotton of the American Museum of Natural History; and Farrish Jenkins, Chuck Schaff, and Bill Amarault of the Museum of Comparative Zoology. Previous drafts of the manuscript were improved by review by Robert Carroll, Robert Holmes, and David Green. This study was supported by the Natural Sciences and Engineering Research Council of Canada.

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FIGURE 1. *Pseudophlegethontia turnbullorum*, n. gen. et sp. FMNH PR 281. A. Entire specimen in dorsal view. B. Close-up of the dorsal skull roof. Scale bar for A equals 4 mm, B equals 10 mm.

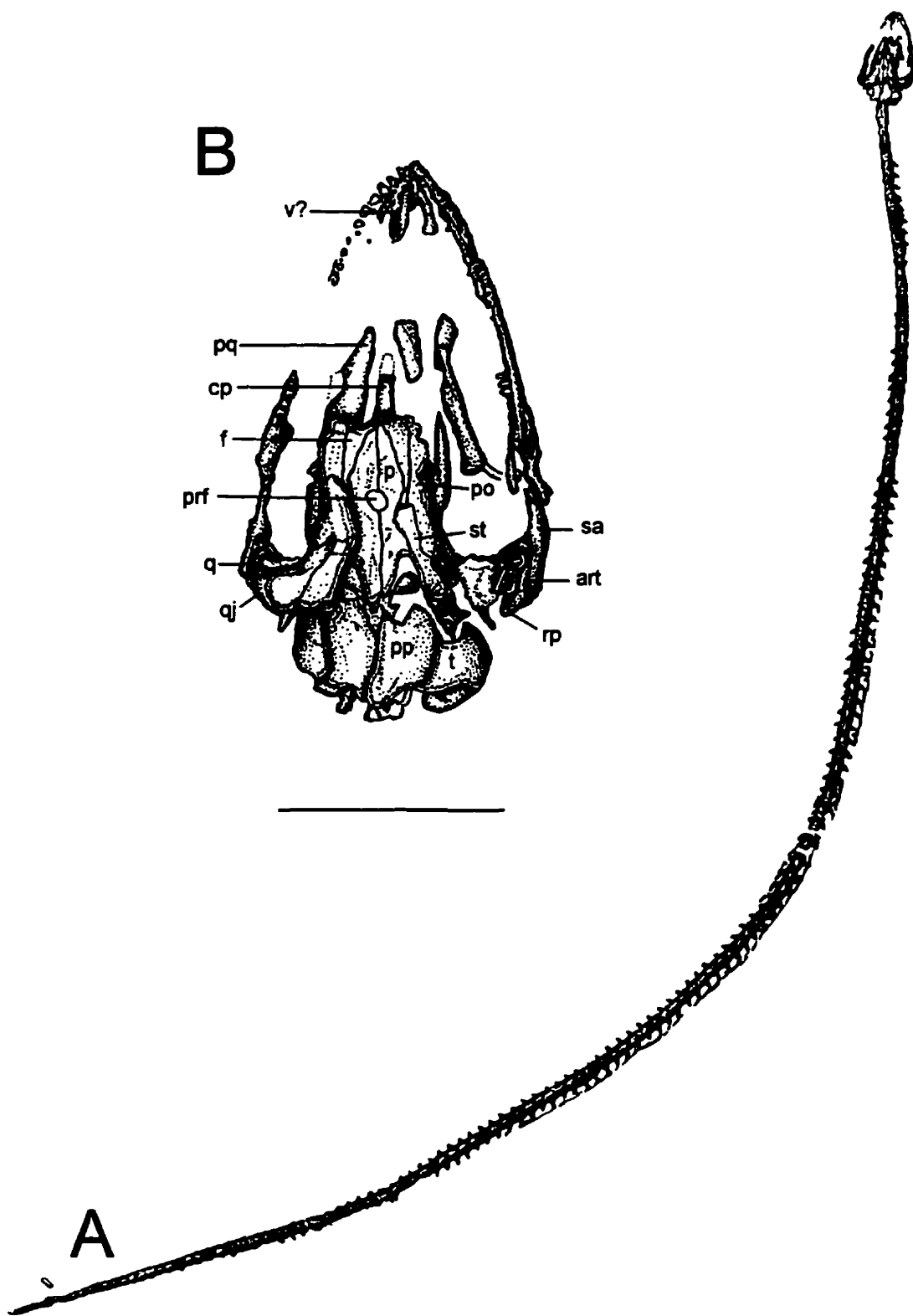




FIGURE 2. Oblique left lateral view of the suspensorium and braincase. The quadrate condyle has broken off the quadrate ramus of the palatoquadrate and became rostrally displaced. Resolution is lost in the central portion of the epipterygoid. Scale bar equals 2 mm.

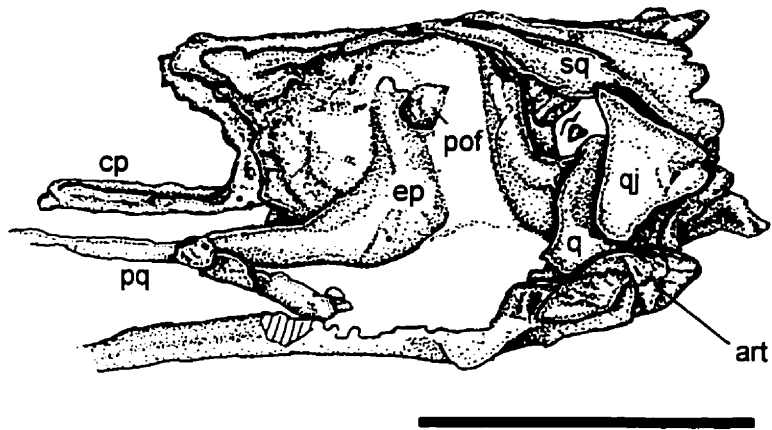


FIGURE 3. X-ray photograph of the holotype nodule in dorsal view. From Turnbull and Turnbull, 1955.



FIGURE 4. Ventral view of the skull and anterior vertebrae. Scale bar equals 4 mm.

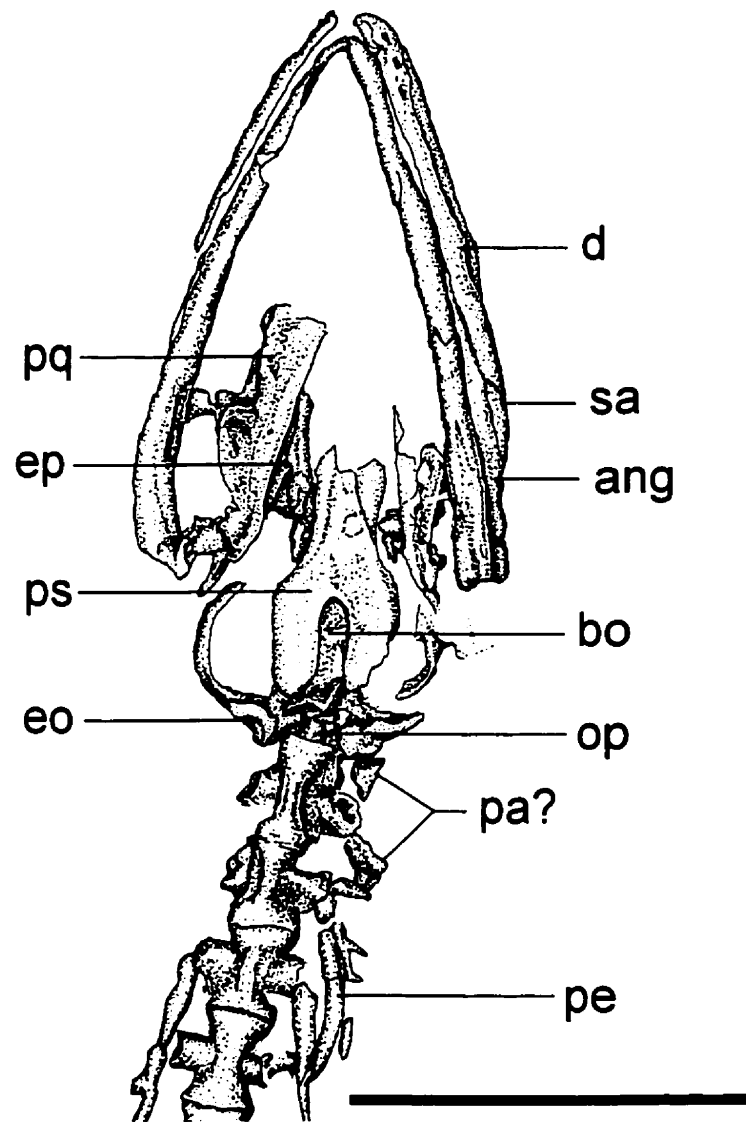


FIGURE 5. Reconstruction of the dorsal skull roof.

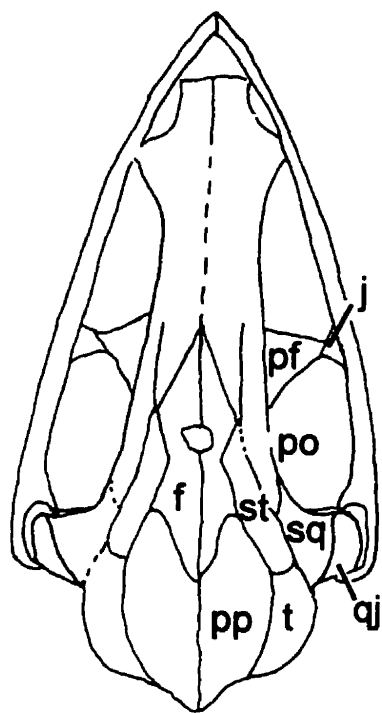


FIGURE 6. Ventral view of the vertebral column, showing progressive changes in location and orientation of the transverse processes. Scale bar equals 5 mm.

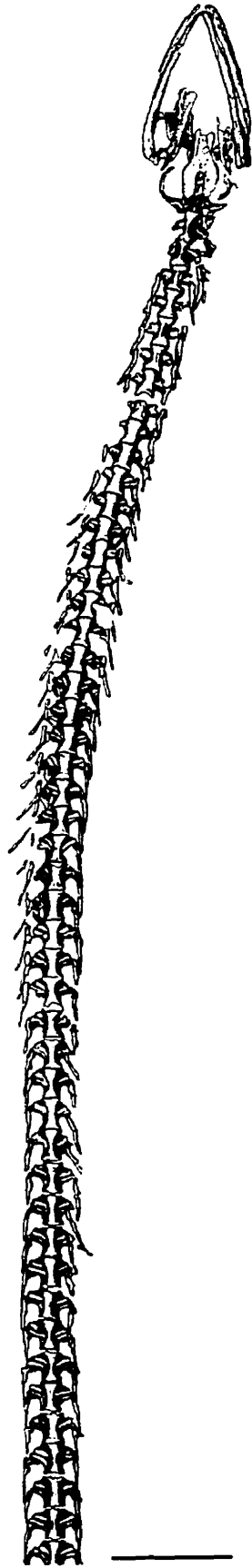


FIGURE 7. Right lateral view of mid dorsal ribs, showing the characteristic “k-shape” common in Pennsylvanian aïstopods. Scale bar equals 1 mm.

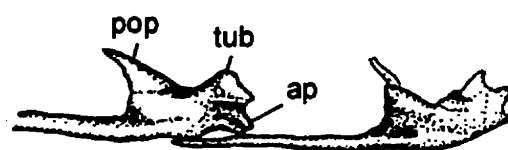


FIGURE 8. Ventral view of mid dorsal vertebrae and gastralia. Anterior is to the top of the page.



CHAPTER 5

NEW INFORMATION ON *LETHISCUS STOCKI*
(TETRAPODA, LEPOSPONDYLI, AĬSTOPODA) FROM
HIGH RESOLUTION COMPUTERIZED
TOMOGRAPHY AND A PHYLOGENETIC
CLASSIFICATION OF AĬSTOPODA

To be submitted as: Jason S. Anderson, Robert L. Carroll, and Tim Rowe. New information on *Lethiscus stocki* (Tetrapoda, Lepospondyli, Aĭstopoda) from high resolution computerized tomography and a Phylogenetic Classification of Aĭstopoda. Prepared for Paleontologica Electronica.

PREAMBLE CHAPTER 5

The information gathered from all of the relatively complete aistopods is vital to the interpretation of less complete forms. *Lethiscus stocki*, the oldest known specimen attributed to this order, is known from only a single, fragmentary specimen. Bone is only visible in broken sections, which commonly pass through the bone itself. Mechanical or chemical preparation would be very difficult, and destructive forms of study (i.e. serial sectioning) are not desirable given the unique nature of the fossil. High resolution computerized tomography provides x-ray slices that can be reassembled and otherwise manipulated using the computer. This chapter presents the results from the application of this technology to *Lethiscus*. It also includes a phylogenetic analysis of the interrelationships of all aistopods, and concludes with a new classification of the group following the principles of Phylogenetic Taxonomy.

ABSTRACT

High power computerized tomography provides an alternative to serial sectioning and other destructive forms of studying fossils. This technology was used to study the oldest, and presumably most basal, aïstopod *Lethiscus stocki*. It is found to have approximately 30 closely spaced teeth on its maxilla and dentary, a short vomer, a palatine running nearly the entire length of the maxilla that is toothed at least posteriorly, and a choana that is located at the premaxilla-maxilla suture. Its has a high articular facet for the quadrate condyle, a lateral masseteric fossa, and a sutural pattern of the lower jaw that closely resemble that of *Oestocephalus*.

All aïstopods were coded and analysed using parsimony. Two most parsimonious trees were found, differing in the arrangement of the outgroup taxa. *Phlegethontia* and *Pseudophlegethonita* are found to be sister taxa to *Coloraderpeton* and *Oestocephalus*, with *Ophiderpeton* and *Lethiscus* as successively more distant taxa. A node-stem triplet was placed at the crown dichotomy, producing new taxa Phlegethontimorpha (stem-based definition), Oestocephalia (stem-based taxon), and Aïstopodia (node based taxon). Aïstopoda is redefined as a stem based taxon.

INTRODUCTION

In a series of papers, Carroll (1998a) and I (Chapters 2, 3, and 4) have reconsidered a group of elongate, limbless Paleozoic tetrapods known as aïstopods, in light of newly available, nearly complete specimens from Nýřany, Czech Republic and Mazon Creek, Illinois. Aïstopods have highly fenestrate skulls, a fused pterygoid, epipterygoid and quadrate forming a palatoquadrate, approximately 60-65 precaudal vertebrae and up to 230-250 vertebrae total. Their vertebrae are distinct in having a single, spool-shaped centrum fused indistinguishably with the neural arch at extremely small size and a spinal nerve foramen just posterior to the transverse process (except for the atlas of *Oestocephalus*). They are part of a larger monophyletic assemblage of tetrapods called Lepospondyli that share: simple, spool-shaped centra; loss of the intertemporal, squamosal notch, atlas intercentrum and labyrinthodont in-folding of the dentine; and an odontoid process on the atlas (Chapter 1).

Aïstopods have been traditionally divided into two families, Ophiderpetontidae and Phlegethontiidae, with a third, Lethiscidae, added recently (Wellstead, 1982). “Ophiderpetontids” have blunt snouts, orbits placed well anterior to the midlength of the skull, ventrally open temporal fenestra, and thick dermal scalation with tightly packed ventral gastralia and trapezoidal to circular dorsal osteoderms (Baird, 1964; Milner, 1994; Carroll, 1998a, b; Chapter 3). Dorsal osteoderms also cover the temporal fenestra of “ophiderpetontids”. “Ophiderpetontids” have the jaw articulation posterior to the occiput. *Oestocephalus*, a subgroup of “ophiderpetontid”, has “k-shaped” ribs, with a tuberculum, costal and posterior process forming the arms of the “k,” as far back on the vertebral

column as can be determined. Phlegethontiids are characterized by narrow snouts, large orbits just anterior to the midlength of the skull, retention of a lower temporal arch, quadrate condyles anterior to the occiput, and thin gastralia but no dorsal osteoderms (Gregory, 1948; Baird, 1964; McGinnis, 1967; Chapter 2). Phlegethontiids have distinct “k-shaped” ribs until the 6th or 7th rib, at which point the posterior process becomes reduced to a tiny remnant. Both have sickle-shaped remnants of the pectoral girdle, possibly the cleithrum (Carroll, 1998b) or fused clavicle and cleithrum (Chapters 2 and 3), located in the region of vertebrae 3-5.

Anderson (Chapter 4) described a new species of aïstopod that shows morphology intermediate to the “ophiderpetontid” and phlegethontiid conditions. In common with phlegethontiids it has a pointed snout, orbits just anterior to the middle of the skull, quadrate condyles anterior to the occiput, thin gastralia and no dorsal osteoderms, despite being larger than the size at which they are known to thickly cover “ophiderpetontids” (Chapter 3). However, it has no lower temporal arch, a skull table with separate, sutured elements, and large posterior processes of the rib at least to the 57th vertebra, which are characters present in “ophiderpetontids”. Anderson (Chapter 4) did not place *Pseudophlegethontia* into either an existing or a new family, pending the present phylogenetic analysis.

Phylogenetic analysis of Aïstopoda requires consideration of *Lethiscus stocki*. It is from the Visean Wardie Shales of Scotland, which predates the deposits of Jarrow, Ireland, and East Kirkton, Scotland (Wellstead, 1982; Milner, 1994). It was known for a hundred years before the description of Wellstead, but was not studied because of the intractable nature of its matrix (Baird, 1964). It is preserved in a long, cylindrical, siderite

concretion that is split into many fragments throughout the preserved column of 78 vertebrae. The matrix is too hard to prepare, and since it is a unique specimen, attempting to etch away the bones and cast the resulting natural molds (Baird, 1955) is undesirable. Wellstead did a remarkable job with the information present; however, many of the states he described seem unusual for aïstopods. This specimen is important because, since it is the oldest, and presumably most basal, representative of Aïstopoda, it could potentially have combinations of plesiomorphic and apomorphic characters crucial to linking aïstopods with one of the many morphologically very different “labyrinthodont” clades.

High resolution computerized tomography (CT) has been increasingly employed by paleontologists to examine internal structures, or morphology at risk of destruction from conventional preparation (Rowe et al., 1999; Brochu, 2000). The type, and only, specimen of *Lethiscus* was brought to the High Resolution Computerized Tomography Facility at the University of Texas at Austin in November, 1998, for scanning. This facility operates a scanner that uses higher energy levels than conventional medical CT scanners, resolving extremely fine details (tens of microns in size). This paper presents the results of the CT scans, and incorporates this new information into a phylogenetic analysis of Aïstopoda, and concludes with the presentation of a new classification of this taxon.

Materials and Methods

MCZ 2185 was transported to the High Resolution CT Facility at the University of Texas at Austin. The scanning was performed by Dr. Richard Ketcham, assisted by

Dr. Matt Colbert, between November 25 and 27, 1998. Each portion of the specimen was suspended in florist foam to keep its position stable. All of the skull except for the dorsal fragment that preserves the mould of the internal skull roof were scanned, as were the vertebral sections #2 (containing vertebrae 5-7 and the putative pectoral elements/sarcopterygian scales), #22 (with vertebrae 53-5) and #24 (vertebrae 59-61). Part and counterpart of the vertebral sections were held together by elastic bands. Scanner settings were as follows for all pieces: II, 180 kV, 0.133 mA, 1 brass plate filter (1/16 inch), air wedge, 160% offset, slice thickness 0.190 mm, S.O.D. 81 mm, 1200 views, 2 samples per view, inter-slice spacing 0.144 mm, recon. offset 500, recon. scale 22. Fields of reconstruction were: 39 mm for the major skull fragment, 33 mm for the left rostrum fragment, 25 mm for vertebral piece #2 and 22, and 34 mm for # 24.

The raw CT data was prepared for processing using Adobe Photoshop 5 and Corel Photo-Paint 8. Resampling, analysis, and production of images and Quicktime movies was done using a MacIntosh PowerPC 7200/75 running OS 8.5 with 50 Megs of RAM and a 512 K level 2 cache, using NIH Image, freeware from the National Institutes of Health, the United States of America (<http://rsb.info.nih.gov/nih-image/about.html>).

Characters relevant to aïstopod systematics discovered through the course of my revision of this taxon (Chapters 2, 3, 4 and the above) were used to examine the ingroup relationships. The matrix included twenty-seven characters (16 cranial, 11 postcranial) and seven aïstopod taxa. Taxa included are: *Lethiscus stocki*, *Ophiderpeton* (a composite of *O. brownriggi* and *O. kirktonensis*), *Oestocephalus amphiuminus*, *Phlegethontia longissima*, *P. linearis*, and *Pseudophlegethontia turnbullorum*. All characters were binary except 25 and 26 (see Appendix 1), which were unordered, permitting direct

transformations between any two states. Missing data was indicated by a question mark, and inapplicable characters by a dash.

The phylogenetic analysis was performed on the same PowerPC. Data were inputted and manipulated using MacClade (Maddison and Maddison, 1992) upgraded to release 3.07 via the internet (<http://ag.arizona.edu/ENTO/macclade/macclade.html>; Maddison and Maddison, 1997). The matrix was analyzed using PAUP* 4.0b4a (Swofford, 1998), using the branch-and-bound algorithm. Bootstrap values were calculated over 1000 branch-and-bound replicates. All tree statistics were calculated using MacClade.

Abbreviations:

Institutional—AMNH, American Museum of Natural History; BM, British Museum (Natural History); CM, Carnegie Museum of Natural History; FM, Field Museum of Natural History; MCP, Mazon Creek Paleontological Collection, Northeastern Illinois University; MCZ, Museum of Comparative Zoology; NMW, Naturhistorisches Museum Wien; UMMP, University of Michigan Museum of Paleontology, Ann Arbor.

Anatomical—ang, angular; art, articular; c, choana; cp, costal process of rib; d, dentary; m, maxilla; mf, masseteric fossa; pm, premaxilla; pq, palatoquadrate; ps, parasphenoid; psp, posterior spine; qc, quadrate condyle; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal; t, tabular; tp, transverse process; tub, tuberculum; v, vomer.

RESULTS

CT Scans

Bone and matrix are of sufficiently different density that they read distinctly. A thin layer of pyrite that coats the bone surface often aids this resolution. Unfortunately, the bone is obscured by two other factors. One, the nodule at the air interface has the same pixel values as bone, which impedes the use of some aspects of the processing software. In effect, this thin layer of similarly colored matrix has created a shell around the objects of interest. Two, and more seriously, the crystalline calcite that frequently infills cavities within the specimen reads with the same density as the bone. This is particularly awkward for the braincase area, which encloses a large crystal of calcite, creating a large, featureless mass of the same pixel value as bone right in the center of the specimen, obscuring morphology. Additionally, the skull is highly disarticulated.

However, some results are striking. Much of Wellstead's (1982) description is confirmed by this new data. The left mandible is folded under the skull, but seemingly more medially placed than portrayed by Wellstead (but this might due to different perspectives between his x-ray images and mine).

In a series of horizontal reslices, the full lateral jaw morphology is shown (Fig. 1). *Lethiscus* closely follows the pattern of articulation with the quadrate present in *Oestocephalus* (Carroll, 1998a; Fig. 2). The articular facet is placed high above the tooth row on the posterior terminus of the jaw; there is no retroarticular process. There is a lateral masseteric fossa, as in *Oestocephalus*, but not *Coloraderpeton* or any other "ophiderpetontid" (Carroll, 1998a; Chapter 3). The surangular is the largest bone on the

posteriolateral surface in terms of depth, and it reaches to the posterior third of the tooth row. The angular is restricted to the ventral portion of the lateral jaw, but it has an anterior extent of almost half the length of the mandible. The dentary covers three quarters of the total length of the jaw, as in *Oestocephalus* and *Coloraderpeton*. Unfortunately, it remains unknown whether a splenial was present.

Teeth are uniform in size and are tightly packed together, forming a long cutting surface in the style of *Oestocephalus*. At least 30 teeth were present on the maxilla and dentary (Figs. 3 and 4). This is a much higher tooth count than early ophiderpetontids like *Ophiderpeton kirktonense*. Closely spaced marginal teeth are present in many outgroup taxa such as *Greererpeton* (Smithson, 1982) and *Proterogyrinus* (Holmes, 1984) as well as most basal lepospondyls, including adelospondylids (Andrews and Carroll, 1991; Carroll and Andrews, 1998), and is presumably primitive for aïstopods. However, Milner (1994) distinguished between *Ophiderpeton* (comprised of the Viséan East Kirkton and Jarrow specimens) and *Oestocephalus* (specimens from Nýřany, Linton and Mazon Creek; see Chapter 3) in part by dentition. The older, and presumably more primitive, *Ophiderpeton* has widely spaced teeth, and the Upper Carboniferous *Oestocephalus* has closely spaced teeth. With *Lethiscus* having closely spaced teeth, it suggests that widely spaced teeth is a derived, not primitive, character in aïstopods. The additional presence of widely spaced teeth in *Coloraderpeton* (Chapter 3) which is otherwise nearly indistinguishable with *Oestocephalus* cranially, brings into question the utility of the dentition in aïstopod systematics above the level of the species.

Both premaxillae are preserved in articulation (Fig. 4). They come together in a narrow, but blunt, point. The maxillary ramus is rather short, occupying only a fraction of the distance covered by the maxilla.

The palatine is visible in a resample of the small skull fragment (Fig. 4). As preserved, it is an elongate rectangular bone that runs alongside the maxilla to the choana. Teeth are present in at least one row immediately adjacent to the maxillary tooth row. The cultriiform process reaches the premaxillae. Lateral to the cultriiform process is a short rectangular vomer, which has a posterior recess that forms the anterior margin of the choana. The choana is positioned at the junction of the vomer, palatine, premaxilla and maxilla. The two choanae are close to one another due to the narrow rostrum.

Quadrate condyles are posterior to the occiput (Fig. 5), as in “ophiderpetontids,” but in contrast with phlegethontiids and *Pseudophlegethontia*. The parasphenoid is shown in greater detail than was figured by Wellstead (1982). Again, the basiptyergoid processes are clear, but the posterior limits of the parasphenoid are more clearly defined in the CT images. The basal plate is narrowly rectangular, rather than widely triangular as figured by Wellstead (1982), although this delimitation was obscured by the overlying otic capsules in Wellstead’s x-rays.

The scan through the anterior vertebral segment did not show the rounded scales described by Wellstead (1982). These were evidently superficial structures with no internal depth. Neither were found possible pectoral elements or a proatlas. Examination shows them to have a slightly different coloration and texture that is present on well defined bone. Microscopic investigation of these features under oblique lighting suggests that they are not even skeletal features but rather concoidal fractures on the surface of

slightly different lithologies. Other such rounded features with the same color are present on fragments 11 and 16, which are not superficial but are deep, rounded concavities on the matrix surface, suggesting that the inclusion of different lithology was lost, perhaps as a result of the weathering the specimen underwent.

Throughout the specimen, fractures centered on the vertebral centrum and passed along the planes of the neural spine and transverse processes (Fig. 6). This suggests that the unusual (for an aïstopod) height of the neural spine described by Wellstead (1982) as present in vertebra nine is a taphonomic artifact. In the scans of neural spines that do not have fractures passing through them, the spines have the low morphology more typical of aïstopods. These vertebrae do not have a deep medial groove on their posterior neural spines.

Transverse processes are as described by Wellstead. They seem to have a single rib bearing facet, which suggests that the “capitulum” figured by Wellstead (1982: Text-Fig. 10 A and B) is a costal process. A rib on fragment 24 is visible in articulation with the transverse process (Fig. 7). It shows the entire articulation was at one of the rib “heads,” here interpreted as the tuberculum, while the other is anteroventrally directed. All aïstopods have single headed ribs, although *Coloraderpeton* and *Pseudophlegethontia* have remnants of two rib facets on the transverse processes (Chapter 3, 4). No evidence for the presence of posterior processes was present on any rib of *Lethiscus*.

Ventral gastralia are similar in shape and size with those found in *Ophiderpeton* and *Oestocephalus*. Wellstead (1982) called a series of round to trapezoidal fragments that run along the length of the specimen “gas bubbles,” citing a study by Wood (1977) that stated that these were preserved in other fossils from the Wardie Shales. Wellstead

made this determination because the “bubbles” are pyrite surrounding a calcite core. However, elsewhere in the specimen (the braincase being a prime example), crystalline calcite fills empty spaces, obliterating surrounding bone morphology. Additionally, pyrite coats most bone in the specimen, so this suggests that bone was initially present. The “gas bubble” hypothesis also does not explain why the “bubbles” are always separated from the ventral gastralia (Wellstead, 1982: Text-Figs. 7-9) into discrete layers. I agree with Baird (1964) that these are dorsal osteoderms of an “ophiderpetontid” pattern. Interestingly, the ventral osteoderms are located dorsal to the vertebrae in the anterior part of the specimen. The dislocation of part of the skin agrees with the disarticulation present throughout the skeleton, which suggests a period of post-mortem exposure and degradation before burial.

Phylogenetic Analysis

Two most parsimonious trees were found, differing in the position of *Adelogyrinus* and *Asaphestera* at the base of the outgroup (Fig. 8). These trees have a length of 44 steps, a consistency index of 0.68, and a retention index of 0.76. Bootstrap support at all nodes was strong (80% or higher) except the placement of *Ophiderpeton* (57%) and the *Oestocephalus*-*Coloraderpeton* clade (68%). This may be due to character uncertainty stemming from the incompletely known *Ophiderpeton* (18% unknown characters, the highest in the matrix). Additionally, while *Oestocephalus* and *Coloraderpeton* are very similar in skull morphology, their differing dentition may be attracting *Coloraderpeton* toward *Ophiderpeton*. Additional characters might settle this topology.

DISCUSSION

Lethiscus has more similarities with “ophiderpetontids” than previously appreciated. The jaw morphology is identical. The apparent single tooth row on the palatine is similar to *Oestocephalus* (MCP 323: Carroll, 1998). *Coloraderpeton* has three or four rows of teeth on its broad palatine. The pattern of dermal osteoderms is the same as seen in all “ophiderpetontids” except “*Oestocephalus*” *nanum*, which has only patches of dorsal osteoderms. The absence of a posterior process of the rib is more similar to *Ophiderpeton* than *Oestocephalus*, but the possible presence of a costal process suggests that all aïstopods have single-headed ribs.

The traditional families are not supported by the new phylogeny. Ophiderpetontidae is a paraphyletic grade, with the more derived “ophiderpetontids” as sister taxa to *Pseudophlegethontia* and phlegethontiids proper. The lower bootstrap support for the “ophiderpetontids” might suggest that, with additional characters or new taxa, *Ophiderpeton* could be placed as sister taxon to *Oestocephalus*+*Coloraderpeton*, rather than the *Oestocephalus*+*Phlegethontia*. However, additional characters and taxa could solidify the present topology. Phlegethontiidae is stable (assuming *Sillerpeton*, not included in the present analysis, would place as sister taxon to either *Phlegethontia* species), with *Pseudophlegethontia* as its closest outgroup. Given the uncertainties related to the paraphyly of Ophiderpetontidae, the “distinctiveness” of *Lethiscus* with respect to *Ophiderpeton*, and the position of *Sillerpeton*, and to bring aïstopod systematics into the phylogenetic method (de Queiroz and Gauthier, 1990; de Queiroz and Gauthier, 1992), I propose doing away with the traditional familial names in favor of

a phylogenetic classification (see <http://www.ohiou.edu/phylocode/> for a current discussion related to phylogenetic taxonomy).

In the phylogenetic system, taxon names are given ostensibly. Since they are proper names rather than classes (Gheselin, 1966; Hull, 1976), they must be defined, not diagnosed, as the traditional practice requires (Ghiselin, 1984; Rowe, 1988). Sereno (1999) proposed a rationale for the use of stem versus node based definitions (de Queiroz and Gauthier, 1990, 1992) where taxa would be established using stem-node triplets. Following Sereno (1999), a stem-node triplet would be placed at the dichotomy between *Oestocephalus*+*Coloraderpeton* and *Phlegethontia*+*Pseudophlegethontia*. I define the first stem taxon, Oestocephalia, as “all taxa closer to *Oestocephalus* than to *Phlegethontia*.” The second stem taxon, Phlegethontimorpha, is defined as “all taxa closer to *Phlegethontia* than to *Oestocephalus*.” The triplet is completed by defining the node taxon, Aïstopodia (note that in the phylogenetic system suffixes do not denote a particular rank), as “all taxa arising from the most recent common ancestor of *Oestocephalus* and *Phlegethontia*.” Aïstopoda I define as a stem taxon, as “all taxa closer to Aïstopodia than to any other lepospondyl.” Lepospondyli requires an explicit phylogenetic definition. Considering the uncertainties that persist regarding the relationships between the constituents, this is probably premature. A working definition could be “all taxa descending from the most recent common ancestor of Aïstopoda, Microsauria, Adelospondyli, Lysorophia, and Nectridea,” however, some authors question the utility of using more than two anchor taxa (Sereno, 1999). Until new specimens are found that begin to bridge the gaps between the major lepospondyl groups, this definition should be considered tentative.

The paraphyly of “Ophiderpetontidae” is not surprising. Even within the family there seemed to have been a progressive acquisition of characters which, with the description of *Pseudophlegethontia*, led towards the condition of *Phlegethontia*. It remains to be seen how this hypothesis withstands new fossils. *Ophiderpeton*, which is not completely known, is derived relative to *Lethiscus* and most other Paleozoic tetrapods in the possession of widely spaced teeth. According to the present hypothesis, they were either lost separately in *Oestocephalus* and phlegethontimorphs, or acquired in parallel by *Ophiderpeton* and *Coloraderpeton*.

There is an on-going debate within the systematics community regarding the utility of maintaining Linnean binomials (Pleijel, 1999; Cantino et al., 1999). I agree that the enforcement of Linnean ranks, especially mandatory ranks such as the genus (Cantino et al., 1999) is untenable within a classification system based on monophyly. I cannot, however, accept the proposed solution by some that only the specific epithet be maintained, with some sort of indication (a numeric code, say) to distinguish one “maculatus” from the next (Pleijel, 1999). This would cause undue confusion especially within the literature, something that our classifications are supposed to prevent, not foster. Furthermore, we already have a code to distinguish one “grandis” from another: the generic name. All the binomials used above are part of the species epithet; no genus is stipulated or accepted in this classification. This conceptual change in the meaning of the binomial, from mandatory rank to a component of a two-part species name, is one of the solutions offered by Cantino et al. (1999), and I hope it is the one accepted by the biological community since it would best preserve continuity in the literature.

CONCLUSIONS

Lethiscus is similar to ophiderpetontids in the anatomy revealed by High Resolution CT, but much more remains to be learned about this species. *Coloraderpeton* is very similar to *Oestocephalus* in cranial morphology, but is different in post cranial anatomy. The postcrania of *Coloraderpeton* and *Pseudophlegethontia* suggest the ancestral presence of double headed ribs, however the presence of single rib heads in all known taxa, including *Lethiscus* and other taxa that do not have remnants of two facets on the transverse processes, suggests that more taxa remain to be found.

Phylogenetic analysis has supported the close affinity of *Pseudophlegethontia* and *Phlegethontia*, not “ophiderpetontids.” Phlegethontimorphs are sister group to the Oestocephalia, forming the node based taxon Aïstopodia, with Ophiderpeton and *Lethiscus* as successively more distant sister taxa.

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APPENDIX 1

Character description and matrix used in this study.

1. **Snout.** 0: blunt; 1: pointed.
2. **Parietal-tabular contact.** 0: absent; 1: present.
3. **Frontals.** 0: paired; 1: fused.
4. **Postorbital.** 0: enters orbital margin; 1: restricted from orbit; 2: absent.
5. **Postorbital.** 0: contacts supratemporal-tab; 1: no contact with supratemporal.
6. **Parietals.** 0: present; 1: absent.
7. **Parietal foramen.** 0: present; 1: absent.
8. **Temporal fenestra.** 0: absent; 1: present.
9. **Occipital condyle.** 0: transversely wide; 1: round.
10. **Braincase.** 0: composed of multiple bones; 1: fully fused.
11. **Stapes.** 0: columella present; 1: columella absent.
12. **Fenestra ovale.** 0: lateral; 1: ventral.
13. **Quadrate to occipital condyle.** 0: posterior; 1: anterior.
14. **Palatoquadrate.** 0: absent (distinct pt, q, epi); 1: present.
15. **Marginal dentition.** 0: rounded; 1: laterally compressed.
16. **Marginal dentition.** 0: tightly packed; 1: widely spaced.
17. **Proatlas.** 0: absent; 1: present.
18. **Neural spine.** 0: high; 1: low.
19. **Transverse process.** 0: short; 1: wider than 2x span of zygopophysis.
20. **Spinal nerve foramina.** 0: absent; 1: present.
21. **Accessory vertebral articulations.** 0: absent; 1: present.

22. **Pectoral girdle.** 0: fully represented; 1: endochondral elements absent.
23. **Neural arch.** 0: sutured to centrum; 1: fused to centrum.
24. **Costal process of rib.** 0: absent; 1: present.
25. **Posterior process of rib.** 0: absent; 1: prominent anteriorly only; 2: prominent throughout trunk.
26. **Dorsal osteoderms.** 0: present, absent from cheek; 1: present, present in cheek; 2: absent.
27. **Ventral gastralia.** 0: thick, densely packed; 1: thin, spaced.

Taxa	Characters	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1
<i>Lethiscus</i>		0	0	0	0	0	0	0	1	1	0	?	?	1	1	0	0	0	0/1 ?
<i>Ophiderpeton</i>		0	0	0	1	1	0	0	1	1	0	?	?	0	?	0	1	?	1 ?
<i>Oestocephalus</i>		0	1	0	2	-	0	0	1	1	0	1	1	0	1	1	0	1	1 1
<i>P. longissima</i>		1	-	1	2	-	1	1	1	1	1	1	1	1	1	0	0	1	1 1
<i>P. linearis</i>		1	-	1	2	-	1	1	1	1	1	?	?	1	1	0	0	?	0 1
<i>Pseudophlegethontia</i>		1	0	0	1	0	0	0	1	1	0	?	?	1	1	0	0	?	1 1
<i>Scincosaurus</i>		0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0 0
<i>Asaphestera</i>		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1 0
<i>Adelogyrinus</i>		0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0 0
<i>Coloraderpeton</i>		0	1	0	2	-	0	0	1	1	0	?	?	0	1	0	1	?	1 1
<i>Brachydectes</i>		0	1	0	2	-	0	1	1	0	0	0	0	1	0	0	0	0	0 0

Taxa	Characters	2	2	2	2	2	2	2
		0	1	2	3	4	5	6
<i>Lethiscus</i>		1	0	?	1	0	0	0
<i>Ophiderpeton</i>		1	?	1	1	0	0	1
<i>Oestocephalus</i>		1	1	1	1	1	2	1
<i>P. longissima</i>		1	0	1	1	1	1	2
<i>P. linearis</i>		1	0	1	1	1	1	2
<i>Pseudophlegethontia</i>		1	0	1	1	1	2	2
<i>Scincosaurus</i>		0	1	0	1	0	0	0
<i>Asaphestera</i>		0	0	0	0	0	0	0
<i>Adelogyrinus</i>		0	0	1	0	0	0	0
<i>Coloraderpeton</i>		1	1	1	1	1	2	1
<i>Brachydectes</i>		0	0	0	0	0	0	2

FIGURE 1. Two sequential slices through the left jaw of *Lethiscus*. A) is more medial than B).

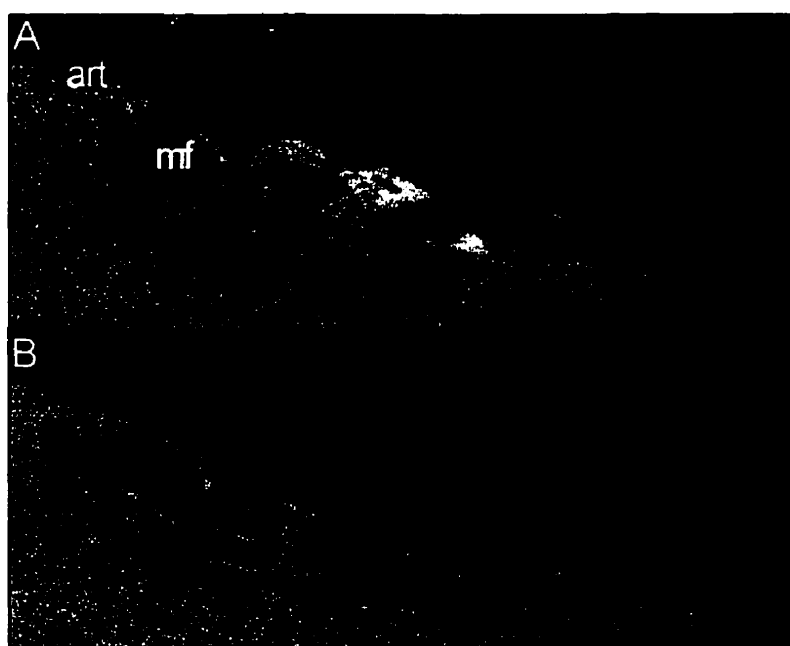


FIGURE 2. Lower jaw of *Oestocephalus amphiuminus*. Modified from Carroll (1998a).



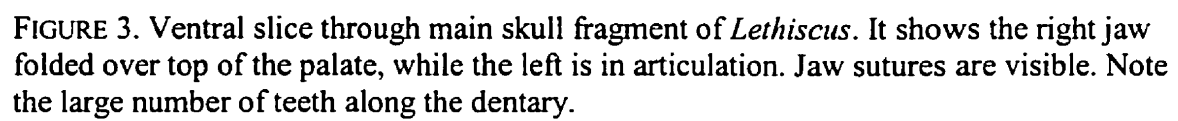


FIGURE 3. Ventral slice through main skull fragment of *Lethiscus*. It shows the right jaw folded over top of the palate, while the left is in articulation. Jaw sutures are visible. Note the large number of teeth along the dentary.

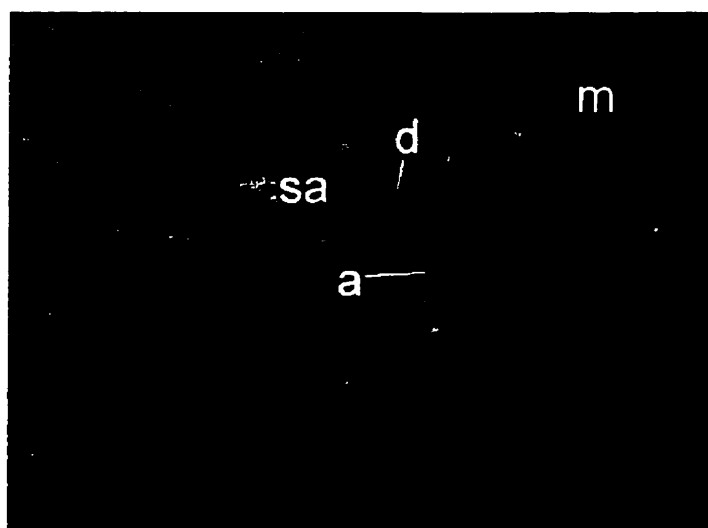


FIGURE 4. Three slices through the anterior skull of *Lethiscus*, showing details of the palate and dentition.

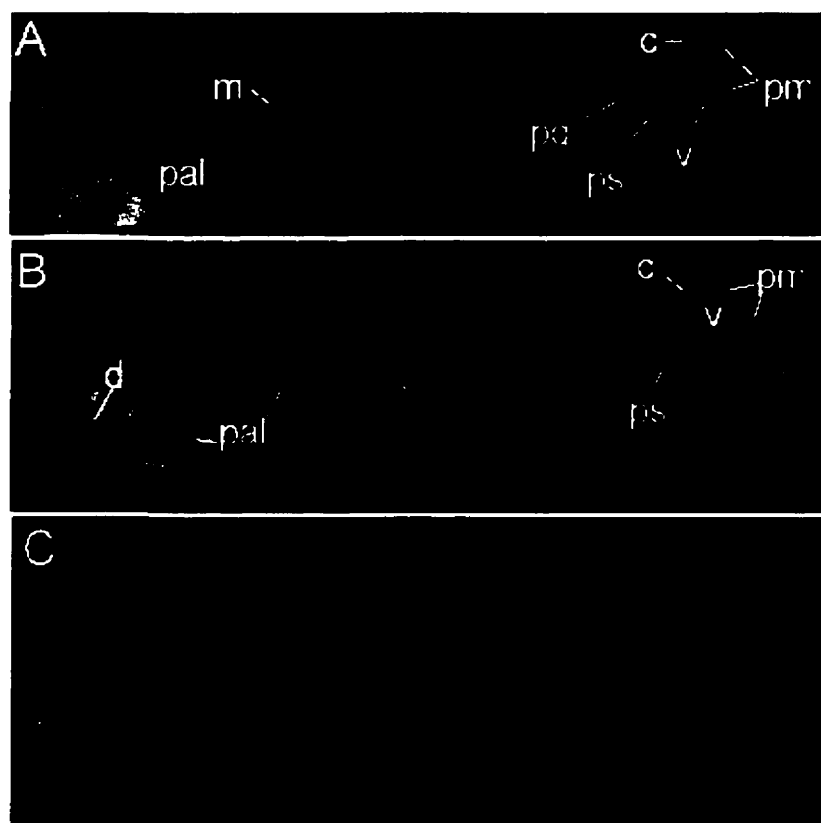


FIGURE 5. Ventral view of the skull of *Lethiscus*. The central structure is the entire parasphenoid, showing basipterygoid processes and long cultriform process. Also note the jaws are placed posterior to the occiput. Anterior is dorsal.

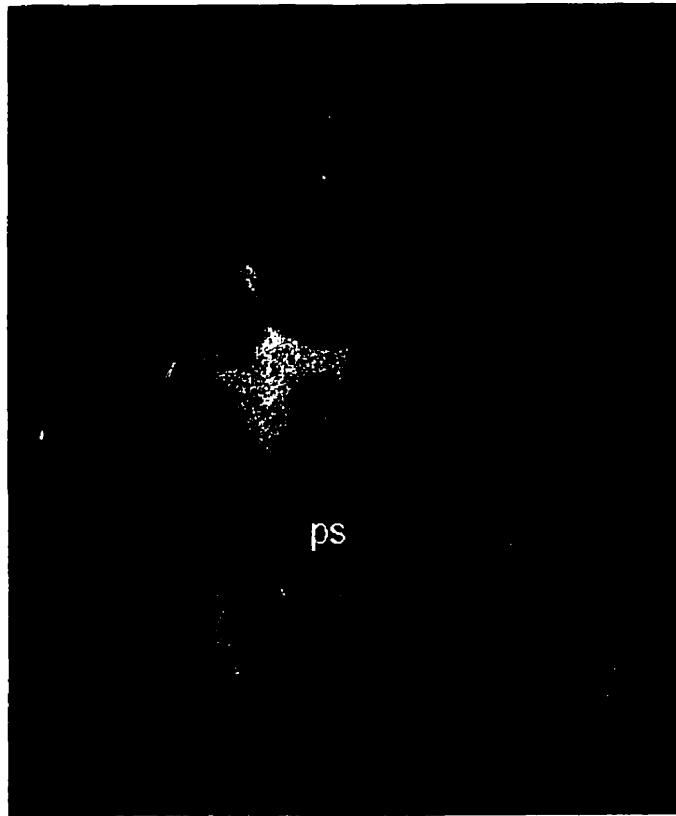


FIGURE 6. Two vertebrae of *Lethiscus*. A) Transverse slice showing the centrum (lower circular structure) and neural arch (dorsal to the centrum). Transverse processes are placed at the neural arch-central junction. Note that the neural spine (projecting from the middle of the top of the neural arch) is short. B) Slice showing fractures running along the transverse processes and neural arch, centered on the centrum.

A

B

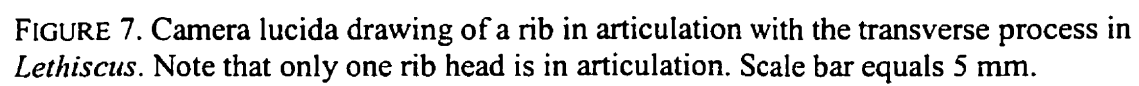


FIGURE 7. Camera lucida drawing of a rib in articulation with the transverse process in *Lethiscus*. Note that only one rib head is in articulation. Scale bar equals 5 mm.

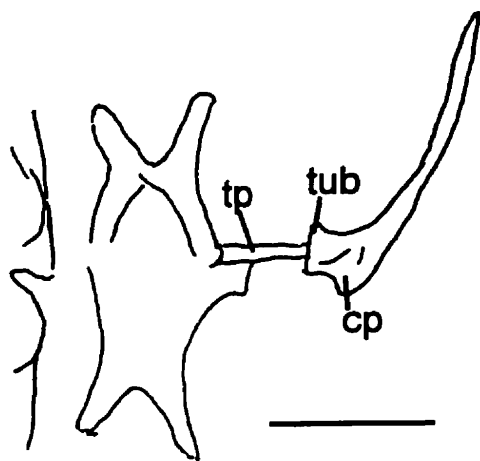
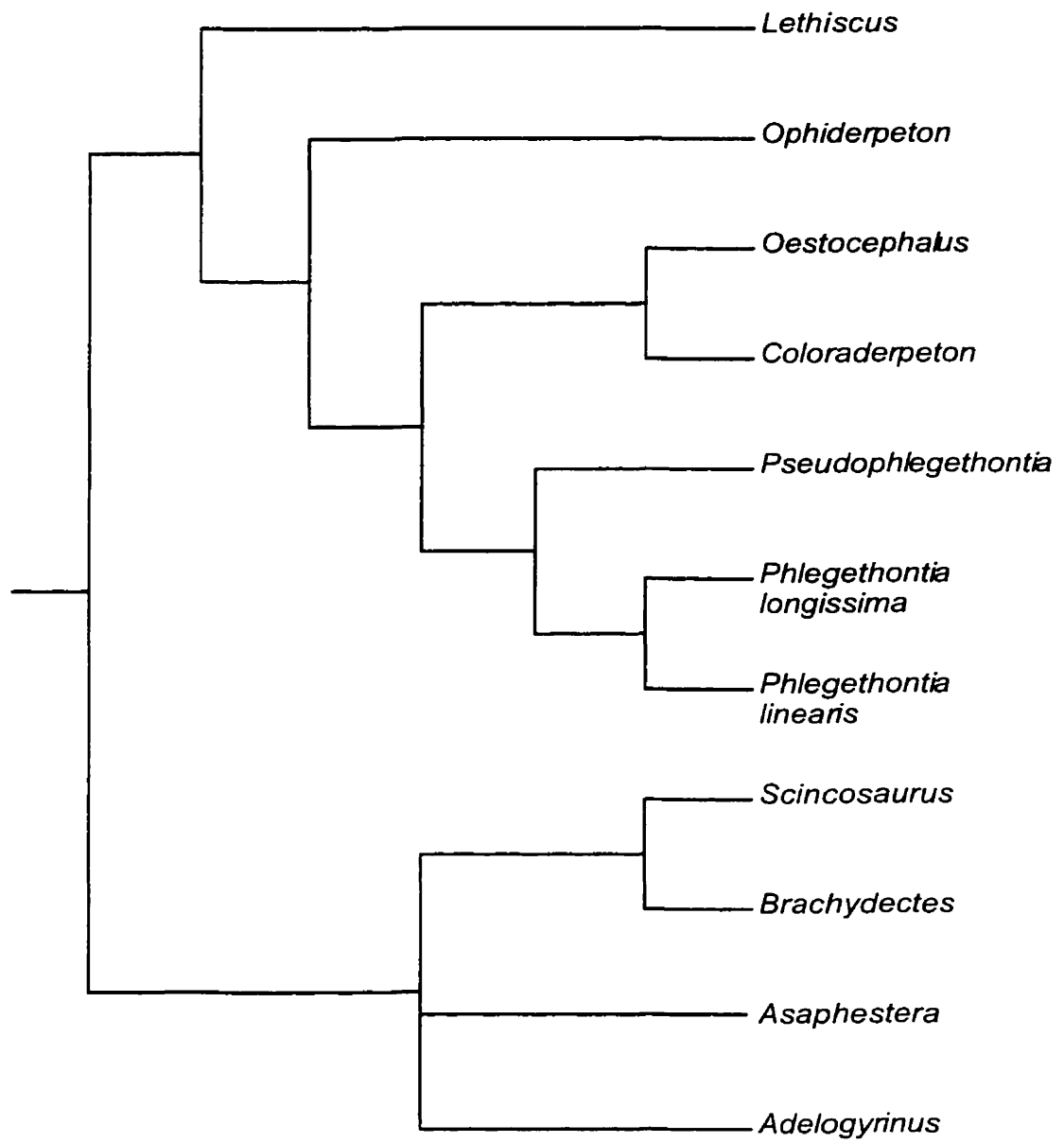


FIGURE 8. Strict consensus of two most parsimonious trees, showing hypothesis of aïstopod relationships.



SUMMARY

This thesis has examined the anatomy and relationships of the Aïstopoda. New complete specimens and comparative study has provided an integrative view of this odd group of elongate, limbless tetrapods. Aïstopods are a monophyletic clade within a monophyletic Lepospondyli, which includes at least caecilians among modern amphibians (Chapter 1). The three traditional families have been examined in turn. Phlegethontids include *Sillerpeton* and two species of *Phlegethontia*: *P. linearis*, represented only by the type specimen, and *P. longissima*, which includes all other specimens. *Sillerpeton* may be distinguished from *Phlegethontia* by its retention of a distinct foramen for cranial nerve III. *P. linearis* is distinguished by having centra on at least the first four anterior vertebrae that are half as long as the same vertebrae in *P. longissima*, and by having high instead of low neural spines on the same vertebrae. *Phlegethontia longissima* has 64 precaudal vertebrae, at least 85 vertebrae bearing ribs, and a total of 200-220 vertebrae. *P. linearis* has 230-250 vertebrae in total, but additional details are unknown (Chapter 2).

The specimen described as “*Phlegethontia mazonensis*” by (Turnbull and Turnbull 1955) is identified as a new taxon, *Pseudophlegethontia turnbullorum* (Chapter 4). *Pseudophlegethontia* shares characteristics of both “ophiderpetontids” and phlegethontiids. It has a pointed snout and more posteriorly placed orbits (although they are still located anterior of the midline), quadrate condyles anterior of the otic capsules, gastralia reduced in degree of ossification and in numbers, and an absence of dorsal osteoderms, shared with *Phlegethontia*. However, it has in common with *Oestocephalus* “k-shaped” ribs well posterior to the 8th vertebra, all bones of the skull table are present (and not incorporated into a mammal-like calvarium as in *Phlegethontia*), and a shorter

vertebral column (although still very long compared with the majority of Paleozoic tetrapods). *Pseudophlegethontia* has approximately 89 ribbed vertebrae, about as many as *Phlegethontia*, but only 50 ribless caudal vertebrae compared with the 100+ present in *Phlegethontia*.

Ophiderpetontidae as previously defined is a paraphyletic grade. All “ophiderpetontids” possess densely packed gastralia and dorsal osteoderms, which fill the temporal opening. *Ophiderpeton* is outgroup to a dichotomy with the other “ophiderpetontids” *Coloraderpeton* and *Oestocephalus* on the one side, and phlegethontiids and *Pseudophlegethontia* on the other. *Ophiderpeton*, as characterized by Milner (1994), has a broad snout, a postorbital restricted from the orbit, and single headed ribs. *Oestocephalus* and *Coloraderpeton* have lost the postorbital, and have “k-shaped” ribs far posterior on the vertebral column. *Coloraderpeton* retains two articulating facets on the transverse process; however, the articulation of the rib as reconstructed by Gallup (1983) would position it in an unlikely position. It probably had a rib articulation similar to *Oestocephalus*, *Phlegethontia* (for the anterior 7-8 rib bearing vertebra), and *Pseudophlegethontia*, where one of the lower arms of the “k,” the tuberculum, articulates with the transverse process, positioning the rib shaft posteroventrally. The costal process is angled anterodorsally, directed at the transverse process of the preceding vertebra. The posterior process is directed posteriorly, and is oriented horizontally. It overlaps the succeeding rib when in close articulation. *Oestocephalus* has a count of 107-109 vertebrae, to which none are added with growth. Ribs were present until at least the 70th vertebra, leaving only 37-39 rib free caudal

vertebrae, the lowest count among aïstopods. Caudal vertebrae may be present at the 60 vertebra, however, this identification is tentative (Chapter 3).

CT scans of the oldest aïstopod *Lethiscus* reveals many similarities with *Oestocephalus*, especially in jaw structure (Chapter 5). *Lethiscus* has a lateral masseteric fossa with a high coronoid process medially and an articular cotyle placed above the tooth row. *Lethiscus* bears at least 30 closely packed teeth of even height. Quadrate condyles are posterior of the occiput. It shows the anterior palate in more detail than any other aïstopod.

Phylogenetic analysis places *Lethiscus* at the base of the clade, followed by *Ophiderpeton*, and finally all other known aïstopods (Chapter 5). The phylogenetic hypothesis presented here suggests that there is a trend within the Aïstopoda for progressive elongation that is primarily achieved by addition of rib free caudal vertebrae. There is a second trend of hyperossification of the endochondral portions of the braincase coupled with a reduction in the degree of ossification in the dermal skull and gastralia, and the loss of the dorsal dermal ossicles. This coupled hyperossification of the endochondral skeleton and reduced ossification of the dermal skull has been noted by Hanken (1983) within modern miniaturized amphibians. In the modern forms, hyperossification of vertebrae and limb bones results in truncation of growth. Additional complete specimens of aïstopods will be required to examine this scenario in more detail.

Following the principles of phylogenetic taxonomy (de Queiroz and Gauthier, 1990, 1992), taxon names are given explicit definitions with respect to the pattern of relationship. The traditional families, the monotypic Lethiscidae, paraphyletic Ophiderpetontidae, and monophyletic Phlegethontiidae, are abandoned. Instead, a stem-

node triplet (Serenó, 1999) is placed at the crown dichotomy. Phlegethontimorpha is a stem taxon, and includes *Phlegethontia*, *Pseudophlegethontia*, and *Sillierpeton* (although its exact placement is unknown). Oestocephalia, the second stem taxon, includes *Oestocephalus* and *Coloraderpeton*. These two stem taxa anchor the definition of the node-based Aïstopodia, which is defined as “all taxa descended as the most recent common ancestor of the Oestocephalia and Phlegethontimorpha. Aïstopoda itself is redefined as a stem taxon, as “all taxa closer to Aïstopodia than to any other group.”

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