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Juul, Lars

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THE PHYLOGENY OF BASAL ARCHOSAURS

by

Lars Juul

Bernard Price Institute for Palaeontological Research,
University of the Witwatersrand, Johannesburg, Private Bag 3, Wits 2050, South Africa.

ABSTRACT

Archosaur systematics has received much attention from the mid 1970s and several influential works on this topic have emerged. As discrepancy exists among proposed phylogenies, some of the most important of the papers in question are assessed here. Characters used in cladistic analysis have often been selected too uncritically or phrased too vaguely to be of diagnostic value, and previously used, seemingly valid apomorphies have been disregarded by later workers, sometimes for no apparent reason.

In the present paper a character matrix for the Archosauria was assembled by critically incorporating, and often modifying, characters used in earlier works on archosaur systematics. A phylogeny resulting from cladistic analysis of the matrix compiled here supports the monophyly of Archosauria, Crown-group Archosauria Crurotarsi, Ornithodira, Dinosauromorpha and Dinosauria, and disputes the existence of Suchia less Ornithosuchidae and of a monophyletic Crocodylotarsi. A new taxon, Dromaeosuchia, is erected for a clade consisting of Ornithosuchidae, Crocodylomorpha and *Gracilisuchus* plus *Postosuchus*.

KEYWORDS: phylogeny, archosaurs, assessment.

GENERAL INTRODUCTION

The purpose of this paper is to review and critically assess what are here construed to be the most important and influential, recent phylogenies (see below) proposed for basal archosaurs. This is a justifiable task as these phylogenies differ somewhat in their placement and composition of the constituent taxa. Furthermore not all characters listed in the earlier studies are discussed in the later ones in which some previously used, apparently valid apomorphies/characters were left out; additionally a number of characters that have been employed are too vaguely defined to have systematic meaning. Thus, as a consequence, the objective here is also to establish a comprehensive, better defined character assemblage as basis for archosaur systematics.

It is the paraphyletic assemblage of basal archosaurs previously known as the "Thecodontia" (e.g. Charig, 1976b; Bonaparte, 1982) that is the main concern of the present paper; the interrelationship of these animals and their relationships with other taxa is often less well understood than in the case of other archosaurs. Thus the group in question corresponds to the non-crocodyliform, non-dinosaurian, non-pterosaurian archosaurs; note that basal crocodyliforms +Protosuchidae, *Orthosuchus*, *Gobiosuchus* and *Sphenosuchus* (Benton and Clark, 1988) are not included above and will not be treated in detail in this study as these have been and still are considered closely affiliated with the taxa included in Mesoeucrocodilia (see also Sereno and Wild, 1992).

BACKGROUND

At present two conflicting definitions of Archosauria are in use: "traditionally" the clade consisting of Proterosuchidae and all later evolved relatives has been termed Archosauria (e.g. Charig, 1976a; Paul, 1984; Benton, 1985, 1990a). However, recently the concept has been redefined as consisting of the two extant (archosaurian) taxa, Aves and Crocodylia, their most recent common ancestor and all its fossil descendants (Gauthier, 1986; crown group concept of Hennig, 1971) and the term Archosauriformes has been applied to this new Archosauria + the successive outgroups Proterochampsidae (and more recently *Euparkeria*), Erythrosuchidae and Proterosuchidae (Gauthier, 1986). Here the traditional definition will be adhered to.

The notion that dinosaurs evolved from 'thecodont', or 'thecodontian' (Charig, 1976b), ancestry is a long held one, but there has been much disagreement among authors about the exact relationship between 'thecodonts' and dinosaurs. This discrepancy has existed partly because of an incomplete fossil record, but also due to a lack of applied stringent cladistic method in earlier archosaur systematics; resulting in, among other things, that Dinosauria has been conceived as a polyphyletic group (e.g. Charig, 1976a; Bonaparte, 1978; Cruickshank, 1979) because of the use of primitive characters in phylogenetic reconstruction.

However from the mid 1980s, with the work of Gauthier (1986) on saurischian monophyly and the origin of birds, in connection with which he supplied a diagnosis of a monophyletic Dinosauria, grew a consensus among palaeontologists that dinosaurs had but a single origin. This had been suggested earlier, notably by Bakker and Galton (1974), but did not gain broad acceptance at the time. At present only few workers seriously question dinosaurian monophyly; e.g. Charig (1991a).

MATERIAL AND METHODS

The phylogenies reviewed are: Gauthier (1986), Gauthier *et al.* (1988), Benton and Clark (1988), Benton (1990a), and Sereno (1991b); also Novas (1992), Sereno and Novas (1992) and Parrish (1992; 1993) will be referred to below.

These papers are here seen as epitomising the knowledge of the systematics of archosaurs and basal dinosaurs resting on the foundation of other recent and older studies such as Romer (1956; 1972b), Bakker and Galton (1974), Bonaparte (1982), Chatterjee (1982), Paul (1984) and Benton (1985).

Numbers (1-263) in parentheses below refer to characters/character states in the relevant diagnoses in appendix 1; references to nodes also pertain to the cladograms in appendix 1.

Unless otherwise specified, definitions and diagnoses by Benton are from Benton and Clark (1988), those of Gauthier from Gauthier (1986) and those of Sereno from Sereno (1991b).

All characters, which are not contradicted by original descriptions or fossil material examined by the present author, are used to construct a cladogram of the Archosauria. Some characters here deemed as being phrased too vaguely were left out.

Prolacerta, *Youngina* and Rhynchosauria were used as archosaur outgroup taxa. Specimens of *Prolacerta* (BP/1/2675 and BP/1/2676), the type specimen of *Pricea* (BP/1/471), the skull of which does not differ morphologically from that of *Prolacerta* (Gow 1975), and specimens of *Youngina* (BP/1/2871 and BP/1/3859), augmented by descriptions by Broom (1922) and Gow (1975), were used to determine the relevant character states in these taxa. As representatives of Rhynchosauria specimens of *Mesosuchus* (SAM 5882, SAM 7416 and SAM 6536) and *Howesia* (SAM 5886 and SAM 5884) were examined because these genera are the most likely to exhibit character states plesiomorphic for rhynchosaurs (pers. comm. David Dilkes); in instances where this was not the case descriptive work on other rhynchosaur genera was consulted (Benton, 1990b; Benton and Kirkpatrick, 1989).

The 'branch-and-bound' search option of the computer implemented algorithm PAUP *Phylogenetic Analysis using Parsimony* (version 3.0s) developed by David Swofford (Swofford, 1990) was used to derive most parsimonious cladograms. All characters were treated as unordered ("Fitch characters") and scaled to equal weight, i.e. a base weight of 1000 was assigned to binary characters, a weight of 500 to 3-state characters, a weight of 333 to 4-state characters etc. This is recommended by Swofford (1990) whenever multistate characters are in operation so that these will not count for more steps than binary ones during search for shortest tree(s). The DELTRAN *or delayed transformation* option, which resolves ambiguities in character configurations by preferring parallelisms over reversals (Swofford, 1990), was chosen for optimising the character states in the new diagnoses (apomorphy list) (appendix 2).

The following abbreviations precede specimen numbers referred to in the text and identify the place of storage of the specimens: BP/1/, Bernard Price Institute for Palaeontological Research (vertebrates); GHG, Geological Survey, Pretoria; SAM, South African Museum; SMNS, Staatliches Museum für Naturkunde, Stuttgart.

If not clearly stated otherwise then *only* those taxon names followed by a specimen number refer to personal observations by the present author.

CRITICAL REVIEW

Introduction

The four papers that are the main subjects of this review (Gauthier 1986, Gauthier *et al.* 1988, Benton and Clark 1988 and Sereno 1991b) differ in certain aspects: no discussion of the characters listed was provided by Gauthier *et al.* (1988) and only synapomorphies of dinosaur taxa were discussed to any extent by Gauthier (1986). Benton briefly examined characteristics of different archosaurian taxa and stated that his analysis was an initial attempt at discovering the interrelationships of these, and in order not to ignore potential synapomorphies rather imprecise characters were included in the diagnoses, which will become apparent below. In contrast Sereno gave good account of the characters he employed and often reviewed synapomorphies previously used by others, frequently disregarding these. Most of the findings offered by Sereno were anticipated or reached in an earlier paper (Sereno and Arcucci, 1990).

All workers used PAUP to obtain their respective cladograms and all appear to have coded their characters as unordered with equal weight (unweighted). The configuration of taxa presented by Benton is not the most parsimonious resulting from his analysis; according to the author himself Ornithosuchia was placed as the sister group of *Postosuchus* plus Crocodylomorpha in the cladogram entailing the fewest steps, but because this arrangement involved numerous reversals a 'slightly less parsimonious' cladogram was preferred. This procedure amounts to a *posteriori* coding of some characters as irreversible ('Camin-Sokal' characters).

For clarity the following discussion falls in four parts pertaining to levels or clades in the archosaur phylogenies; the first three of these divisions do of course not correspond to any monophyletic groupings or clades, but are only practical conventions: (1) non-crown group Archosauria, (2) non-crocodylomorph crocodile-line Archosauria; basal crocodylomorphs (*Pseudohesperosuchus*, *Saltoposuchus*, *Dibothrosuchus* and *Sphenosuchus*) are not treated in this analysis as these and Crocodyliformes are held here to, unproblematically, constitute a monophyletic taxon, (3) non-dinosaur bird-line archosaurs, and (4) basal branching points within Dinosauria. Such a partitioning is possible because there is a general consensus among the authors, whose phylogenies are being discussed here, about which taxa reside at the various levels.

Some overlap between the sections is of course unavoidable; not least because of the fact that the character distributions on the different phylogenies sometimes conflict in listing the same synapomorphies as diagnostic of different or incompatible clades.

Non-Crown Group Archosauria

As shown by the cladograms, there is consensus among the authors whose papers are reviewed here that Erythrosuchidae and Proterosuchidae constitute successive outgroups to the rest of Archosauria. Earlier, the Proterosuchidae and Erythrosuchidae had been included in a paraphyletic 'Proterosuchia' (Charig and Sues, 1976), sometimes with Proterochampsidae (Romer 1972b; Carroll, 1987) or *Euparkeria* (Cruickshank, 1972). Bonaparte (1984) also hypothesised an erythrosuchian ancestry for Rauisuchidae and included the two taxa in a suborder, 'Erythrosuchia'; previously Hughes (1963) had proposed similar ideas. These groupings, however, were based on phenetic similarity (overall resemblance) and did not reflect a 'natural' phylogenetic pattern.

The diagnoses of Archosauria by Gauthier *et al.* (1988) and Benton share four characters: (1) postfrontal reduced, (3) antorbital fenestra present, (6) presence of an ossified laterosphenoid and (9) possession of a fourth trochanter on femur. Presence of an antorbital fenestra (3) is undoubtedly synapomorphic for this clade as it is present in all its members except advanced crocodilians, and not present in the archosaurian outgroups Rhynchosauria (*Mesosuchus*; SAM 2871), Prolacertiformes (*Prolacerta*; BP/1/2675, *Pricea/ Prolacerta*; BP/1/471) and *Youngina* (BP/1/2871). Character (1) has some credit to it as the postfrontals in the just mentioned three taxa are larger than the postfrontals in archosaurs, but the way the character is phrased is too weak for it to be of diagnostic value. Given a new specimen with postfrontals of a size intermediate between that of *Proterosuchus* and the immediate outgroup taxa of Archosauria there is no way, other than a subjective evaluation, of deciding whether the postfrontals of such a specimen would be reduced enough to be diagnosed by synapomorphy (1). It is necessary to redefine this type of character in a quantified manner such that e.g. the length of the feature in question is given as a proportion of another osteological measurement. Even though the possibility that such two measurements may not display isometry throughout ontogeny remains, it is here believed preferable to quantify characters instead of using terms such as reduced, elongated, broad, etc. to specify conditions as the result of the former procedure is more open to objective testing.

In addition to Benton and Clark (1988) and Gauthier *et al.* (1988), Parrish (1992) also holds the presence of a laterosphenoid (6) to be an archosaurian synapomorphy, although Cruickshank (1972) explicitly stated that this feature is not possessed by *Proterosuchus*. Benton quoted a personal observation of J. M. Clark of this feature in *Proterosuchus* in support of his use of the character; a recent study by Clark *et al.* (1993) verifies the presence of a laterosphenoid in *Proterosuchus*. Contra Gauthier *et al.* (1988) and Benton who believed it to be a characteristic of all archosaurs, Parrish (1992) claimed that the possession of a fourth trochanter (9) only diagnoses a clade consisting of Erythrosuchidae and higher archosaurs, and it is indeed impossible to discern a raised fourth trochanter on femora from published drawings of proterosuchids (Cruickshank, 1972; Parrish 1986), and Cruickshank (1972) did not *mention* any such feature in his account of the femur in Proterosuchus, nor did Hughes (1963).

Romer (1972d) claimed that there was no evidence for the presence of a fourth trochanter in *Gracilisuchus*.

Parrish furthermore listed the possession of a lateral mandibular fenestra (17) as synapomorphic for Archosauria (Archosauriformes in his terms); Benton and Gauthier *et al.* (1988) purported this to be diagnostic of Erythrosuchidae + all higher archosaurs only and Cruickshank (1972) did not figure a mandibular fenestra in his reconstruction of *Proterosuchus* claiming the apparent presence of this feature in some *Proterosuchus* specimens to be an artefact. After personal examination of a *Proterosuchus* specimen (GHG 231) with both lower rami preserved, found after 1972, I am convinced that the mandibular fenestra is present in this taxon. In addition see Clark *et al.* (1993) and Welman and Flemming (1993), however, the mandibular fenestrae are relatively much bigger in specimen GHG 231 than reconstructed by the latter two authors.

Character (12), 'marginal teeth laterally compressed', in contrast is potentially synapomorphic for Prolacertiformes + Archosauria as it is present in *Prolacerta* (BPI/1/2675) and all non-ornithodiran archosaurs (with the notable exceptions of Stagonolepidae (Walker, 1961) and *Doswellia* (Weems, 1980); in addition, only part of the dentition in parasuchians (e.g. Chatterjee, 1978) show the apomorphic state), it is however, not very pronounced in *Proterosuchus* (GHG 231) and *Erythrosuchus* (BP/1/5207). The character is absent in Youngina (BP/1/2871) and rhynchosaurs (*Mesosuchus* SAM 6536; see also e.g. Benton, 1990b).

Among the more dubious apomorphies noted by Gauthier *et al.* (1988) at node 1 (their Archosauriformes) is 'upper temporal fenestra dorsally oriented' (5): a dorsally oriented upper temporal fenestra is also present in the archosaurian outgroups Prolacertiformes (*Pricea/Prolacerta* BP/1/471), *Youngina* (BP/1/2871) and Rhynchosauria (Carroll, 1987), thus the character must be considered invalid; note that Benton did not list this character in his diagnosis of the same clade. The latter author, however, listed 'posterior border of infratemporal fenestra bowed' (11) as an archosaurian synapomorphy; the meaning of this character is unclear and the infratemporal fenestra posterior borders are bowed, in at least some rhynchosaurs, as well as in *Pricea* (BP/1/471), in different manners. Benton's

character (13) 'no ectepicondylar groove or foramen on humerus' is almost identical to character (25) by Gauthier *et al.* (1988) of node 2; the outgroup taxa *Prolacerta* (BP/1/2675), *Youngina* (Gow, 1975) and *Mesosuchus* (per. obs) all feature an ectepicondylar groove albeit that in *Mesosuchus* is not very pronounced. A specimen that is possibly a proterosuchid features an ectepicondylar groove on the humerus (Charig and Sues 1976: 17) and there is a deep ectepicondylar groove on the humerus of *Stagonolepis*. Thus this character will need further work before its distribution can be ascertained with certainty.

The occurrence of thecodont dentition (Gauthier *et al.*, 1988); characters (8), 'premaxillary teeth implanted in deep sockets', and (18), 'maxillary and dentary teeth in deep sockets', node 1 and 2 respectively) character (50) of Benton who has listed thecodont dentition as a single trait of node 3) has been reported in a confusing manner. Hughes (1963) and Charig and Sues (1976: 13) purported 'Proterosuchia' (Proterosuchidae and Erythrosuchidae) as having 'subthecodont' dentition. However, Charig and Sues later in the same paper when describing the marginal dentition of *Chasmatosaurus* (*Proterosuchus*) in general (not only that of the premaxillary; character (8) by Gauthier *et al.*, 1988) confusingly used the term thecodont. The teeth in the premaxilla of *Archosaurus* (only tooth bearing bone recovered of this genus) were also referred to as being of thecodont implantation; so was the dentition of *Garjainia* (Erythrosuchidae), and *Arizonasaurus*, this genus, though, may be rauisuchian (Galton, 1977; Chatterjee, 1985) rather than erythrosuchid, has 'deep oval tooth sockets'. Only *Erythrosuchus*, was described as having 'subthecodont' marginal dentition (Charig and Sues, 1976); this is indeed an ill-defined condition as noted by Romer (1956). A large fragment of an erythrosuchid maxilla (BP/1/4540) features very deeply rooted teeth; at a point where the height of the maxilla is 115 mm a tooth root is present which is 65 mm in length. The crown of this tooth is not complete, but an approximate estimate is that the length of the root is more than 45 percent of that of the total tooth length. This also seems to be the case for the premaxillary dentition of *Proterosuchus*, however, the teeth of the maxilla of the same animal are less deeply rooted (pers. obs). Because it was not possible to obtain a quantitative expression of the relative lengths of root to crown for many archosaurs and thereby make meaningful distinction between the terms 'subthecodont', and 'thecodont' characters (8) and (18) are not considered further here. In addition subthecodont is also used by some workers to refer to the condition where interdental plates are present rather than as a measure of root length. On the basis of the material available to the present author it was not possible to establish the exact distribution of interdental plates within Archosauria; nevertheless they are present in rauisuchids ('Kupferzell rauisuchid'; SMNS unnumbered), *Postosuchus* (Wu and Chatterjee, 1993), *Herrerasaurus* (Sereno and Novas 1994) and a number of theropods, appear to be so in *Ornithosuchus* (Walker, 1964) and in modified form in the maxilla of *Massospondylus* (SAM K 1314). Interdental plates are not present in rhynchosaurs or *Prolacerta* (pers obs.).

Serrated teeth (7) are present in *Proterosuchus* (GHG 231), *Erythrosuchus africanus* (BP/1/5207) and other toothed archosaurs except stagonolepids, and pterosaurs and some dinasaurs, but not in rhynchosaurs, *Prolacerta* (BP/1/2675), *Youngina* (BP/1/2871) or *Milleretta* (BP/1/2876 and BP/1/3318).

Synapomorphy (2) 'postparietal fused' is corroborated by the presence of this condition in e.g. *Proterosuchus* (Cruickshank, 1972), *Shansisuchus* (Charig and Sues, 1976), *Euparkeria* (Ewer, 1965) and the presence of discrete postparietals in *Youngina* (Romer, 1956) and *Petrolacosaurus* (Carroll, 1987); however because postparietals are absent in *Prolacerta*, *Trilophosaurus*, rhynchosaurs and possibly some eosuchians (Romer, 1956) the character is only incorporated tentatively here.

There is some disagreement among authors about the presence/absence of intercentra in different segments of the axial column in basal archosaurs: Gauthier *et al.* (1988) believe that the absence of intercentra 'from all postcervical trunk vertebrae' (23) (note that their character (22) is included in (23) making it redundant) is diagnostic at their and Benton's node two, and that the absence of intercentra from postaxial cervicals diagnoses node three, while Benton holds that no intercentra are present behind the axis in the presacral column at node two (29). As pointed out by Sereno it is problematic for the phylogeny proposed by Gauthier *et al.* (1988), and that of Benton, that intercentra occur all along the spine of *Euparkeria*; thus the latter authors are forced to recognise reversals of respectively characters (23 and 41 'intercentra absent from postaxial cervicals') and (29) in this genus. Charig and Sues (1976) reported that in Erythrosuchidae '...presence of intercentra not certain but probable' in *Erythrosuchus*, 'cervical centra....without intercentra' in *Garjainia*, 'no intercentra between axis and tail' in *Shansisuchus* and 'no precaudal intercentra' in the possible erythrosuchid *Cuyosuchus*. According to Parrish (1992) *Fugusuchus* is the 'only erythrosuchid for which an intercentrum is preserved' and that 'anteroventral and posteroventral bevelling of the cervical and trunk centra in *Vjushkovia triplicostata* and of the cervical centra in *Garjainia prima* (for which trunk centra are unknown) indicates that these species possessed intercentra as well'. Charig and Sues (1976) did not explicitly discuss indirect evidence (shape of centra) for intercentra in Erythrosuchidae, even though they suspected their presence. Parrish's observations however, and the osteology of *Fugusuchus*, seem to invalidate the assignment of Gauthier *et al.*'s (1988) character (23) and Benton's character (29) to node two. Sereno arguing similarly chose to move *Euparkeria* to a basal position in the archosaur phylogeny because of its full

complement of intercentra, which are not present in Proterochampsidae and crown group archosaurs, and on grounds of tarsal anatomy.

There is an apparent discrepancy between the character lists of Gauthier *et al.* (1988) and Benton at node two; this is because Gauthier *et al.* concerned themselves with dental characters while Benton focused on pelvic morphology. In addition to the problem of thecodont dentition, which has been discussed above, the issue of palatal tooth characters is raised here. 'Teeth on transverse process of pterygoid absent' (21) seems a valid apomorphy for node two, but again the position of *Euparkeria* in Gauthier *et al.*'s (1988) phylogeny is problematic (as acknowledged by the author himself (1986: 43)): *Euparkeria* exhibits teeth on vomer, palatine and pterygoid; no crown group archosaur does that. In Erythrosuchidae, palatal teeth are absent (Sereno; Parrish 1992; contra Gauthier: 176) and this is hypothesised to constitute an apomorphy for that family (i.e. to have been lost independently in Erythrosuchidae and crown group archosaurs) by Parrish (1992), as palatal teeth are present in *Proterosuchus* (Cruickshank, 1972), Proterochampsidae (Walker, 1968; Romer, 1971c; Sues, 1976) and Doswellia (Weems, 1980). Gauthier, however, because of his placement of *Euparkeria*, is forced to invoke parallel loss of palatal teeth in his Pseudosuchia (77) and Ornithosuchia (166) or, alternatively, a reversion of this character in *Euparkeria* to the plesiomorphic condition.

Character (18) refers to the question of thecodont dentition which has already been discussed and character (20) 'dentary teeth with an enlarged tooth within few teeth from symphysis' is not readily supported by the relevant literature; further because of the way it is formulated it could too easily comprise more than a single character and is therefore hardly valid.

Of the four pelvic characters listed in Benton's diagnosis of node two, 'iliac blade has a small anterior process'(34), 'pubis has a strongly downturned tuber when seen in side'view' (35) and 'ischium has a large posteroventral process (the ischium is longer than the iliac blade)' (36) are well supported in literature e.g. compare Cruickshank (1972, Figure 8a) and Carroll (1987, Figure 13-2a,c,d) with Charig and Sues (1976, Figure 8L) and Parrish (1986, Figure 4-11)); overlooked by Gauthier *et al.* (1988) who do not address pelvic morphology at this node in the cladogram at all. Although the conditions described by (34) and (35) are somewhat difficult to delimit these characters are applicable to taxa at this level; in contrast character (33) "pelvis is markedly three-rayed, with a long down turned pubis and ischium" is too loosely defined to be of much systematic value and is partly covered by (34).

Both Gauthier *et al.* (1988) and Benton noted characters pertaining to the humerus and pectoral girdle at node two, but without overlap of diagnoses. Gauthier *et al.* "scapula narrow above glenoid" (24), although it describes a recognisable condition different from that of *Proterosuchus*, is likely to characterise a more inclusive clade as it is found in, at least, *Protosaurus* (Carroll 1987), *Trilophosaurus* (Romer, 1956) and the rhynchosaurs *Scaphonyx* (Benton and Kirkpatrick, 1989), Rhynchosaurus (Benton 1990b) and to a lesser extent *Paradapedon* (Carroll 1987). Benton's 'deltopectoral crest extends at least one-quarter of the way down the shaft of the humerus' (31), though it appears well defined, cannot be affirmed as it is not possible to determine exactly where on the humerus the deltopectoral crest ends; see below under (235) for an alternative phrasing of this kind of character. His use of the character 'loss of anterior proximal 'hook' on the metatarsal V' (39) at node two is invalidated by the presence of a "hooked" fifth metatarsal, in at least, the erythrosuchid *Shansisuchus shansisuchus* (Charig and Sues, 1976), *Euparkeria* (Ewer, 1965), *Stagonolepis* (Walker, 1961), *Parasuchus* (Chatterjee, 1978) and *Saurosuchus* (Rauisuchidae) (Sill, 1974); see below, synapomorphy (241), for further discussion of this feature.

At node three Benton placed Proterochampsidae + *Doswellia*, Gauthier *et al.* (1988) Proterochampsidae, and Sereno, who did not treat the first two nodes in his analysis, *Euparkeria* as sister group to the rest of Archosauria. As reason for his placement of *Euparkeria* in the cladogram Sereno lists two characters ((67) 'postaxial intercentra absent'; (68) 'contiguous crural facets on astragalus') shared by Proterochampsidae and crown-group archosaurs, not shared by *Euparkeria*, and considered most of the characters (40, 41, 42, 44, 45, 47, 49, 50, 51, 52, 53) listed by Gauthier *et al.* (1988) and Benton, in support of their configuration of taxa at node three, problematic. Indeed this appears to a great extent to be true: character (40) 'parietal foramen absent' also diagnoses node two as all but one of five genera of erythrosuchids listed by Parrish (1992) share the absence of a parietal or pineal foramen. This is the most parsimonious interpretation since it is not the most basal of the erythrosuchid genera in which a parietal opening is present. However, this character has a very peculiar distribution; thus a parietal foramen is also present in some individuals of *Plateosaurus* according to Galton (1990), but the present author was unable to positively identify this feature in any BPI specimen of the closely related *Massospondylus*. Characters (41) 'intercentra absent from postaxial cervicals' and (50) 'thecodont dentition' have already been discussed above. Characters (42) "humerus with reduced epicondyles", (47) "femoral condyles not projecting markedly beyond shaft" and (49) "otic notch well developed" will here be disregarded for reasons similar to those given in the discussion of character (1); in addition see Sereno (p. 9) for further critique of the former two of these characters. The condition specified by (44),'inner two digits of hands and feet more robust than outer two', also seems to be present in *Shansisuchus* (Charig and Sues, 1976, Figure 10T), and furthermore good manual material is lacking for a number of archosaur taxa (see below) which makes the application of (44) too speculative. An intertrochanteric fossa (45)

is present in the outgroup taxa used here (*Prolacerta*, *Youngina* and *Rhynchosauria*), *Proterosuchus* (Cruickshank, 1972) and Erythrosuchidae; the members of the latter family are unique in retaining an intertrochanteric fossa and also possessing a fourth trochanter (Parrish, 1992). An intertrochanteric fossa is absent in Proterochampsidae, *Euparkeria* (Parrish, 1992), and crown-group archosaurs. In *Proterosuchus* all ribs seem to be either one- or two-headed and in Erythrosuchidae two-headed ribs is the plesiomorphic condition while three headed ribs is apomorphic for *Vjushkovia* (Parrish, 1992) – all of which makes character (51) 'ribs all one- or two-headed' problematic. Semi-erect or erect gait (52) appears to be a characteristic of node three, however this character may in fact encompass a whole suit of characters (e.g. pelvic, femoral and tarsal). Benton's character (53) 'possession of 'crocodiloid' tarsus...' must be the character Sereno claimed corresponds to his 'loss of a bony astragalocalcaneal canal' (57) even though he disregarded parts of Benton's apomorphy later in the same paper (Sereno: 10; note that the same author is incorrect in stating that Benton and Gauthier *et al.* (1988) listed respectively his character '3' and '5' (here 48 and 58) as synapomorphies for this group).

Characters pertaining to body armour were also listed: (54) 'single paramedian osteoderm pair per cervicodorsal vertebra' and (55) 'dorsal body osteoderms' by Benton and Sereno respectively. The dorsal body armour of *Chanaresuchus* (Proterochampsidae) consists of a single median row of osteoderms, 2.85 per vertebra in the cervicodorsal series (see Romer, 1972c); *Doswellia*, in contrast, was heavily armoured with scutes arranged in paramedian files (Weems, 1980), but what the exact number of lateral scute rows per vertebra was in this animal, is unclear. In *Euparkeria* there is an approximately one to one correspondence of vertebrae to paramedian scutes; this is also the case for *Ornithosuchus* (Walker, 1964) and many crocodile-line archosaurs including parasuchians (Chatterjee, 1978), *Stagonolepis* (Walker, 1961) and *Protosuchus* (Colbert and Mook, 1951). In rauisuchids, however, the situation is somewhat different, e.g. in *Ticinosuchus* there are two paramedian scutes per vertebra (Krebs 1965, plate 3); in '*Mandasuchus*' two and a half (Charig pers. comm.). Rounded osteoderms has been found for *Erythrosuchus* (BP/1/5207), however, the arrangement of these is uncertain. Of the other synapomorphies listed at node three by Sereno 'interclavicle with reduced, tablike lateral processes' (56) is not well supported in literature: the relevant part of the interclavicle is missing in *Euparkeria* (Ewer, 1965), neither clavicles nor interclavicles are present in *Chanaresuchus* (Romer, 1972c) and although character (56) is present in *Doswellia* (Weems, 1980) the systematic position of this animal is uncertain (Sues, 1992) (Gauthier *et al.* (1988) listed a similar character (72) as synapomorphic for crown group archosaurs, but noted that it might characterise a more inclusive taxon).

The two characters ((67), (68) respectively 'postaxial intercentra absent' and 'contiguous crural facets on astragalus') cited by Sereno in support of the monophyly of Proterochampsidae + crown group archosaurs (excluding *Euparkeria*) stand against the five (62-66) characters listed by Benton in favour of a monophyletic taxon consisting of *Euparkeria* and crown group archosaurs, but exclusive of Proterochampsidae, and the seven (41, 62, 69-73) characters listed by Gauthier *et al.* (1988) being synapomorphic for crown group archosaurs including *Euparkeria*.

Character (67) is valid at this level and (68) seems to be so also. The most parsimonious distribution of (62), the presence of antorbital fossa, on the archosaur cladogram, depends on resolution of the interrelationships of Proterochampsidae: if *Gualosuchus* turns out to be the most basal member of this family (62) will be diagnostic of a clade including *Euparkeria*, Proterochampsidae and crown group archosaurs because *Gualosuchus* is the only proterochampsid in which an antorbital fossa or depression is present; furthermore this feature is of similar construct as that of *Euparkeria* where the dorsocaudal process of the maxilla has a sharp prong which overlaps the lacrimal inside the fossa. If *Gualosuchus* does occupy a basal position within Proterochampsidae we would, in the phylogenies of both Benton and Sereno, have to invoke a secondary loss of (62) in proterochampsids other than *Gualosuchus* and the character would require two-steps in both phylogenies, but if the latter genus is not the most basal member of its family the configuration of character (62) will require a total of at least three steps in Sereno's cladogram, but only a minimum of two in that of Benton (as well as in that of Gauthier *et al.*).

Benton did also specify in (62) that the antorbital fenestra lying in the fossa be large; a large antorbital fenestra may also have been the ancestral condition in Proterochampsidae, but dorsoventral flattening of the snout region could be the reason why this skull opening is less pronounced in proterochampsids, and extreme lengthening of e.g. the premaxilla and maxilla in these animals also makes the antorbital fenestra look relatively smaller. An antorbital fossa is also present in the erythrosuchids *Vjushkovia sinensis*, *Shansisuchus*, and *Erythrosuchus* (BP/1/5207; Parrish, 1992; character 16 of table 1) in the latter genus the fossa has a striking resemblance to that of *Euparkeria* (Parrish 1992, Figure 6).

The condition specified by character (63) 'nasals run forwards between the nares' is present in at least one of specimen *Proterosuchus* (GHG 363), some erythrosuchids (Charig and Sues 1976, Figure 6), but could not be verified for *Prolacerta* (BP/1/471) contra Gow (1975; Figure 12), and (64) 'diapophysis is placed fairly high on the neural arch of cervical vertebrae' in at least *Erythrosuchus* and *Shansisuchus*. Characters (65) 'parapophysis transfers to the neural arch in anterior dorsal vertebrae' and (66) 'diapophysis and parapophysis fuse in the posterior dorsal vertebrae and the ribs become single-headed' may very well also be

valid for *Chanaresuchus* and Proterochampsidae (Romer, 1972c).

Characters (41) and (72) have already been discussed; character (69) 'exoccipital fused with opisthotic in adult' does not seem to be a characteristic of *Euparkeria* (Ewer 1965, Figure 2a), but is present in *Proterochampsa* (Sill, 1967; Figure 3) and *Chanaresuchus* (Romer, 1972c), and (73) 'calcaneal tuber posteriorly directed' seems to be featured by Proterochampsidae (see Romer 1972c). *Euparkeria*+crown group archosaurs, however, share two characters: (54) 'possession of dermal armour with one pair of osteoderms per vertebra' and (70) 'apex of neural spine expanded in dorsal view'. The former character was originally listed by Benton as being synapomorphic for a more inclusive group, but does only characterise *Euparkeria* and crocodile-line archosaurs, and note that both characters are most parsimoniously interpreted as defining a monophyletic *Euparkeria*+crocodile line archosaurs, were it not for the three characters (see below) shared by crown group archosaurs (exclusive of *Euparkeria*) and for the two characters, (67) 'postaxial intercentra absent' and (68) 'contiguous crural facets on astragalus', shared by Proterochampsidae and crown group archosaurs.

The systematic status of *Doswellia* is problematic; Benton placed this genus as the sister group of Proterochampsidae (node 3.1) on account of two apomorphies shared by these taxa: (60) 'loss of postfrontal (parallelism with Crocodylomorpha)' and (61) 'pelvis massive, and not three-rayed'. This is obviously rather weak evidence; the latter of these characters is not a well defined one and the former not an autapomorphy for the group. Sues (1992) claimed that a detailed comparative study revealed no other synapomorphies for *Doswellia* plus Proterochampsidae. In addition to (60) *Doswellia* displays other features which have been used to characterise crocodile-line archosaur clades, such as broad, medial interpterygoidal contact (Crocodylotarsi), 'spine tables' (see below), lateral deflection of iliac crest (*Protosuchus*) and additional vertebrae incorporated into sacrum (Ornithosuchidae, some rauisuchians). However, some aspects of this enigmatic archosaur's morphology are quite primitive; e.g. pterygoid dentition, weakly differentiated proximal femur and extensive participation, of pubis in acetabulum.

Crown-Group Archosaurs

Before dealing with crocodile-line archosaurs the characters uniting these and the bird-line archosaurs in the crown group clade (node four in Gauthier's cladogram; node five in Benton's and Sereno's cladograms) will be examined. All the synapomorphies listed at this node by Gauthier have been discussed above and none seem valid unless *Euparkeria* is included in crown group Archosauria. Of the characters cited by Benton only (77)'palatal teeth absent' is clearly apomorphic at this level; (74) 'parietals send posterior processes into the occiput which meet the supraoccipital' is also present in Proterochampsidae (Romer, 1971c; Sill, 1967) and *Euparkeria* (Ewer, 1965) and it is uncertain at which level (75) 'discrete postparietal and exoccipitals absent beyond juvenile stages of development' applies: According to Westphal a discrete postparietal is present in some parasuchians (Westphal, 1976), and the exoccipital seems not to be fused with the opisthotic in *Nicrosaurus gregorii* (same ref., Figure 3a); Chatterjee, however, reconstructs *Parasuchus hislopi* with fused exoccipital and opisthotic, but finds no postparietal (=interparietal) in this species (probably juvenile specimens) (Chatterjee, 1978). The exoccipital and opisthotic bones are also coossified in *Angistorhinus* (another parasuchian), but, as in the case of *Parasuchus*, no postparietal appears to have been present (Mehl, 1915a). *Stagonolepis* may, like *Typothorax*, have had a separate postparietal, nevertheless the exoccipitals and opisthotics are fused in this animal (Walker, pers. comm.); in *Gracilisuchus* a discrete postparietal appears to be present, but nothing definite can be said about the condition of the exoccipitals (Romer, 1972d) and the state of the character is hard to discern from literature for many other taxa as well as the ontogenetic stage of these. Thus the use of part of character (75), as two characters: 'exoccipitals and opisthotics fused' and 'absence of discrete postparietal', here may be premature. If character (76) "pterygoids meet medially in the palate" is rephrased as: 'pterygoids with medial contact for at least a third of their length' it may diagnose crocodile line archosaurs as it is present in *Parasuchus* (Chatterjee, 1978), *Rutiodon* (Westphal, 1976) *Angistorhinus* (Mehl, 1915a), *Stagonolepis* (Walker, 1961), *Postosuchus* (Chatterjee, 1985), *Pseudhesperosuchus* and *Hemiprotosuchus* (Bonaparte, 1971). In contrast pterygoids in *Coelophysis* and *Syntarsus* have no medial contact (Colbert, 1989) and in *Lesothosaurus* these bones meet at their extreme anterior end, and through a pair of processes posteriorly (Sereno, 1991a); it is not certain what the state of this character originally was in Sauropodomorpha.

In addition to 'palatal teeth absent' (77) Sereno lists 'calcaneal tuber directed more than 45 degrees posterolaterally' (78) and 'Calcaneum with contiguous articular surfaces for fibula and distal tarsal 4' (79) as crown group synapomorphies. The calcaneal tuber in crown group archosaurs seems to be more posteriorly directed than in basal archosaurs and character (79) is not contradicted by original descriptions or fossil material available to the present author.

Non-crocodylomorph crocodile-line Archosauria

The question of tarsal anatomy is raised in earnest here as Gauthier, Benton and Sereno all cite several synapomorphies, uniting crocodile line archosaurs, pertaining to this anatomical region. This question has received more than its fair share of attention by workers in archosaur systematics and the structure of 'astragalus and calcaneum' has preoccupied minds to a degree which has sometimes led to an almost overshadowing

of other aspects of morphology. This subject will therefore be treated at some length here again.

It has long been recognised that two rather different tarsal constructs are present among archosaurs: Romer (1971b) referred to Krebs (1963) as being the worker who first clearly brought out the distinction between a crurotarsal and mesotarsal ankle joint; previously also Walker (1961) gave good account for the function of the crurotarsal ankle joint. In the crurotarsal ankle, rotation of the pes relative to the crus, in the parasaggital plane, occurs through a joint between the astragalus, which is functionally part of the lower limb, and the calcaneum which moves with the foot. In the mesotarsal type of ankle the axis of rotation of the pes on the crus runs mediolaterally between the proximal- and distal tarsals. Krebs later (1974) grouped pseudosuchians (?sensu Benton) and crocodylomorphs together in Suchia because these archosaurs all have an ankle joint of the former type. Further distinction was made by Bonaparte (1971: 97) who chose to distinguish between two ankle types of the crurotarsal configuration; these have later come to be known as the 'crocodile-normal' (CN) and the 'crocodile reversed type' (CR) (Chatterjee, 1978). In the CN ankle the pivotal articulation between the astragalus and calcaneum occurs through a peg on the former element and a receiving socket on the latter, while in the CR type the peg is on the calcaneum and the socket on the astragalus. The (CN) ankle is found in crocodile-line archosaurs and the CR ankle is only recognised, today, as being present in Ornithosuchidae.

Cruickshank (1979) put forward a phylogeny which suggested a fundamental dichotomy of 'thecodonts' into CN and CR lines, arising from a 'Proterosuchian' ancestor with a mesotarsal ankle and leading to respectively Prosauropoda, Ornithischia + Coelurosauria and Sauropoda + Carnosauria. This scheme was elaborated upon by Chatterjee (1982) who proposed a phylogeny of 'thecodont' tarsi where, an ankle construct of a 'primitive mesotarsal' type, found in *Proterosuchus*, gave rise to CN and CR tarsal forms which were further transformed into respectively 'advanced mesotarsal normal' and 'advanced mesotarsal reversed' ankle forms; the latter two types occurring in different dinosaurian taxa. Cruickshank and Benton (1985) revising Cruickshank's and Chatterjee's earlier proposals chose to recognise only one 'advanced mesotarsal' ankle type supporting a monophyletic Dinosauria, and introduced yet another term 'modified primitive mesotarsal' referring to the ankle construct found in *Euparkeria*, *Chanaresuchus* and *Erythrosuchus*; the latter genus, however, is more likely to possess a tarsus closely resembling that of *Proterosuchus* (Chatterjee 1982; Parrish 1992). In the primitive mesotarsal (PM) ankle a double articulation, two pairs of pegs and sockets, exists between the two proximal elements with an upper peg on the calcaneum and a lower peg on the astragalus, separated by a perforating foramen. In the 'modified primitive mesotarsal' (MPM) tarsus the perforating foramen between the astragalus and calcaneum has been lost and the articulation surface between the two proximals is relatively smaller and less sculptured than in PM, CN and CR forms. In the AM ankle the astragalus is very much enlarged at the expense of the calcaneum and has an ascending process that locks the tibia; the two proximal tarsi articulate with each other through plain facets and are closely adpressed against each other and against the tibia and fibula.

The different ankle constructs have been correlated with various gait or posture 'grades' attributed to archosaurian taxa: the PM ankle with a 'sprawling posture', the CN and CR ankles with a 'semi-improved posture' and AM ankles with a 'fully improved posture' (Chatterjee, 1982).

Sereno disregarded the CN-CR nomenclature claiming that the two ankle types are basically of the same design, with a large ventral and a smaller dorsal articulation between the two proximal elements, and that they really only differ in the polarity of the ventral astragalocalcanear articulation: in CN archosaurs this articular surface of the astragalus is convex while it is concave in CR archosaurs. But proximal tarsals in many archosaurs are not readily comparable because topographical details often differ widely and when looking at the astragalocalcanear articulation, Sereno's view does not seem to receive more support than the 'traditional' CN-CR one from the many excellent drawings made of archosaur tarsi. Indeed it appears, looking only at intratarsal articulation morphology, one can choose to see the tarsus in ornithosuchids as having been derived from a 'CN' ancestor, as would be a consequence of Sereno's phylogeny, or as having evolved from a mesotarsal ankle (MPM) type, as hinted at by Cruickshank and Benton (1985), equally well were it not for the fact that both the CN and CR ankles are both of the rotary, crurotarsal type where the astragalus is functionally part of the crus. Sereno also cited other tarsal characters in favour of derivation of "CR" archosaurs from a 'CN' ancestor: (88) 'hemicylindrical calcaneal condyle for articulation with fibula', (89) 'astragalus with flexed tibial articular surface' (108 of Gauthier), (90) 'robust calcaneal tuber with shaft wider than high', and (91) 'calcaneal tuber with flared distal end'; all easily distinguishable characters which lend support to a monophyletic Crurotarsi (inclusive of Ornithosuchidae), as defined by Sereno.

In addition to tarsal morphology Gauthier and Benton, but not Sereno, cited 'cervical ribs short and stout' (82) as synapomorphic for crocodile line archosaurs. This character is present in parasuchians (Chatterjee 1978; Westphal 1976), *Gracilisuchus* (Romer, 1972d), *Stagonolepis* (Walker, 1961), *Postosuchus* (Chatterjee, 1985) and less extreme in *Ticinosuchus* (Krebs, 1965) and *Ornithosuchus* (Walker, 1964). In contrast cervical ribs are slender in *Euparkeria*, *Chanaresuchus*, long and slender in *Lagerpeton*, *Herrerasaurus* (Sereno, 1993; Figure 16)

Coelophysis (Colbert, 1989), *Anchisaurus* and in *Lesothosaurus diagnosticus* the cervical ribs are short, but slender (Weishampel and Witmer, 1990a). For character (84) 'deltopectoral crest extends less than one quarter of the way down the humerus shaft' in Benton's list at node six I refer to the treatment of character (31) in the previous section. Sereno cited three characters with reference to the appendages, (85) 'proximal humerus strongly arched under inner tuberosity', (86) 'anterior trochanter of fibula robust and knobshaped' and (87) 'distal end of fibula wider than proximal end' in support of his Crurotarsi. These claimed synapomorphies are hardly valid for reasons pointed out by Parrish (1993) and I refer to him for critique of these characters.

Moving to the next node in the crocodile-line clade Gauthier, Benton and Sereno (node six, seven and seven respectively) all agree to leave Parasuchia branching off as the basal-most taxon member. The former two authors both believed that the absence of the septomaxilla (94) is synapomorphic for the taxa included at this node. Sereno, in contrast, saw this condition as being plesiomorphic for crown group archosaurs as Parasuchia is the only one of these taxa possessing a septomaxilla; thus he considered the presence of a septomaxilla a parasuchian apomorphy and denied the possibility that the feature, because of its singular morphology in parasuchians, is homologous with the septomaxilla in primitive diapsids (Sereno p.16). Let it be noted here that no septomaxilla was reported for *Euparkeria* (Ewer, 1965), *Proterochampsa* (Sill, 1967), *Gualosuchus* and *Chanaresuchus* (Romer, 1971c) and that septomaxillae are possibly present in *Proterosuchus* (Cruickshank, 1972); the data on the distribution of this character are here considered too sparse for them to be included in the analysis below. Postparietal morphology (95) will be treated in detail below. Where only adult specimens are available character (96) 'fusion of second intercentrum and first centrum in juvenile or earlier stages of ontogeny', listed by Gauthier, of course cannot be assessed with confidence, and 'triradiate pelvis' (97) is here considered too imprecise to have diagnostic meaning; furthermore the pelves of e.g. *Chanaresuchus* (Romer, 1972c) and *Cuyosuchus* (Erythrosuchidae) (Charig, 1976a; Figure 9c) may also very well be considered 'triradiate'. Character (98) "screw joint' tibio'astragalar articulation', also by Gauthier, was considered imprecise by Sereno and he rephrased it 'astragalus with flexed tibial articular surface' (89), so that it also was diagnostic of Parasuchia, considering the form of the tibio-astragalar joint in this taxon to be basically similar to that of higher crocodile line archosaurs; this seems in concordance with the osteological evidence (e.g. Parrish, 1986). Characters (99) 'fully developed crocodile-normal crurotarsal joint' and (107) 'advanced crocodile-normal tarsus', by respectively Gauthier and Benton, do not refer to any specific condition found in the members of this clade not found in Parasuchia, but rather mirror the fact that tarsal characters already present in Parasuchia are in some sense proliferated or accentuated in higher crocodile-line archosaurs; e.g. the calcaneal tuber is further posteriorly directed, the astragalar peg for articulation with the calcaneum more prominent and the proliferation of the proximal articulation surfaces of the astragalus more pronounced.

Gauthier also 'noted osteoderms on ventral surface of tail' (100) for this clade; such dermal ossifications seem to be present in only the members Stagonolepidae, *Saurosuchus* (Bonaparte, 1981) and *Ticinosuchus*, as noted by Sereno; the extent to which this character is distributed in Rauisuchidae cannot be fully appreciated as many members of this family are very poorly preserved. In any case ventral dermal armour is also present in some parasuchians (Gregory, 1962) and it may be a primitive feature for crocodile-line archosaurs.

Benton's 'lower temporal fenestra is reduced in size and triangular in shape, with a dorsal point' (101) is also quoted by Sereno, but in a slightly rephrased form: 'postorbital-squamosal temporal bar anteroposteriorly short with subtriangular laterotemporal fenestra' (110). Even though 'reduced in size' is somewhat imprecise Benton's phrasing of the character is preferable, if applied to a clade of crocodile-line archosaurs exclusive of Parasuchia and Ornithosuchidae (in the latter taxon the laterotemporal fenestra is neither reduced nor particularly triangular in shape), as a (sub)triangular lower temporal fenestra with a dorsal point is present in *Gracilisuchus* (Romer, 1972d), Stagonolepidae (Walker, 1961), *Postosuchus* (Chatterjee, 1985) and *Saurosuchus* (Bonaparte, 1981), and because the postorbital-squamosal temporal bar in the rauisuchians *Luperosuchus* and possibly *Heptasuchus* (Bonaparte, 1984) does not seem to have been any shorter than that of ornithosuchids (Bonaparte, 1971; Walker, 1964). In addition (101) and (110) show a lot of variation within terminal taxa, e.g. *Prestosuchus*, *Pseudhesperosuchus* and *Lotosaurus* (Parrish, 1993) do not exhibit a reduced laterotemporal fenestra and nor, as in Ornithosuchidae, is it triangular in shape in the latter two taxa, and can only safely be said to characterise *Stagonolepidae*, *Gracilisuchus* and *Postosuchus*. It is doubtful if character (102) 'axial diapophysis is reduced or absent' is diagnostic at this level as axial diapophyses are only very weakly developed in *Euparkeria* (Ewer, 1965) and *Chanaresuchus* (Romer, 1972c), and Sereno did not use this character at any level in his cladogram. Neither character (103) "no pubo-ischiadic plate, and much reduced contact between pubis and ischium" will here be regarded synapomorphic at node seven in Benton's cladogram; broad puboischiadic contact, with a plate-like development present, exists in *Stagonolepis* of approximately the same extent as that seen in the parasuchids *Parasuchus* and *Rutiodon* (Westphal, 1976). In the rauisuchid *Ticinosuchus* (Krebs, 1965) the puboischiadic symphysis, though not as prominent as the one found in *Stagonolepis*, is at least of the same length as those in *Euparkeria* and *Chanaresuchus*. Benton acknowledged that several of the characters he included in the diagnosis of this clade are paralleled in

his Ornithosuchia: (103), (104) 'pubis is long and narrow and subvertically oriented', (105a) 'pubis is longer than ischium' and (108) 'digit V of the foot is reduced (shorter than I)'. These characters are equivocally distributed on his cladogram as pointed out by Sereno. This is not true for the parallelisms (97) 'triradiate pelvis', (98) 'screw joint..' between the two clades listed by Gauthier because he included *Euparkeria* as the most basal member of his Ornithosuchia; this, however, causes other serious problems as acknowledged by Gauthier and described above.

Character (104) 'pubis is long and narrow and subvertically oriented' does describe a pubic structure different from that found in *Euparkeria*, *Chanaresuchus* and parasuchians, and is valid as such, but, like characters (33, 61 and 98), it may be too loosely defined. In contrast (105a) 'pubis is longer than ischium' refers to a more exact pelvic condition which clearly distinguishes itself from the pubo ishiadic allometry of the just mentioned three taxa; character (105a) is valid for all non-crocodylomorph crocodile-line archosaurs (except for some rauisuchids and, of course, Parasuchia) where the relevant elements are preserved. After examining the prosauropod femurs in the collection of the Bernard Price Institute I would refrain from using character (106) 'proximal head of femur is turned inwards at about 45°' as post-mortem distortion of the femur seems to be common and obscures the true inflection of the proximal head of this bone; thus creating serious uncertainty with regard to (106) where only a single or very few specimens are preserved. 'Digit V of the foot is reduced (shorter than I)' (108) is also present in *Chanaresuchus*, and ornithodirans, see e.g. (Romer, 1971b) (Reig, 1963); in *Euparkeria* these digits are about the same length. If rephrased 'digit V shorter than I' the character will support the monophyly of Proterochampsidae + crown group archosaurs. The rephrasing is necessary because digit V of some higher crocodile-line archosaurs is not reduced compared to the same digit in *Euparkeria*, as pointed out by Sereno (p. 12).

Sereno's definition of this clade differs from those of Benton and Gauthier mainly by the inclusion of Ornithosuchidae. The latter two authors believed this family to be the sister taxon of Ornithodira. By using parts of Benton's and Gauthier's characters (105a) and (116) 'length of pubis exceeds three times width of acetabulum' respectively Sereno arrived at a character, 'pubis is longer than ischium and at least three times anteroposterior diameter of acetabulum' (105b), which is not paralleled in basal ornithodirans, such as *Lagosuchus* (Sereno; Figure 25), and, hence, is synapomorphic of his Suchia (except for *Stagonolepis*, some advanced crocodilians, as noted by the author himself, and some rauisuchids) + Ornithosuchidae, and also of higher dinosauriforms. In the latter group the character is present in *Dilophosaurus* (Welles, 1984; Figs. 30, 31), *Coelophysis* (Colbert, 1989; Figure 77), *Lesothosaurus* (Sereno, 1991a; Figure 10), in one specimen of *Sellosaurus* (SMNS 17928) (Galton, 1984; Figure 1e) and *Herrerasaurus* (Novas, 1993; Figure 5), but not in *Staurikosaurus* (Galton, 1977; Figure 2b) nor quite in *Lagosuchus* (Sereno Figure 25). Character (105b) is thus synapomorphic for at least Eudinosauria among bird-line archosaurs and character (105a) for at least *Lagosuchus* and all other Dinosauriformes (the terms Dinosauriformes and Eudinosauria are used here in accordance with Novas, 1992; see appendix 1). Character (109) 'posterior pubic acetabular margin recessed' seems to be present only in Ornithosuchidae, *Postosuchus*, possibly in some stagonolepids, and among crocodylomorphs in at least *Terrestrisuchus*; this character was concordantly only used by Sereno as a tentative synapomorphy at node seven in his cladogram.

Sereno did not try to resolve the relationships of his Suchia and proposed only one synapomorphy (110) "postorbital-squamosal bar short with subtriangular laterotemporal fenestra', which has been discussed above, for this taxon.

Benton, in contrast, had *Gracilisuchus* the next taxon branching off from the crocodile line and quoted several synapomorphies for the remaining taxa (node eight): (96) and (100) have been treated above; the question of the presence/absence of postparietals (95) have also been touched upon before, but will be dealt with in more detail here: In Parasuchia taxa possessing a postparietal do occur (Westphal, 1976) and, as noted above, in Stagonolepidae a postparietal is present in *Typothorax*, however, its presence could not be established for *Stagonolepis* because of incomplete preservation of the occiput (Walker, 1961). *Gracilisuchus* retains the bone (Romer, 1972d), but it appears to be absent in *Postosuchus*, (Chatterjee, 1985), crocodylomorphs; e.g. *Terrestrisuchus* (Crush, 1984) and *Pseudhesperosuchus* (Bonaparte, 1971), and in ornithosuchids (Walker, 1964; Bonaparte, 1971). Among rauisuchids *Prestosuchus* (Barberena, 1978) possesses a postparietal, but for other members of the taxon the state of character (95) is difficult to ascertain because of poorly preserved or even missing hindskulls; this is true for e.g. *Teratosaurus* (Benton, 1986), *Rauisuchus* (Huene, 1935-1942), *Luperosuchus* (Romer, 1971a), *Fasolasuchus* (Bonaparte, 1981), '*Mandasuchus*' (fragmentary maxillae and a fragment of the right dentary were the only skull material recovered for this animal; Charig, 1956) and also *Ticinosuchus*; even though the type specimen is always figured as a complete skeleton, only the maxilla and dentary have been prepared and the rest of the skull is reconstructed with *Euparkeria* as model! (Krebs, 1965). Complete skull material exists for three taxa: *Heptasuchus clarki* (Dawley *et al.*, 1979), *Prestosuchus chiniquensis* (Barberena, 1978) and *Saurosuchus galilei* (Bonaparte, 1981). A satisfactory description of the latter specimen has never been given; Sill (1974) gave a detailed account of a fragmentary specimen of this species and Dawley *et al.* only supplied a preliminary description of *Heptasuchus*.

According to Benton character (111), 'Pit between basioccipital and basisphenoid', corresponds to 'foramen intertypanicum' of living crocodilians and the author cites J. M. Clark's unpublished Ph.D. thesis in support of the character. The term 'foramen intertypanicum' does not appear to be otherwise used in descriptions of archosaurs, nor is it used by Romer (1946; 1956), Romer and Parsons (1986) or Carroll (1987). In *Stagonolepis* an excavation or a fossa is present between the basioccipital and the basisphenoid (Walker, 1961; Figure 5), this is also the case in *Postosuchus* (Chatterjee, 1985; Figure 7). Whether or not any of these features are the foramen intertypanicum of modern crocodiles I am unable to say. In *Pseudhesperosuchus* the basicranium is not preserved (Bonaparte, 1971) and in *Terrestrisuchus* no basisphenoid could be identified (Crush, 1984), and Crush did not mention if a fossa or pit could be judged present at the suture between the basioccipital and the basisphenoid from the appearance of the former element. In *Ornithosuchus* the preservation state of the braincase does not allow comparison with respect to basioccipital – basisphenoid morphology, nor does Bonaparte's description of the basicranium of *Riojasuchus* (Bonaparte, 1971). In rauisuchids studies of the relevant skull parts were not available. No foramen intertympanicum or fossa is present in *Euparkeria*, *Parasuchus* (Chatterjee, 1978), *Dilophosaurus* (Welles, 1984), *Lesothosaurus* (Sereno, 1991a) or *Sellosaurus* (Galton and Bakker, 1985).

Of the taxa included at node eight in Benton's cladogram *Stagonolepis* is not diagnosed by 'accessory neural spine on caudal vertebrae' (112); the character was not noted by Chatterjee (1985) for *Postosuchus*, but is present in *Terrestrisuchus* (Crush, 1984), probably in *Pseudhesperosuchus* (Bonaparte, 1971; Figure 27d) and a number of rauisuchians: *Ticinosuchus* (Krebs, 1965), '*Mandasuchus*' (pers. obs.), *Prestosuchus loricatus* and *Rauisuchus triradentes* (Huene, 1935-1942). The character may also be present in other rauisuchians, but this was either not noted or the relevant axial material has been too incompletely preserved.

The first of the characters (113) 'first (atlantal) intercentrum much longer than wide' listed by Gauthier as synapomorphic for his node seven is inaccurate; it is not present in e.g. *Ticinosuchus*, *Postosuchus* or *Terrestrisuchus*. Character (114) 'axial diapophysis reduced or absent' is phrased identically to (102), but has been given a separate number here because of the imprecise meaning of 'reduced', a relative term which, when used at different nodes compares the characters to two different sets of outgroup taxa. However, the axial diapophyses are just as reduced in *Gracilisuchus* (Romer, 1972d) and *Parasuchus* (Chatterjee, 1978) as in e.g. *Postosuchus* (Chatterjee, 1985) and equally reduced in *Gracilisuchus* (Romer, 1972d), *Ticinosuchus* and *Riojasuchus* (Bonaparte, 1971). Information on the character is not available for *Stagonolepis* (Walker, 1961) and many rauisuchids.

'Enlarged, pneumatic, basipterygoid processes' (115) is also a very dubious synapomorphy at this level. Basisphenoid elements are missing in *Terrestrisuchus* (Crush, 1984), *Pseudhesperosuchus* (Bonaparte, 1971) and rauisuchids, except for possibly *Prestosuchus*; only in *Postosuchus* are large basipterygoid processes present, somewhat larger than in *Parasuchus*, *Stagonolepis* and *Gracilisuchus*. To what extent these processes are pneumatic in the different taxa is impossible to determine from descriptive studies. Because of the extent of the missing data on character (115) it will not be considered further here. Character (116) 'length of pubis exceeds three times width of acetabulum' turns out to be identical to (105b) for all practical purposes as the length of the pubis is never exactly three times the width of the acetabulum.

Gauthier also listed 'fewer than four phalanges in pedal digit five' (117) as being synapomorphic at node seven in his cladogram; this character also diagnoses *Euparkeria* (Ewer, 1965), *Chanaresuchus* (Romer, 1972c) and *Riojasuchus* (Bonaparte, 1971).

In contrast to Gauthier who placed Rauisuchidae and Stagonolepidae (Aetosauria) as successive outgroups to Crocodylomorpha, Benton saw the two former taxa as constituting a monophyletic sister group (his Pseudosuchia) to crocodylomorphs and listed five synapomorphies (118-122) in support of monophyletic Rauisuchidae plus Stagonolepidae: Character (118) 'dorsal centra very constricted in ventral view' is verified by literature for *Rauisuchus, Prestosuchus chiniquensis* (Huene, 1935-1942), *Saurosuchus* and *Stagonolepis*, but in addition diagnoses, at least, *Postosuchus* and *Ornithosuchus* as well; for many other taxa description does not permit secure establishment of the presence/absence of the condition specified by (118). Character (119) 'acetabulum is subhorizontal and faces downwards, giving a 'pillar like' erect posture of the hindlimb' can only be said to be semi-present in *Stagonolepis* (Walker, 1961, Figure 17) and *Ticinosuchus* as the tilt of the acetabulum towards the horizontal is only slight in these animals; in contrast the acetabular portion of the ilium faces fully downwards in 'advanced' rauisuchids such as *Saurosuchus* (Bonaparte, 1984). 'Iliac blade is oriented subhorizontally' (120) is diagnostic at this node even though the ilium of *Stagonosuchus* does not conform to this specification; however, the vertical orientation of the iliac blade in this animal could be interpreted as a reversal because *Stagonosuchus* displays a number of advanced rauisuchid characters (e.g. ventrally facing acetabulum and three sacral vertebrae). Character (121), 'iliac blade is long and low', does not apply to *Stagonolepis* any more than to *Euparkeria* or some parasuchians (Westphal, 1976); however a number of rauisuchids display a distinctive looking low iliac blade in which the posterior process is very elongate. Hence a version of (121), exact, morphometrically defined, may prove a rauisuchid synapomorphy. Character (122) 'pubis attaches to anteroventral face on the ilium' is found in many archosaurs other than rauisuchids and

stagonolepids, e.g. *Ornithosuchus*, *Euparkeria* and *Chanaresuchus*.

Benton also diagnosed a monophyletic Rauisuchidae using *Ticinosuchus* and *Luperosuchus* as representatives of this family. The rauisuchids were never a clearly delimited group as e.g. the stagonolepids, ornithosuchids or parasuchians. This is in part due to the fact that many rauisuchid genera are represented by very fragmentary fossil material only, and partly due to the use of primitive – or otherwise invalid characters in the diagnoses of Rauisuchidae and Rauisuchia; e.g. two of four diagnostics listed by Chatterjee and Majumdar (1987) for Rauisuchia 'teeth robust recurved, laterally compressed with serrated edges' and 'pubis and ischium elongate with long median symphysis' are clearly also characteristic of other archosaurs; the former trait is found in *Riojasuchus*, *Herrerasaurus*, many theropods and erythrosuchids, and both characters are present in *Ornithosuchus*. The same author also listed 'maxillary teeth less than 12', 'short cervicals', 'closed acetabulum', 'lack of foot in pubis' and 'quadrupedal pose' as synapomorphies of Rauisuchidae within Rauisuchia; none of these are valid: the tooth count in ornithosuchids and *Stagonolepis* is also less than 12; the cervicals in Parasuchia and ornithosuchids are of the same length as those of *Ticinosuchus* and '*Mandasuchus*', and 'closed acetabulum', 'lack of foot in pubis' and 'quadrupedal pose' are found in numerous other archosaurs.

Benton in comparison, gave a number of potential synapomorphies for Rauisuchidae; these will here be discussed in relation to the genera: *Rauisuchus*, *Saurosuchus*, *Ticinosuchus*, *Luperosuchus*, *Prestosuchus*, *Stagonosuchus*, *Heptasuchus*, *Tikisuchus*, *Fasolasuchus* and *Teratosuchus* and the poposaurids *Poposaurus* and *Postosuchus*. Other nominal or potential rauisuchids and poposaurids are *Basutodon* (Kitching and Raath, 1984), *Lotosaurus* (Parrish, 1993), (the 'Kupferzell rauisuchid'; SMNS unnumbered) and (following Benton, 1986 and Chatterjee, 1985; the '?' marks are the former author's) ?*Wangisuchus*, ?*Fenhosuchus*, ?*Arizonasaurus* (listed as an erythrosuchid by Charig and Sues, 1976), *Anisodontosaurus*, ?*Procerosuchus*, and a number of unnamed or undescribed forms from England, Germany, America, Canada, India and South Africa. These latter taxa are mostly omitted or only briefly mentioned in the following discussion because the fossil material is fragmentary and only displays characteristics also found in most other lower archosaurs; in some cases the descriptions of these forms were unavailable to me and some of the taxa are as yet undescribed. In addition three rauisuchids has been described from the Russian region: *Vjushkovisaursus* (Ochev, 1982), *Vytshegdosuchus* and *Dongusuchus* (Sennikov, 1988). *Vjushkovisaursus* is represented by a small fragment of a pterygoid, some vertebrae and a humerus. The pterygoid fragment and vertebrae are not diagnostic; the humerus is strongly arched under its inner tuberosity (85) and could belong to a rauisuchid or a stagonolepid equally well. *Vytshegdosuchus* is also represented by very fragmentary remains only. The most interesting of these is part of an ilium which has a small anterior process, relatively low blade (incomplete posteriorly) and a supraacetabular crest; this combination of features makes it likely that *Vytshegdosuchus* is a rauisuchian. The *Dongusuchus* material consists of miscellaneous limb bones that could belong to a number different archosaurian taxa.

'*Mandasuchus*' appears to be closely related to *Prestosuchus* (Charig, 1956) and *Ticinosuchus* on account of the similarity of the dorsal osteoderms, which are of almost exactly the same shape, in these genera; furthermore the ilium is slightly horizontally inclined in both '*Mandasuchus*' and *Ticinosuchus* (Charig pers. comm.).

Character (123) 'extra slit-like fenestra between maxilla and premaxilla' is present in *Saurosuchus*, *Luperosuchus* (Romer, 1971a), *Heptasuchus*, *Tikisuchus*, *Teratosaurus* and *Postosuchus*, but not in *Prestosuchus*; for many other taxa data regarding this feature are missing. The character may also be present in *Jushatyria* (a taxon of uncertain affinity), (Kalandadze and Sennikov, 1985) and possibly *Euparkeria* (the material available to the present author did not allow secure establishment of whether the feature is present in this taxon); a fenestra between the premaxilla and maxilla is also present in *Shansisuchus* (Erythrosuchidae) (Parrish, 1992), *Erythrosuchus africanus* (BP/1/5207; most clearly seen on the left aspect of the specimen) contra Parrish, (1992) and *Chalishevia* (a probable erythrosuchid) (Ochev, 1980). Though the feature is figured as being subcircular rather than slit-like for these taxa at least one specimen of *Erythrosuchus* (BP/1/5207) has a dorsoventrally elongated fenestra between the premaxilla and maxilla. A fenestra or foramen also occurs between the premaxilla and maxilla of *Herrerasaurus* (Sereno *et al.*, 1993), many carnosaurs (Molnar *et al.* 1990), *Diplodocus* (Mcintosh, 1990), and amongst prosauropods in at least *Massospondylus* (e.g. BP/1/5241) and *Plateosaurus* (SMNS 13200) (Juul in prep.). A subnarial foramen, of about the same relative size as that found in *Herrerasaurus* appears to be present in *Proterosuchus*, and *Mesosuchus*, but not in other rhynchosaurs (David Dilkes, pers. comm.). Synapomorphy (124) 'movable joint between the maxilla and premaxilla' appear to be positively present in at least *Tikisuchus* (Chatterjee and Majumdar, 1987) *Teratosaurus*, and (125) 'main antorbital fenestra is low in front' is here considered a too vaguely phrased character. In contrast (126) 'tall orbit with a 'stepped' postorbital/jugal bar behind' is better defined and supported for *Saurosuchus*, *Heptasuchus*, *Prestosuchus* and *Tikisuchus*, but, as (123), diagnose *Postosuchus* in addition to rauisuchids. Character (127) 'lacrimal forms a heavy ridge over the orbit' is clearly invalid as the lacrimal is not part of the roof above the orbit in any of taxa for which good skull material has been recovered. The presence or non-presence of 'Proximal distance

between the ischia is less than that between the pubes' (128) is extremely difficult to establish for most rauisuchids and outgroup taxa from literature; however, (128) is definitely present in *Saurosuchus* (Bonaparte, 1981; Figure 24), but also in *Stagonolepis* (Walker, pers. comm). "Pubis is shorter than the ischium' (129) is present in at least *Saurosuchus* and *Ticinosuchus* (among rauisuchids), non-crown group archosaurs and Parasuchia, but not in *Gracilisuchus*, *Postosuchus*, *Ornithosuchus* or *Lagosuchus*.

Recently Parrish (1993) has published a phylogeny of crocodylotarsan archosaurs in which he separates *Prestosuchus*, *Ticinosuchus* and *Saurosuchus* from the 'traditional' Rauisuchidae into a family of their own, the Prestosuchidae; a similar idea was proposed by Charig (1956). It is not surprising if Rauisuchidae (as generally perceived), being so vaguely characterised, is a paraphyletic assemblage. However, the feeling here is that it is a serious shortcoming of Parrish' (1993) analysis that a number of relevant characters, listed above, were not employed; e.g. (126).."stepped" postorbital/jugal bar, (119) orientation of the acetabulum, etc. Furthermore in some instances there is no correspondence between his character list (table 1) and character state matrix (table 2), e.g. character 11 is given as a binary character in the character list, but 3 states are indicated in the matrix for the same character. Thus the matrix is difficult to test and lacking important characters. Nonetheless three characters (checked against original descriptive work) from Parrish (1993) are incorporated in the present analysis and in deference to this author his Prestosuchidae (and not 'other' rauisuchids) is employed as they incorporate the better described, often more complete taxa.

Benton also saw *Postosuchus*, *Terrestrisuchus*, *Protosuchus* and Crocodylia (the latter three taxa forming a restricted Crocodylomorpha) constituting a monophyletic group. Two of the characters, (115) 'enlarged, pneumatic, basipterygoid processes' and (116) 'length of pubis exceeds three times width of acetabulum', cited in support of this grouping have been discussed previously; (115) is not substantiated by literature for *Postosuchus*, *Terrestrisuchus* and *Protosuchus*. In contrast (116) is present in the three taxa just mentioned and in *Saurosuchus* (Bonaparte, 1981; Figure 24A), *Ornithosuchus* and some dinosaurs; among rauisuchids at least *Ticinosuchus* does not display the condition specified by this character, but *Saurosuchus* does. Character (130) 'posterior border of lower temporal fenestra is not bowed' is a reversal of (11); again the phrasing of this character is considered too vague here. 'Short descending process of squamosal and tall quadratojugal that contacts the postorbital' (131) is present in *Postosuchus*, *Protosuchus* (Crompton and Smith, 1980), *Hemiprotosuchus* (Bonaparte, 1971) and *Orthosuchus* (Walker, 1970), but no quadratojugal-postorbital contact exists in *Terrestrisuchus* (Crush, 1984), *Sphenosuchus* or *Crocodylus* (Walker, 1970). Character (132) 'maxillary-vomer secondary palate' is dubious as synapomorphy at this level: after examining *Postosuchus* material Parrish (1991) stated that the nature of the maxillary-vomer relationship in this animal could not be determined. Otherwise (132) is slightly developed in *Terrestrisuchus* (Crush, 1984) and extensively in Eusuchia (Romer, 1956). However, a secondary palate is not present in *Pseudhesperosuchus* (Bonaparte, 1971; Figure 24), and in *Protosuchus* this feature is rudimentary formed by either vomers or palatines; no maxillary participation was mentioned by Crompton and Smith (1980). Character (132) is also present in *Chanaresuchus* (as noted by Benton); in *Proterochampsa* a secondary palate is also developed, but without participation of the vomers (Sill, 1967).

Clavicles (133), 'reduction or loss of clavicle', were not described for *Terrestrisuchus* (Crush, 1984), *Protosuchus* (Colbert and Mook, 1951), *Pseudhesperosuchus* (Bonaparte, 1971) (all crocodylomorphs) or *Postosuchus* (Chatterjee, 1985), but are definitely present in *Ticinosuchus* (Krebs, 1965), *Stagonolepis* (Walker 1961), *Ornithosuchus* (Walker, 1964), *Euparkeria* (Ewer, 1965) and *Proterosuchus* (Cruickshank, 1972). Character (134) 'forelimb: hindlimb ratio is about 0.5' is, like character (132), not a very convincing synapomorphy at this level: the forelimb: hindlimb ratio of *Postosuchus* (Chatterjee, 1985) is approximately 0.4, in *Gracilisuchus* (Romer, 1972d) it is 0.54, in *Euparkeria* (Ewer, 1965) about 0.62, in *Ticinosuchus* 0.66 (Krebs, 1965) and ranges from 0.63 to 0.67 in crocodylomorphs (all measurements are taken from skeletal reconstructions or calculated from figures given in the respective descriptions).

'Acetabulum perforated' (135) is, apart from being paralleled in ornithosuchians, unproblematically apomorphic at node nine in Benton's cladogram. A 'supra'acetabular crest on ilium' (136) appears to be possessed by *Saurosuchus*, Poposaurids, *Terrestrisuchus*, *Protosuchus*, *Ornithosuchus* (Walker, pers. comm), *Lagerpeton* (Sereno and Arcucci, 1993), *Lagosuchus* and dinosaurs. No ilium is preserved for *Pseudhesperosuchus* (Bonaparte, 1971). In basal pterosaurs the pelvis is too transformed for valid comparison; here the upper border of the acetabulum is formed by the extremely low iliac blade and it is unclear if a supra-acetabular crest proper is present. 'Pedal digit V has no phalanges' (137) was also listed by Benton in support of a monophyletic Crocodylomorpha plus *Postosuchus*; this character is present in *Postosuchus*, *Protosuchus*, higher crocodylomorphs (e.g. *Crocodylus* and *Stenosaurus*), *Chanaresuchus* (Proterochampsidae), *Lagerpeton*, *Lagosuchus* (Romer, 1971b) and the early dinosaurs *Coelophysis* (Colbert, 1989) and *Dilophosaurus* (Welles, 1984), but not in *Sauropodomorpha*, *Herrerasaurus* (Reig, 1963; Sereno and Novas 1992; Figure 2, Novas, 1993) and pterosaurs where a fifth toe is retained; the pes is missing in *Staurikosaurus*

(Colbert, 1970) and the phalangeal formula for the fifth digit is unknown in basal ornithischians (Weishampel and Witmer, 1990a). It is problematic to attribute stances or gaits to fossils and character (138) 'stance is digitigrade' relies too heavily on conjectural evidence for use in cladistic analysis; it would of course be ridiculous not to assume that the elongate and closely appressed metatarsals of e.g. *Terrestrisuchus* and *Lagosuchus* implies some sort of digital stance *in vivo*, but it is less straightforward to interpret taxa like *Pseudhesperosuchus* and Ornithosuchidae in this respect.

Non-dinosaur bird-line archosaurs

Here are included the basal members of the other main lineage of archosaurs; the lineage giving rise to dinosaurs and, eventually, birds.

Their evolutionary success has been contributed to, among other things, the erect posture, parasaggital gait and hindlimb morphometrics of early bird-line archosaurs which enabled these to function as high speed cursors; the key morphological acquisitions being deep, perforated acetabulum, inturned, offset femoral head, prominent fourth trochanter, elongate epipodials and metatarsus, and an advanced mesotarsal ankle. Naturally these and similar characters have been widely used to diagnose bird-line archosaurs in phylogenetic studies; not all equally well defined as will become apparent below.

'Ornithosuchia'

As mentioned previously Gauthier, in contrast to Benton, chose to include *Euparkeria* in Ornithosuchia (node eight), however, the characters cited in favour of this arrangement are not impressive: 'squamosal reduced and descending ramus gracile' (139); in *Shansisuchus*, *Vjushkovia* (Erythrosuchidae) (Parrish, 1992; Figure 7 and 9) and *Luperosuchus* the squamosal does not seem relatively larger nor does its descending ramus appear less gracile than in *Riojasuchus*. Furthermore the squamosal looks very dissimilar in e.g. *Euparkeria*, *Riojasuchus* and *Herrerasaurus*, and in the latter genus its descending ramus can hardly be called gracile (Sereno and Novas, 1992, Figure 1b). The meaning of character (140) 'centra steeply inclined in at least the first four postatlantal cervicals' is probably similar to that of (209), see below, and 'modifications in the hindlimb and girdle correlated with semierect gait' (141) clearly describes a character complex rather than a single character and should have been listed accordingly in order to be useful in cladistic analysis. It is uncertain what the absent 'ventral flange' of the astragalus (142) is, and character (143) has been discussed above; a 'crocodile reversed ankle joint, with peg on calcaneum and socket on astragalus' is only present in Ornithosuchidae. Character (144) 'pedal digit five with fewer than four phalanges' is also present in *Chanaresuchus* as well as the taxa at node seven in Gauthier's cladogram; thus this character requires three steps when distributed on the cladogram whether it originated once at node three or three times at nodes three, seven and eight.

Benton listed numerous apomorphies in support of a less inclusive Ornithosuchia. (145, 146, 148-150) all are paralleled in Suchia and have been evaluated above; so have (139, 142). Of the remaining characters 'manual digit I is short and equipped with a diverging claw' (147) is hard to test for Ornithosuchidae and *Lagerpeton* as good manual material is lacking in these taxa, however, ornithosuchids appear to possess a first manual digit that is relatively short compared to the three middle digits, as do pterosaurs, *Lesothosaurus* (Sereno, 1991a), *Herrerasaurus* (Sereno and Novas, 1992), *Coelophysis* (Colbert, 1989), *Dilophosaurus* (Welles, 1984) and prosauropods; only in the latter two taxa is a diverging claw present on this digit. A lesser or anterior trochanter (151) is only present in Ornithosuchidae (Walker, 1964; Bonaparte, 1971) *Lagosuchus*, *Pseudolagosuchus* (Novas, 1992), dinosaurs, but not in *Lagerpeton* (Sereno and Arcucci, 1994; Figure 2); in pterosaurs no lesser trochanter was noted by Wellnhofer (1978). Character (152) 'fourth trochanter is a sharp flange' is distributed in the same manner as (151) apart from also being present in *Lagerpeton*. Character (153) 'shaft of femur is bowed dorsally' is too imprecise and does not define a condition characteristic of Ornithosuchia only; the femurs of e.g. *Chanaresuchus* and *Ticinosuchus* also conform to the phrasing of (153). A prominent cnemial crest is present on the tibiae (154) of *Gracilisuchus*, Ornithosuchidae, dinosaurs and probably *Lagerpeton* (Sereno; Figure 18C); pterosaurs also feature, as do many other archosaurs, a cnemial crest on the tibia, but only a weakly developed one.

Gauthier diagnosed a similar clade (his Ornithosuchia exclusive of *Euparkeria*), several of the synapomorphies he listed in support of it are paralleled in crocodile-line archosaurs or have been discussed already in other connections: (155, 156, 160 and 161). Of the remaining characters (162) 'anterior trochanter on femur appears early in post-hatching ontogeny' is clearly dubious; the phrasing 'early post-hatching ontogeny' is imprecise and ontogenetic series are not available for most of the relevant taxa. Neither is 'coracoid tubercle lies close to glenoid fossa and coracoid foramen' (157) accurate enough for the current purpose. Also (164) 'fifth metatarsal gracile' is too vague; furthermore the fifth metatarsal does not seem anymore gracile in ornithosuchids than in any other archosaurs, e.g. *Gracilisuchus* and *Terrestrisuchus*. Character (158) 'first metacarpal with offset distal condyles, and pollex directed medially and bearing enlarged ungual' is two rather than one character; the part of it which pertains to ungual proportions has been dealt with above. The other part of this character, first metacarpal with offset distal condyles, is present in Ornithosuchidae (Walker, 1964; Bonaparte, 1971), *Herrerasaurus* (Sereno and Novas, 1992), *Coelophysis* (Colbert, 1989), many prosauropods and *Lesothosaurus* (Sereno, 1991a), but does not seem to be so in pterosaurs or any other

archosaurs; manual material is missing in *Staurikosaurus* (Colbert, 1970), *Lagerpeton* (see Sereno; Figure 18C) and *Gracilisuchus* (considered an ornithosuchid by Romer, 1972d). Because digits are very sparsely preserved in basal ornithosuchians, even more so than metacarpals, character (159), 'manus more asymmetrical than in pseudosuchians, with inner digits much larger than outer digits', cannot be assessed with confidence and (163) 'aliform fourth trochanter' is here seen as just an alternative phrasing of character (152).

Ornithodira

Gauthier, Benton and Sereno (nodes ten, eleven and eight in respective cladograms) included nearly the same taxa in their definition of the next avian clade, *Ornithodira*. Within this clade Sereno placed pterosaurs as the basal-most taxon member while Benton and Gauthier remained inconclusive on the relative systematic positions of Pterosauria and *Lagosuchus* depicting the interrelationship of these taxa with Dinosauria as an unresolved tricothomy on their cladograms.

Gauthier, as the only one, listed two ornithodiran synapomorphies pertaining to the atlas-axis complex: (166) 'atlantal intercentrum enlarged, completely surrounding odontoid ventrally and laterally and fitting into prominent recessed area below odontoid on axis' and (167) 'axial intercentrum, and then odontoid, fuses to axis at cessation of growth'. The former condition seems to be present to the same extent in *Riojasuchus* as it is in the pterosaur *Rhamphorhynchus* ; it is not present in *Dilophosaurus* (Theropoda) and relevant material is lacking in many taxa, e.g. *Staurikosaurus* and basal ornithischians. The latter character cannot be properly tested in the fossil record; hence both (166) and (167) are not included in the present analysis. The postfrontal is absent (165) in proterochampsids, *Doswellia*, crocodylomorphs, pterosaurs and dinosaurs within Archosauria (again exact data were unobtainable for basal dinosauromorphs). Although a bit vaguely formulated (168) 'modification of cervical centra and zygapophyses that combine to yield an S-shaped neck', also listed by Gauthier, does describe a neck morphology only found in ornithodirans among archosaurs; notwithstanding that the neck curvature is very weak in *Lagerpeton*, *Lagosuchus* and early pterosaurs. Character (169) 'zygapophysial facets nearly vertically disposed in all but proximal part of the tail' by the same author, however, could not be verified and in many theropods, e.g. *Coelophysis* and *Dilophosaurus*, zygapophysial facets are almost horizontally inclined. The absence of an interclavicle (170) was regarded synapomorphic at this level by Gauthier, Benton and Sereno; indeed this character is well supported by descriptive literature (although the character could not be verified for *Lagerpeton*, *Lagosuchus* and *Pseudolagosuchus* by the present author). The clavicle is purported to be 'reduced and gracile' (171) and 'rudimentary or absent' (202) by Gauthier and Sereno respectively; again this character could not be tested here with regard to *Lagerpeton*, *Lagosuchus* and *Pseudolagosuchus*, but clavicles are not present in pterosaurs (Wellnhofer, 1978) or most dinosaurs. These two workers also both listed characters pertaining to the deltopectoral crest; (175) 'apex of deltopectoral crest placed distally on humerus' and (203) 'subrectangular deltopectoral crest'. The latter, by Sereno, is preferable because it is more concise and describes a condition easily recognisable in e.g. *Lagerpeton*, *Eudimorphodon*, *Herrerasaurus*, *Dilophosaurus* and *Lesothosaurus*. Two scapulocoracoid characters listed by Gauthier 'glenoid facet on scapulacoracoid faces posteroventrally' (172) and 'coracoid small, with subcircular profile, and lying in nearly the same plane as the scapula' (173) do not seem to be unique to ornithodirans. In contrast (176) 'less than five phalanges in manual digit four and less than three phalanges in manual digit five' by the same author are present in all ornithodirans where the relevant digits are preserved, but it is uncertain whether it also extends to Ornithosuchidae. Character (174) 'Forelimbs less than 55% of hindlimb length, and hindlimb very long relative to length of trunk' (Gauthier) is difficult to assess, the exact forelimb/hindlimb ratio cannot be obtained for ornithosuchids so it is uncertain if (174) also characterises this family; in any case this ratio is approximately .54 in *Gracilisuchus*, .55 in *Lagerpeton*, .52 in *Lagosuchus*, .51 in *Scleromochlus*, .48 in *Herrerasaurus*, .41 in *Coelophysis* and plus .60 in other archosaurs except pterosaurs in which the forelimb is too transformed for comparison (most ratios were calculated from measurements taken from skeletal reconstructions and hence may be prove to contain errors).

'At least three vertebrae involved in sacrum' (177) is not a valid synapomorphy for Ornithodira unless one is willing to accept a reversal to the plesiomorphic condition of two sacral vertebrae in *Lagosuchus*, and probably *Lagerpeton*; the character is present in Pterosauria, *Scleromochlus* (Krebs, 1976) and dinosaurs (except maybe *Staurikosaurus*; see below). In contrast to Gauthier who listed it synapomorphic at this level, a more recent study (Novas, 1992) claims that a brevis shelf on ventral surface of the postacetabular portion of ilium (178) is present only in Saurischia (now also including Herrerasauridae; see below (Sereno and Novas, 1992)) and Ornithischia; this is in concordance with drawn reconstructions of ornithodirans. A shelf-like projection is also present on the ilium of *Poposaurus* (see Mehl, 1915b; Chatterjee, 1985; Figure 25), but it is hardly likely that this feature is homologous with the brevis shelf in dinosaurs. Gauthier also cited several characteristics of the hindlimb in support of Ornithodira: (179) 'birdlike distal end of femur, prominent anterior and posterior intercondylar grooves, with the latter constricted by prominent external tibial condyle...' is an extensive character complex of which many of the sub-characters are found in ornithosuchids and rauisuchids. An anterior intercondylar groove is

absent in *Lesothosaurus*, basal 'thyreophorans', and both anterior and posterior intercondylar grooves are absent in heterodontosaurids; in some more advanced ornithischians (e.g. psittacosaurids; Sereno, 1990) where both these grooves are present it would appear to be a case of parallelism. 'Tibia as long or longer than femur' (180) is present in *Lagerpeton*, *Lagosuchus*, *Pseudolagosuchus*, *Staurikosaurus* (Colbert, 1970), theropods, *Lesothosaurus* and *Terrestrisuchus* (Crush, 1984), but not in prosauropods and, peculiarly enough, *Herrerasaurus*. Having cited (181) 'fibula thin and strongly tapered distally and calcaneum reduced' it is clearly redundant also to list (182) 'astragalus transversely widened', and (183) astragalus and calcaneum with smooth rollerlike articular surfaces abutting against depressed distal tarsals' is a bit vague and could be applied to lower archosaurs also, e.g. *Euparkeria*. Further redundancy, as noted by Sereno (p. 38), is present in listing both (184) 'metatarsals elongate and closely appressed' and (185) 'pes digitigrade'; characters similar to the former have been listed by Benton: (200) 'metatarsals II-IV are closely bunched as a unit' and Sereno 'compact metatarsus with proximal third of metatarsals 1-4 shafts closely appressed'. Benton's or Sereno's versions are superior because they do not address the question of elongation of the metatarsus; this is done separately by Sereno in character (208) 'metatarsal 2-4 elongate with metatarsal 3 more than 50 percent of tibial length'. Character (200) and (208) seem to be autapomorphic for Ornithodira. In contrast there is much homoplasy in Gauthier's 'pedal digit five reduced, does not exceed length of metatarsal IV, and composed of no more than two phalanges' (187). This character is present in *Chanaresuchus*, *Gracilisuchus*, *Postosuchus*, *Crocodylomorpha* and Ornithodirans; in Pterosauria the fifth pedal digit is highly variable in length and it is uncertain what the original condition was in this group, and because of incomplete preservation character (187) cannot be securely assessed for Ornithosuchidae either; in addition the phrasing of the character or its absence is not applicable to many taxa, e.g. Rhynchosauria and *Prolacerta*.

Absence of dermal armour has been construed, in the light of other character evidence, to be the result of a secondary loss in ornithodirans (Gauthier; Sereno; character 188); body armour, though, is present in higher theropods and ornithischians.

Benton listed some additional characters at this level: (189) 'presacral vertebral column is divided into three regions (cervical, cervical-thoracic, lumbar)'; such partitioning of the axial column could also be applied to other archosaurs, e.g. ornithosuchids and crocodylomorphs. 'Centra are steeply inclined in at least cervicals 3-6' (190) is as (140) not clear, but both probably refer to the condition described by Sereno in synapomorphy (209); see below. Character (191) 'zygapophyses of the middle and posterior caudals are inclined posteroventrally' is neither supported nor contradicted by descriptive work; furthermore it is difficult to assess its validity as there is often little more than a hyposphene remaining posteriorly to the neural spine on the arches of the relevant vertebrae. 'Fourth trochanter runs down one third to one-half the length of the femur shaft' (195) is not convincing: Benton noted himself that the character is paralleled in *Erythrosuchus* and *Chanaresuchus*, and present in Ornithosuchidae, but not in pterosaurs. In addition this character seems to be size related: the fourth trochanter is relatively more distally positioned in large than in smaller specimens of *Euskelosaurus* (Juul in prep.). 'Knee articulates at 90°' (196) is extremely difficult of assess as an ornithodiran synapomorphy. (197) 'Mesotarsal ankle joint with astragalus and calcaneum fused to tibia'; in Ceratosauria (Rowe and Gauthier, 1990) and *Heterodontosaurus* (Ornithischia) (Weishampel and Witmer, 1990a) astragalus and calcaneum are fused with the tibia, at least in adult specimens, however, Romer noted that in *Lagerpeton* the proximal tarsals are fused to each other, but not to the tibia. Benton's notion that the ornithodiran calcaneum has no tuber at all (198) is contradicted by the presence of a rudimentary tuber on the calcanae of *Lagosuchus*, *Pseudolagosuchus* and *Ischisaurus* (Herrerasauridae) (Novas, 1989); supporting Sereno's character (206) 'calcaneal tuber rudimentary or absent'. 'Ascending process of astragalus fits between tibia and fibula' (199) could also describe the condition in *Riojasuchus* (compare Sereno; Figure 7B,F,G with Novas, 1989; Figs. 2(5), 5(2,10)), furthermore the ascending process on the astragalus of *Lagerpeton* is situated at the posterior margin of the element (Sereno and Arcucci, 1993), not the anterior as in other dinosauromorphs; thus a detailed study is needed to assess whether the different ascending processes of archosaur astragali are homologous. Indeed in many other archosaurs there is a proximal astragalar process with a tibial facet medially and fibular facet laterally (see e.g. Sereno; Figure 6 and 8). Further characters listed by Benton at his node nine have already been reviewed above (e.g. parallelisms in crocodile-line archosaurs).

Sereno also purported 'anterior cervical centrum length longer than mid-dorsal length' (201), 'femoral shaft bowed anteriorly along at least 80 percent of femoral length' (204), 'posterior groove on astragalus absent' (205) and 'distal tarsal 4 subequal in transverse width to distal tarsal 3' (207) to be ornithodiran synapomorphies. Only the latter appear to be valid: character (201) is present, to various degrees, in a lot of archosaurs other than ornithodirans; e.g. *Ticinosuchus*, *Postosuchus*, some crocodylomorphs and *Gracilisuchus*. Furthermore it is not present in Scleromochlus nor seems to be so in Lagerpeton. The tarsal features of different archosaurs alleged to be 'posterior grooves' in character (205) are morphologically very different and it is questionable if they are homologous (compare Sereno; Figs. 3-8) and estimation of the presence of (204) is highly prone to error as noted by Sereno himself. In contrast character (207) appears to be autapomorphic for Ornithodira.

Dinosauromorpha

The long-limbed avian-clade archosaurs *Lagerpeton*, *Lagosuchus* and *Pseudolagosuchus* are held to define a monophyletic taxon together with dinosaurs by Novas (1992) and Sereno. The latter worker gave a number of characters diagnosing this *Dinosauromorpha*. At least one autapomorphy was included: 'astragalus with acute anteromedial corner' (211), present in *Lagosuchus*, *Pseudolagosuchus* and dinosaurs (Novas, 1989); Sereno also claims its presence in a specimen of *Lagerpeton*, but no mention of Pterosauria was made in this connection nor was I able determine the presence/non-presence of (211) in this taxon.

'Cervical column following strong sigmoid curve with dorsal offset of the anterior face of the centrum present as far posteriorly as the ninth or tenth presacral' (209), 'forelimb 50 percent or less of hindlimb length' (210) and 'distal tarsal 4 with articular surface for metatarsal 5 limited to half of its lateral surface' (213) are all disregarded here as dinosauromorph synapomorphies: (209) is a very unreliable character because of difficulties in gauging relative offset of the anterior and posterior articular surfaces of centra because postmortem distortion can obscure the exact shape of the centra as admitted by Sereno (p. 24); I can confirm that in *Massospondylus* this is very often the case. Likewise it is difficult to delimit the lateral surface of distal tarsal 4 (213) in many archosaurs, e.g. *Ticinosuchus* and *Riojasuchus*, as this bone is often rounded, and Romer's (1971b) reconstructions of *Lagerpeton* and *Lagosuchus* do not conform to character (213). For treatment of (210) I refer to the critique of (174) above.

In contrast character (212) 'distal articular surface of calcaneum with transverse width 35 available or less that of astragalus' is not conflicting with the present literature on dinosauromorphs. 'Metatarsal 5 with articular surface for distal 4 oriented parallel to shaft axis – 'hooked' proximal end absent' (214) appear to be very similar to Benton's character (39) 'loss of anterior proximal' hook' on the metatarsal V'. However, it is unlikely that these authors perceived a 'hooked' metatarsus in the same manner judging from their very different application of the character; thus Benton would probably not refer to the proximal end of the fifth metatarsal in *Riojasuchus* as being 'hooked' because it does not possess a clearly distinguishable medial projection (e.g. as in *Proterosuchus*) whereas Sereno did because he put emphasis on the orientation of the articular surface with distal tarsal 4 in his version of the character.

Character (215) 'Mid-shaft diameters of metatarsals 1 and 5 less than those of metatarsals 2-4' is closely approached by the condition in *Riojasuchus* where metatarsal 1 is the least robust, and metatarsal 5 only insignificantly wider than the second metatarsal and of about the same width as metatarsal 3 and 4 at mid length. In *Terrestrisuchus* the situation is the reverse; here the fifth metatarsal is thinner than the other four and metatarsal 1 is of roughly the same diameter as the three middle ones. In *Postosuchus* the first metatarsal is clearly the most delicate one, but of the outer digit only a short spur remains which makes safe comparison impossible.

Dinosauriformes

Novas (1992) gave a diagnosis of a less inclusive avian clade; Dinosauriformes (=Dinosauromorpha exclusive of *Lagerpeton*). Three of the five characters listed by Novas also apply to taxa outside Dinosauriformes (154 – tibia with prominent cnemial crest; 162 – anterior trochanter on femur; 203 – subrectangular, distally projected deltopectoral crest on humerus). The remaining two may be diagnostic here: 'presence of a trochanteric shelf on the lateroproximal surface of the femur' (216); the trochanteric shelf is more or less confluent with the anterior trochanter and runs laterodistally from the base of the former in *Lagosuchus*, (probably also *Pseudolagosuchus*) *Herrerasaurus* (Novas, 1992) and ceratosaurs (Theropoda); in the latter group it appears to be a sex related character as it is only present in the robust specimens of each species (Rowe and Gauthier, 1990) see also (Raath, 1990). In *Massospondylus* and other prosauropods of the BPI collection the anterior trochanter forms a straight flange or spike on the proximal femur, however, no distinct "trochanteric shelf" can be discerned on the lateroproximal surface of the same bone in these animals (pers. obs.). The lesser trochanters in *Lesothosaurus* and *Heterodontosaurus* are very different from each other and from the corresponding features in the taxa just mentioned, and as in prosauropods a trochanteric shelf does not seem to be present in Ornithischia; there is no mentioning of trochanteric shelves in any of the descriptions of the major ornithischian groups in Weishampel, Dodson and Osmólska (1990). Indeed this absence, together with the fact that the trochanteric shelf is very reduced in tetanurine theropods and sauropodomorphs (missing in the latter group in the opinion of the present author), was used later by Novas (same paper) to diagnose his Eudinosauria (253); the author concordantly interpreted the pronounced trochanteric shelf on the femora of ceratosaurs as synapomorphic for this group of theropods.

The second synapomorphy listed for Dinosauriformes (217) 'distal tibia with lateral longitudinal groove' probably refers to the 'longitudinal channel' on the lateral surface of distal tibia described in an earlier paper by Novas (1989). This character is present in *Pseudolagosuchus*, *Herrerasaurus*, *Staurikosaurus* (Novas, 1989), prosauropods (Galton, 1990) and *Postosuchus* (Chatterjee, 1985); I was unable to confirm the character for any other taxa.

Novas (1992) put forward the claim that *Pseudolagosuchus* is at present the 'thecodont' most closely related to Dinosauria (i.e. the latter's sister taxon) on the basis of the following shared derived characters: (218) 'elongated pubis, nearly as long as the femur' and (219) 'presence of a pyramidal-shaped

ascending process of the astragalus, with a posterior, subvertical facet and presence of an elliptical depression behind the process'. The former is clearly too imprecise to be a valid character and although the ascending process of the astragalus seems to have been pyramidal-shaped in *Pseudolagosuchus* an 'elliptical depression' is not figured by Novas (1989; compare Figure 2.6 and 3.9) for this genus. Furthermore the ascending process of the astragalus in *Lagosuchus* is very similar to that of *Pseudolagosuchus* (compare Novas, 1989; Figure 3(9) and Sereno; Figure 9C).

'Ornithotarsi'

Benton alternatively listed four synapomorphies shared by Pterosauria and Dinosauria, Ornithotarsi, without claiming that the taxon is necessarily valid. One of these, absence of a postfrontal (165), has been treated above and for critique of 'caudal zygapophyses nearly vertical' (220) I refer to the treatment, also above, of the very similar character 'zygapophysial facets nearly vertically disposed in all but proximal part of the tail' (169). 'No more than four phalanges in manual digit IV' (221) cannot be tested for ornithosuchids and *Lagerpeton* because manual material is lacking in these animals (Romer 1971b; 1972a; Arcucci, 1986; 1987). The character is present in pterosaurs, dinosaurs and in the crocodylomorphs *Terrestrisuchus* and *Crocodylus*, but not in *Protosuchus*, however, because of the important data missing, character (221) is disregarded here. 'Proximal head of femur fully offset' (222), also cited by Benton in favour of Ornithotarsi, does not seem to apply any more to *Herrerasaurus*, *Staurikosaurus* and *Lesothosaurus* than to *Riojasuchus* or *Lagosuchus*; in addition the proximal femur in pterosaurs, with only a prominent major trochanter developed, is very aberrant looking and hardly comparable to that of the just mentioned taxa with respect to character (222).

Basal Dinosauria

Logically the taxa included at this level should only be those which exhibit the synapomorphies diagnosing Saurischia plus Ornithischia because the genera on which Owen (1842) erected his Dinosauria belong to either of these orders. However a few carnivorous archosaurs, notably *Herrerasaurus*, *Staurikosaurus* and *Ischisaurus* (taxa originally believed to be saurischian dinosaurs (Reig, 1963; Colbert, 1970)) which only possess some of the diagnostic characters of the saurischian-ornithischian clade have also been included in Dinosauria as some sort of basal members branching off on the cladogram being successive outgroups of the 'Owenian' dinosaurs (e.g. Benton 1990). Recently *Ischisaurus* and *Frenguellisaurus* (another early dinosaur) have been regarded junior synonyms of *Herrerasaurus* and this taxon together with *Staurikosaurus* was united in the Herrerasauridae on the basis of a number of shared derived characters (Novas, 1992). Even more recently the first complete skeleton of *Herrerasaurus* was found and on the basis of the new information supplied by this material the taxon has been referred to Theropoda (Sereno and Novas, 1992). The evidence supporting the reassignment of *Herrerasaurus* includes the presence of a pubic foot and elongate prezygapophyses in distal caudal vertebrae; the former of these conditions imply affinity to tetanuran theropods, but the latter may characterise Theropoda in general. However, the lack of a fully incorporated third vertebra in the sacrum and the presence of a femur: tibia ratio of more than 1.0 in *Herrerasaurus* appear to dispute its inclusion in Theropoda.

The taxonomic status of the very enigmatic segnosaurs will not be addressed in this paper.

Both Gauthier and Benton provided extensive character lists supporting the monophyly of Dinosauria (including *Herrerasaurus* and *Staurikosaurus*). Only one synapomorphy pertaining to the skull is listed by these authors: 'vomers elongate, reaching posteriorly at least to level of antorbital fenestra' (223); it is present in *Coelophysis*, carnosaurs, *Lesothosaurus*, *Plateosaurus* (Galton, 1990), ornithosuchids, *Chanaresuchus*, *Stagonolepis*, *Postosuchus* and *Terrestrisuchus*, and in Pterosauria the vomers are elongate in some taxa; unfortunately information is not available for a number of archosaurs for character (233). In contrast 'lateral exposure of quadrate head' (245), cited by Sereno and Novas (1992) is only present in the basal archosaur *Proterosuchus* (and possibly *Lagerpeton*, *Lagosuchus* and *Pseudolagosuchus*; however, good skull material is lacking in these taxa) and, widely, in Dinosauria, e.g. in *Herrerasaurus* (Sereno and Novas, 1992), *Syntarsus* (Colbert, 1989), *Allosaurus* (Molnar *et al.*, 1990) Ornithomimidae (Barsbold and Osmólska, 1990) (Theropoda), *Plateosaurus* (Prosauropoda) (Galton, 1990), *Lesothosaurus* (Sereno, 1991a), basal 'thyreophorans' (Coombs *et al.*, 1990) and Hadrosauridae (Ornithischia) (Weishampel and Horner, 1990). These authors (Sereno and Novas, 1992) also purported other characters to be synapomorphic for dinosaurs: 'extension of adductor musculature onto the frontal' (244) and 'reduction of the posttemporal opening to a foramen' (246). The former is treated below, under Saurischia and the latter is not a convincing dinosaurian synapomorphy; it is present in e.g. *Herrerasaurus*, *Syntarsus*, *Plateosaurus*, *Lesothosaurus* and *Heterodontosaurus* (Weishampel and Witmer, 1990a). Nevertheless there is some variation in this character relative to outgroup taxa; the posttemporal opening or foramen is only slightly more reduced in *Coelophysis* than in *Ornithosuchus*, and even less so compared to *Rhamphorhynchus* (Sereno) and *Araripesaurus* (Pterosauria) (Wellnhofer, 1978), and comparative material is lacking for *Lagosuchus* and *Pseudolagosuchus*.

Character (165) 'absence of a postfrontal' (Sereno and Novas, 1992) was treated in connection with synapomorphies listed for Ornithodira; increased asymmetry (225) of the hand is also potentially synapomorphic for Dinosauria as all members of this clade have lost the ungual of the fourth manual digit,

but as noted above important manual material is missing in e.g. ornithosuchids and *Lagerpeton*, precluding conclusive testing.

Three sacral vertebrae (232) may be a derived condition at this level, but full incorporation of third vertebra in the sacrum must have happened independently in the main dinosaurian lineages if Herrerasauridae is included in Theropoda; the lowest sacral count is three in Prosauropoda, four in Sauropoda, five in Ornithischia, and five in theropods other than herrerasaurids. In *Herrerasaurus* the last dorsal has been incorporated as an incipient third sacral; its ribs are narrow, compared to those of the other two sacrals, and do reach the medial walls of the iliac blades (Sereno and Novas, 1992). Colbert (1970) identified three sacral vertebrae in *Staurikosaurus*, but Galton claimed that only two are present in the type specimen, and that the first caudal had been mistaken for a sacral (Galton, 1977). If this is true then either *Staurikosaurus* is not a dinosaur or the plesiomorphic number of sacral vertebrae in archosaurs is retained for Dinosauria.

Characters pertaining to the deltopectoral crest were also cited at this level by respectively Benton, and Sereno and Novas (1992): (235) 'deltopectoral crest is low and runs one-third or one-half of the way down the shaft' and 'elongate deltopectoral crest on humerus'. To be valid this character will have to be stated more unambiguously, e.g. as 'elongate deltopectoral crest with apex situated at a point corresponding to at least 38% of the length of the humerus measured from the proximal end'; this proportional figure is 31% in *Lagerpeton*, almost 36% in *Eudimorphodon*, almost 39% in *Herrerasaurus* (no humerus exists in the type material of *Staurikosaurus*) and higher than 39% in *Coelophysis*, *Sellosaurus* and *Lesothosaurus* (measurements used to obtain these figures are taken from drawings and plates in Wellnhofer (1978) (*Eudimorphodon*), Sereno (1991b) (*Lagerpeton*), Sereno and Novas (1992) (*Herrerasaurus*), Colbert (1989) (*Coelophysis*), Galton (1984) (*Sellosaurus*) and Weishampel and Witmer (1990a) (*Lesothosaurus*)).

'Glenoid faces fully backwards' (234), listed by Benton, does not appear to be any more pronounced in *Dilophosaurus* (Rowe and Gauthier, 1990), *Megalosaurus* (Molnar *et al.*, 1990), *Struthiomimus* (Theropoda) (Barsbold and Osmólska, 1990), *Heterodontosaurus* and *Euoplocephalus* (Ornithischia) (Coombs and Maryanska, 1990) than in *Lagosuchus* (Romer, 1972a).

The acetabulum is semiperforate in *Postosuchus*, crocodylomorphs (e.g. Crush, 1984; Crompton and Smith, 1980) *Ornithosuchus* and *Lagosuchus* (Sereno; Figure 25), largely perforated in Herrerasauridae and fully open in other dinosaurs; hence 'largely to fully open acetabulum' (237) by Benton is preferable to similar characters listed by Gauthier and Novas (226). I was unable to confirm any of the trochanteric characteristics alleged to be dinosaurian synapomorphies; (227) 'ventral orientation of the antitrochanter' and (247) 'antitrochanter within the acetabulum that is divided by a notch'. The antitrochanter does not appear 'notched' in any reconstructions, but it is facing ventrally in ceratosaurs (Rowe and Gauthier, 1990), *Plateosaurus* and pachycephalosaurs (Maryanska, 1990); however, comparison with outgroup taxa is difficult because the antitrochanter is hardly ever described or figured clearly for these animals. Novas (1992) reported that an 'ischium with slender shaft and with ventral 'keel' (obturator process) restricted to the proximal third of the bone' (241) is characteristic for dinosaurs; this does not hold true for a number of taxa, e.g. *Syntarsus*, Oviraptorosauria (Barsbold *et al.* 1990) (Theropoda) prosauropods, and *Lesothosaurus*, and the character is not likely to be synapomorphic at this level.

The 'brevis fossa' listed by Sereno and Novas (1992) must be the feature, for the origin of M. caudofemoralis brevis, which is present concurrent with the brevis shelf (178), mentioned above, and is thus for systematic purposes the same character and synapomorphic for dinosaurs.

The different femoral characteristics in the combined lists for this clade do not describe conditions seen in dinosaurs only: '...inturned head of femur' (227) is present in e.g. *Lagosuchus*, 'proximal head of femur is fully offset' – 'femoral head more distinctly set off from shaft of femur' (238) could also diagnose *Riojasuchus* (and maybe *Ornithosuchus*) and 'subrectangular femoral head' (248) applies to *Lagerpeton* as well (see Romer, 1972a; Figure 1). If the two latter characters are merged a unique dinosaurian condition is defined: 'femoral head subrectangular and distinctly offset'. Still not very satisfactory and because of the vagueness of the terms this character will be regarded here as tentative synapomorphic.

Contra Gauthier (228) the anterior trochanter is not enlarged in *Herrerasaurus* compared to *Lagosuchus* (see Novas, 1992; Figure 4); an account of this aspect of femoral morphology in dinosaurs is given in connection with assessment of character (251) below. Modifications of the lower leg have also been noted for Dinosauria such as mediolateral expansion of the distal tibia ('twisted' tibia) and 'tibia overlaps anteroproximally and posteriorly the ascending process of the astragalus (i.e. ascending process inserts beneath the tibia), with consequent ventral projection of the posterior process of the tibia' (242). According to an earlier paper by Novas the ascending process of the astragalus also inserts beneath the tibia in *Pseudolagosuchus* (Novas, 1989), however, the posterior process of the tibia is considerably distally projected in *Herrerasaurus*, *Lesothosaurus*, *Pisanosaurus* (Ornithischia) (Novas, 1989) and *Plateosaurus* (Galton, 1990), but not, in *Dilophosaurus* (Rowe and Gauthier, 1990). If limited to 'posterior process of the tibia projected markedly distally with receiving depression on dorsal aspect of astragalus' the character is a 'valid' dinosaurian synapomorphy, however, it will require further rephrasing so as to substitute the term markedly with

an exact definition. The transverse broadening of the distal tibia, part of synapomorphy (229) cited by Gauthier, does not only characterise dinosaurs as it is also exhibited, to a slight extent, by *Pseudolagosuchus* (Novas, 1989; Figure 3.13); it is obvious, though, that a trait like this can be influenced to a great extent by post-mortem compressional distortion. All of the conditions noted by the latter author in character (230) are also present in the tarsi of *Lagerpeton*, *Lagosuchus* and *Pseudolagosuchus* except for the presence of a calcanear tubercle which, contra Gauthier, also appears to be present in some dinosaurs, e.g. *Ischisaurus* and *Riojasaurus* (Novas, 1989).

The proximal articular surface of the calcaneum is concave (243) in *Ischisaurus*, *Coelophysis*, *Allosaurus* (Molnar *et al.*, 1990), *Riojasaurus* and *Hypsilophodon* (Sues and Norman, 1990) (Ornithischia), but not in *Pisanosaurus*, *Lesothosaurus* (Weishampel and Witmer, 1990b), *Pseudolagosuchus*, *Lagosuchus* (Novas, 1989) or basal – and crurotarsal archosaurs; hence Novas' character (243) only diagnoses Saurischia, and not Ornithischia, within Dinosauria. Two further ankle characters were cited by Sereno and Novas (1992) 'reduction of the medial process of the calcaneum' (249) and 'reduction of the heel on distal tarsal 4' (250); unfortunately information on the latter is to a great extent unavailable and the former must also diagnose *Pseudolagosuchus* since the size of the medial process of the calcaneum in this genus is subequal to that of *Ischisaurus* and *Riojasaurus* (compare Novas, 1989; Figure 2.12, 3.10 and 4.11); the character was not used by Novas (1993) subsequently.

A number of clearly invalid apomorphies are found in the diagnoses of Dinosauria: 'scapula at least three times longer than width at base...' (224); if by scapular base is meant either proximal or distal end this morphometric relationship does not obtain in *Herrerasaurus*, *Coelophysis*, *Plateosaurus* or *Lesothosaurus*. If instead the portion of the scapula immediately above the glenoid is considered the base, most lower archosaurs are also characterised by (224). Character (231) 'pedal digit five shorter than metatarsal I; the foot is tridactyl in typical dinosaurian condition' clearly also diagnoses *Lagosuchus* (Romer, 1971b). Another dubious character is (239) 'greatly reduced fibula'; the fibulae of *Herrerasaurus* (Reig, 1963), *Coelophysis* and *Anchisaurus* (Galton and Cluver, 1976) are subequal in relative size to, or only slightly more reduced than the fibula of *Lagosuchus* (Romer, 1972a). Only in gracile bipedal ornithischians is the fibula considerably reduced.

A few characters shared by Saurischia and Ornithischia not found in Herrerasauridae have been listed by Benton (1990a) and Novas (1992); most of these have already been discussed: (232) 'three or more sacral vertebrae', (252) 'transversely expanded distal end of tibia' (part of character 229) and (253) 'trochanteric shelf reduced to a slight prominence'.

'Lesser trochanter on the femur is a spike or a crest' (251) refers to a character which is polymorphic in ceratosaurs: the anterior trochanter is crest-like in robust ceratosaurs and spike-like in gracile specimens similar to the corresponding feature in prosauropods. In Ornithischia the anterior trochanter is often blade-like, e.g. in *Lesothosaurus*, but in some taxa, like *Dryosaurus* (Sues and Norman, 1990) it resembles that of carnosaurs except for being more proximally displaced and separated from the rest of the femoral head by a relatively deeper vertical cleft (compare Sues and Norman, 1990; Figure 24.5I and Molnar *et al.*, 1990; Figure 6.10C). Because the very weakly developed anterior trochanter on the femur of *Herrerasaurus* (Novas, 1992; Figure 4C) could be interpreted as both an incipient 'crest' or -spike' it would clearly amount to redundancy listing both character (251) and 'presence of a prominent anterior (lesser) trochanter on the femur' (228), by Novas, as characters distinguishing saurischians and ornithischians from Herrerasauridae. In the light of the above it is hard to say which of these characters is preferable at present; 'prominent' is not a clear-cut definition and the superficial resemblance of anterior trochanters in some saurischians and ornithischians could very well turn out to be non-homologous. Both characters also apply to Ornithosuchidae in which the lesser (anterior) trochanter is, at least in *Ornithosuchus*, like that of some theropods in being slightly undercut (separated from the rest of the femur by a cleft) proximally (Walker, per. comm.).

Saurischia

Two of the three main clades within Dinosauria, the carnivorous, bipedal theropods and the herbivorous, mainly quadrupedal sauropodomorphs, are held by most workers today to constitute a monophyletic taxon, the Saurischia. Alternative groupings of the major dinosaurian lineages, e.g. a monophyletic Sauropodomorpha plus Ornithischia, have been proposed, but the evidence is not convincing; see Benton (1990a) for a resume.

Numerous saurischian synapomorphies were listed by Gauthier and Benton (1990a):

Character (244) 'temporal musculature extends onto frontal' was listed for Dinosauria by Novas and Sereno (1992); on the basis of fossil – or descriptive material available to the present author it was not possible to determine to which taxa this character applies wherefore it was not included in the analysis below. Even though broad symphysial contact between the maxillary process of premaxilla and the nasal is the rule in Ornithischia, and the same contact appears 'reduced' in lateral view of the skull of saurischians (in *Herrerasaurus* an intermediate condition is present) in comparison, character (255) 'contact between maxillary process of premaxilla and nasal reduced or absent' is hard to assess at present. Good skull material is missing for e.g. *Lagosuchus* and *Lagerpeton* and the character is highly variable among other dinosaurian outgroup taxa: some symphysial contact between the maxillary process of premaxilla and the nasal occurs in *Proterosuchus*, some erythrosuchids, *Euparkeria*, rauisuchids and

Riojasuchus, but is absent, in lateral aspect, in stagonolepids and *Ornithosuchus*. And the character like many others needs to be phrased more precisely. The validity of (256) 'posterior cervicals elongate' becomes apparent when length ratios of posterior cervicals to mid dorsals are compared (length of presacral centrum 8/length of presacral centrum 18): this ratio is 0.89 in *Heterodontosaurus*, approximately 1.1 in *Dilophosaurus*, 1.76 in *Coelophysis* and 1.66 in *Massospondylus*; again there is some variation in outgroup taxa, but a plesiomorphic ratio of less than 1.0 is found in *Lagerpeton* and *Scleromochlus* (and also retained by *Herrerasaurus*!). Gauthier provided good discussion of synapomorphy (257) 'axial postzygapophyses set lateral to prezygapophyses' and little can be added here except that contra Gauthier the condition of this character in *Euparkeria* cannot be deduced from Ewer (1965). It is questionable if character (258) 'epipophysis present on anterior cervical postzygapophyses' is synapomorphic at this level: a number of prosauropods seem to be lacking these processes on cervical vertebrae, e.g. *Sellosaurus* (*'Efraasia'*)(Galton, 1973) and *Lufengosaurus* (Galton and Cluver, 1976) and some possess features on the anterior cervical postzygapophyses which at best can only be described as incipient epipophyses, e.g. *Riojasaurus* (Bonaparte, 1971), however, *Massospondylus* does have epipophyses on at least the first five postaxis cervicals (pers. obs.) ; thus character (258) may have evolved twice in Saurischia. This synapomorphy is further discredited by the fact that epipophyses are present on the postzygapophyses of the atlas and third cervical of *Lesothosaurus* (Sereno, 1991a).

In contrast 'hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae' (259) is a far more substantiated saurischian characteristic; it is present in *Herrerasaurus*, *Dilophosaurus* (but not in *Coelophysis*), occurs widespread in Carnosauria (Molnar *et al.*, 1990) and in Sauropodomorpha, e.g. *Massospondylus* (Cooper, 1981) and *Apatosaurus* (McIntosh, 1990). The character is not seen in ornithischians (Bakker and Galton, 1974) or *Staurikosaurus* (Colbert, 1970). Hyposphene-hypantra articulations are also present in the rauisuchids *Fasolasuchus* (Bonaparte, 1981) and *'Mandasuchus'* (pers. obs.), and in *Postosuchus*; Gauthier also cites Parrish for the observation that these features are present in Aetosauria (Stagonolepidae), however, for *Stagonolepis* this is not the case (Alick Walker, pers. comm.). It is hard to determine if character (260) 'manus more than 45% of length of humerus plus radius' is apomorphic for Saurischia or plesiomorphic for Dinosauria because manual material is lacking for outgroup taxa such as *Lagerpeton* and *Riojasuchus*. The reconstructions of *Lagosuchus* (Carroll, 1987), *Eudimorphodon* (Sereno) and *Riojasuchus* (Bonaparte, 1971;) seem to imply a plesiomorphic status for character (260), at this level, while the condition in *Scleromochlus* (Sereno's reconstruction) favours an apomorphic interpretation. In addition the elongate manus in *Heterodontosaurus* and the reconstruction of the forelimb of *Lesothosaurus* in Sereno and Novas (1992) justifies a preliminary dismissal of this synapomorphy. 'Manus markedly asymmetrical' (with digit two the longest) (261) is probably valid as most 'thecodonts' (with the exception of *Stagonolepis*) and ornithischians display the plesiomorphic condition in which the third manual digit is the longest; in Saurischia (not including *Herrerasaurus*) digit two is the longest in the hand. It is somewhat problematic for this character that manual digit two and/or three are incompletely preserved in *Lesothosaurus*, *Heterodontosaurus* and *Hypsilophodon* (Sues and Norman, 1990) because the ancestral state in Ornithischia can thus only be appraised with considerable uncertainty.

Among theropods it is not possible to assess character (262) 'bases of metacarpals IV and V lie on palmar surfaces of manual digits three and four respectively' with respect to clades other than Ceratosauria (and *Herrerasaurus*, if included in Theropoda) as only members of this taxon preserve a fourth metacarpal. Both *Dilophosaurus* and *Syntarsus* conform to this character in that the proximal end of metacarpal IV is adpressed against the palmar aspect of metacarpal III, however, this is not seen in *Coelophysis* (Colbert, 1989; Figure 66A) to any stronger degree than in *Lesothosaurus* (Sereno, 1991a; Figure 8B). In prosauropods which also preserve a fifth metacarpal character (262) is taken to an extreme in *Massospondylus* (Cooper, 1981) and less so, but still well expressed, in *Plateosaurus* (see Galton and Cluver, 1976; Figure 7L). *Herrerasaurus* also retains a rudimentary fifth metacarpal which, in dorsal view, is completely hidden by metacarpal IV, itself being almost concealed by the third metacarpal (Sereno and Novas, 1992). In contrast the proximal metacarpals of 'thecodonts' and ornithischians overlap far less (e.g. see Santa Luca, 1980; Sereno, 1991a; Krebs, 1976; Chatterjee, 1985). 'Saurischian pollex' (263) is a partly valid synapomorphy as applied by Gauthier; not all the conditions specified in connection with this character are met by both Sauropodomorpha and Theropoda; metacarpal I is longer than half the length of metacarpal II and subequal to or longer than the first phalanx in many prosauropods (see Galton and Cluver, 1976; Figure 7). Nevertheless three characteristics of the manus diagnose saurischians: the distal glingymus of the first metacarpal is markedly asymmetrical, the first phalanx equals or exceeds the length of any other phalanx and bears an ungual which is considerably larger than the ungual of any other digit. *Herrerasaurus* exhibits the two former of these traits; also *Riojasuchus* possesses a first metacarpal with an asymmetrical distal glingymus, where the outer condyle is the larger. It is not possible to establish if the two latter characteristics are present in this ornithosuchid.

PHYLOGENETIC ANALYSES

On the basis of the above review a character matrix of 74 characters for 17 archosaurian –and 3 outgroup taxa was assembled (see appendix 2) and subjected to

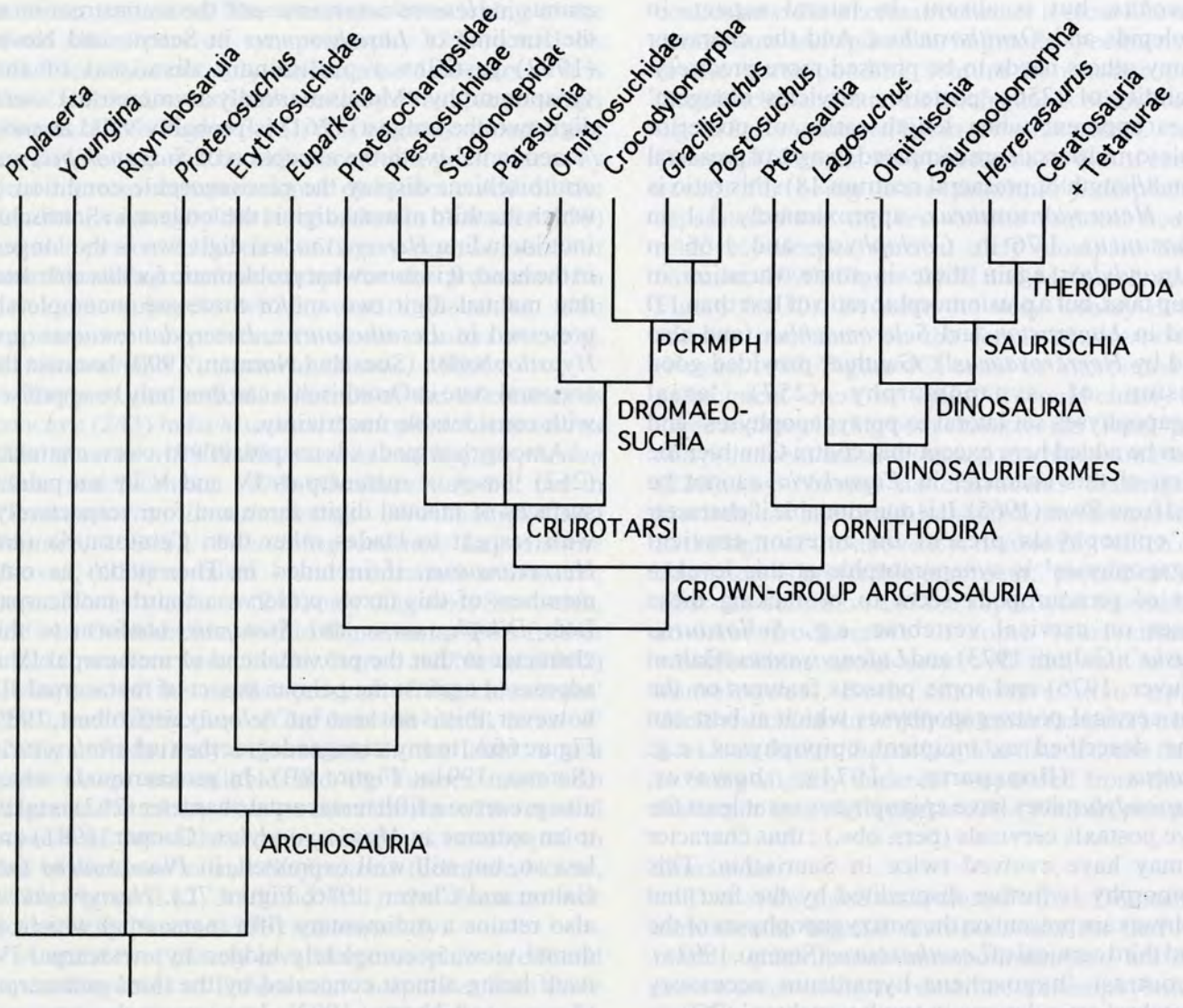


Figure 1. Cladogram resulting from the present analysis of archosaur interrelationships. Characters, character state matrix and diagnoses of the constitutent clades (except terminal taxa) are given in appendix 2. Strict consenus of three trees. The definition of theropoda is here extended to include *Herrerasaurus* in deference to Novas (1993). Abbreviation: PCRMPH, Paracrocodylomorpha.

parsimony analysis as described in 'Material and Methods'.

The PAUP algorithm produced four 'most-parsimonious' trees, however, only three of these are 154 steps long each (C. I. 0.571; C. I. excluding uninformative characters 0.566); the fourth is a 155 step cladogram that differs from a consensus of the remaining three (Figure 1) in placing Stagonolepidae and Prestosuchidae as successive outgroups to Dromaeosuchia (new taxon; see below) rather than have the former two constituting a monophyletic taxon, a modified Pseudosuchia *sensu* Benton.

DISCUSSION

The order of the successive outgroups of crown-group Archosauria, as listed by Sereno, is reproduced on the cladogram (Figure 1) resulting from the present analysis which also strongly supports the monophyly of Crurotarsi (Sereno and Arcucci 1990) (seven syn-apomorphies). The existence of a monophyletic Ornithosuchia, whether or not it includes *Euparkeria*, is disputed here. However if a monophyletic Ornithosuchia *sensu* Benton is combined, the shortest tree obtainable using MacClade (version 3.0), given the present character matrix, is only 3 steps (157, C. I. 0.561) longer than the consensus tree figured above. On the former tree Ornithosuchia is the sistergroup of Paracrocodylomorpha, a similar configuration was the original result of Benton's analysis (see Benton and Clark, 1988), and a crurotarsal ankle joint thus attains paraphyletic distribution.

If Gauthier's option (=Ornithosuchidae and *Euparkeria* being successive outgroups of Ornithodira) is enforced the shortest possible tree is 165 steps long (C.I. 0.533); with Sereno's placement of Ornithosuchidae and Parasuchia as successive outgroups of Suchia the most parsimonious tree is 155 steps long (C.I. 0.568).

Well supported clades other than Crurotarsi are: Archosauria, Erythrosuchidae + higher archosaurs,

Proterochampsidae + crown-group Archosauria, Ornithodira and Dinosauria (see appendix 2). As indicated above a number of the synapomorphies listed for Dinosauriformes are also exhibited by *Lagerpeton* (left out of the present analysis because of the very incomplete nature of the fossil material available for this genus) and may thus come to diagnose a more inclusive taxon.

The existence of a monophyletic Paracrocodylomorpha (Parrish, 1993) is also corroborated, however, here with a different internal configuration than purported by the latter author.

A new character, 'squamosal overhanging quadrate and quadratojugal laterally, and contacting the laterotemporal fenestra dorsally' (74 in Appendix 2), present only in *Gracilisuchus* and Crocodylomorpha, is distributed equivocally within Paracrocodylomorpha.

A new taxon, Dromaeosuchia, is defined as consisting of the last common ancestor of Crocodylomorpha and Ornithosuchidae and all of its descendants, and currently includes Ornithosuchidae, Crocodylomorpha, and *Gracilisuchus* + *Postosuchus* (and possibly other poposaurids) (for a diagnosis of Dromaeosuchia see appendix 2). The name of the taxon refers to the fact that most of its early members (e.g. ornithosuchids, *Gracilisuchus*, *Postosuchus*, *Pseudhesperosuchus* and *Terrestrisuchus*) were semi-erect to erect limbed crurotarsans with adaptations in the pelvis for improved, terrestrial locomotion, and Dromaeosuchia probably includes the better cursors among non-ornithodiran archosaurs. The close association of *Gracilisuchus* and ornithosuchids was anticipated by Romer (1972d).

The systematic position of *Herrerasaurus*, supported by Novas (1993), on the present cladogram as a basal theropod requires the acceptance of a number of reversals in this genus (not included in the list of diagnoses below). These include the shortening of presacral centrum 8 relative to presacral centrum 18, loss of a fully incorporated third vertebra in the sacrum, loss of brevis shelf on ilium, atrophication of the lesser trochanter, and shortening of the tibia relative to the femur. The last transformation has also taken place in Prosauropoda and the 'atrophied' lesser trochanter may be ascribed to sexual dimorphism as indicated above, however, at least the loss of a fully incorporated third sacral seems a somewhat counter intuitive development.

One character 'Articular surfaces for fibula and distal tarsal IV on calcaneum continuous' (79) listed by Sereno as a synapomorphy for crown-group archosaurs is claimed by Parrish (1993) to be present in *Euparkeria* and Proterochampsidae also. After examining type material of *Euparkeria* (SAM 5867) the present author agrees with Sereno that character (79) is not present in the latter taxon; without having had access to relevant material of the former taxon I have chosen to follow Sereno's character state designation for Proterochampsidae with respect to this synapomorphy.

A number of characters reviewed above have been phrased too vaguely to be of value in phylogenetic investigations and have had to be rephrased or discarded altogether. In addition the fossil basis for some other characters has been deemed insufficient. An attempt to reach a better defined character base for archosaur systematics has thus been made here. Some of the characters employed by Gauthier and Benton in their analyses have not been used in the later phylogenetic studies by Sereno and Arcucci (1990), Sereno (1991b) and Parrish (1993) even though valid. Here these characters have been reemployed; the interrelationships of archosaurs can only be understood with greater confidence if the data base underlying research in this field becomes progressively more comprehensive.

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APPENDIX 1

Definitions, diagnoses and cladograms from papers reviewed above.

Node 1
Gauthier *et al.* (1988)
Archosauriformes. DEFINITION: this taxon includes Proterosuchidae, Erythrosuchidae, Proterochampsidae, Pseudosuchia and Ornithosuchia.

DIAGNOSED BY: (1) postfrontal reduced; (2) postparietal fused; (3) antorbital fenestra present; (4) upper temporal fenestra small; (5) upper temporal fenestra dorsally oriented; (6) presence of an ossified laterosphenoid; (7) serrated teeth present; (8) premaxillary teeth implanted in deep sockets; (9) possession of a fourth throchanter on femur.

Benton and Clark (1988)
Archosauria. DEFINITION: Proterosuchidae, Erythrosuchidae, Proterochampsidae +*Doswellia*, *Euparkeria*, Crocodylotarsi and Ornithosuchia are included in this taxon.

DIAGNOSED BY: (1); (3); (6); (9); (10) postparietals fused or absent; (11) posterior border of infratemporal fenestra bowed; (12) marginal teeth laterally compressed; (13) no ectepicondylar groove or foramen on humerus.

Node 2*
Gauthier *et al.* (1988)
Unnamed taxon. Definitions as above, but less Proterosuchidae.

DIAGNOSED BY: (14) supratemporal absent; (15); post-temporal fenestra medium sized; (16) paroccipital process of opisthotic expanded distally; (17) possession of a lateral mandibular fenestra; (18) maxillary and dentary teeth in deep sockets; (19) Tooth attachment by periodontal ligament; (20) dentary with an enlarged tooth within few teeth from symphysis; (21) teeth on transverse process of pterygoid absent; (22) intercentra absent from anterior dorsals; (23) intercentra absent from all postcervical trunk vertebrae; (24) scapula narrow above glenoid; (25) ectepicondylar groove absent; (26) lateral centrale fused to astragalus in adult; (27) distal tarsal I absent.

Benton and Clark (1988)
Unnamed taxon. Definitions as above, but exclusive of Proterosuchidae.

DIAGNOSED BY: (14); (17); (24 – ossified portion of the scapula very tall and narrow (at least twice as tall as the width of base)); (28) coronoid reduced or absent (enlarged in some crocodylomorphs); (29) presacral intercentra are absent behind the axis; (30) coracoid is small, and glenoid faces largely backwards (enlarged in crocodilians); (31) deltopectoral crest extends at least one-quarter of the way down the shaft of the humerus; (32) distal end of the humerus is narrower than the proximal; (33) pelvis is markedly three-rayed, with a long down turned pubis and ischium; (34) iliac blade has a small anterior process; (35) pubis has a strongly downturned tuber when seen in side-view; (36) ischium has a large posteroventral process (the iscium is longer than the iliac blade); (37) tarsus contains only four elements; (38) metatarsals II, III and IV subequal in length, with III the longest; (39) loss of anterior proximal 'hook' on the metatarsal V.

Node 3**
Gauthier *et al.* (1988)
Unnamed taxon. Defined by Gauthier and Benton as at node 1 exclusive of Proterosuchidae and Erythrosuchidae.

DIAGNOSED BY: (40) parietal foramen absent; (41) intercentra absent from postaxial cervicals (may be diagnostic for a clade consisting of Protorosauria + Archosauriformes); (42) humerus with reduced epicondyles; (43) longest digit in hand and foot digit III, (44) Inner two digits of hands and feet more robust than outer two; (45) intertrochanteric fossa absent; (46) medial inflection of femoral head; (47) Femoral condyles not projecting markedly beyond shaft; (48) femoral shaft with prominent sigmoidal curve.

Benton and Clark (1988)
Unnamed taxon. Defined by Gauthier and Benton as at node 1 exclusive of Proterosuchidae and Erythrosuchidae.

DIAGNOSED BY: (40); (49) otic notch well developed; (50) possession of thecodont dentition; (51) ribs all one- or two-headed; (52) hindlimbs are under the body (semi-erect or erect gait); (53) possession of 'crocodiloid' tarsus (foramen is lost, and rotation between astragalus and calcaneum possible); (54) possession of dermal armour with one pair of osteoderms per vertebra.

Sereno (1991b)
Unnamed taxon. Defined by Gauthier and Benton as at node 1 exclusive of Proterosuchidae and Erythrosuchidae.
DEFINITION: *Euparkeria*, Proterochampsidae, Crurotarsi and Ornithodira.

DIAGNOSED BY: (48); (55) dorsal body osteoderms; (56) interclavicle with reduced, tablike lateral processes; ; (57) loss of a bony astragalocalcaneal canal; (58) absence of ossification of distal tarsals 1 and 2; (59) pedal digit IV significantly shorter than III.

From hereon there is no longer correspondence between nodes in the different cladograms, and node numbers will be given in the definition/diagnoses referring explicitly to the cladogram of the author in question.

Benton and Clark (1988) Node 3.1
Unnamed taxon. According to Benton's analysis Proterochampsidae + *Doswellia* define a monophyletic clade, forming the sistergroup of *Euparkeria*+ 'crown group' archosaurs, diagnosed by: (60) loss of postfrontal (parallelism with Crocodylomorpha); (61) pelvis massive, and not three-rayed (reversal of character (33)).

Benton and Clark (1988) Node 4
Unnamed taxon. DEFINITION: taxa included are *Euparkeria*, Crocodylotarsi and Ornithosuchia.

DIAGNOSED BY: (62) antorbital fenestra large and it lies in a depression; (63) nasals run forwards between the nares; (64) diapophysis is placed fairly high on the neural arch of cervical vertebrae; (65) parapophysis transfers to the neural arch in anterior dorsal vertebrae; (66) diapophysis and parapophysis fuse in the posteriordorsal vertebrae and the ribs become single-headed.

Sereno (1991b) Node 4
Unnamed taxon. In contrast to Benton and Gauthier, Sereno does not recognize a supra generic taxon including *Euparkeria*, but exclusive of Proterochampsidae.

PALA AFRICANA — C

DEFINITION: taxa included are Proterochampsidae, Crurotarsi and Ornithodira.

DIAGNOSED BY: (67) postaxial intercentra absent; (68) contiguous crural facets on astragalus.

Node 4 (Diagnoses for this clade are identical in **Gauthier**, 1986 and **Gauthier *et al.*, 1988**; for the remaining nodes only the former is applicable).
Archosauria, Gauthier 1986. DEFINITION: taxa included are Pseudosuchia and Ornithosuchia. This is the crown group definition of Archosauria, but it differs from those of Benton (above) and Sereno (1991) (below) by the inclusion of *Euparkeria* (within Ornithosuchia).

DIAGNOSED BY: (41); (62 – presence of an antorbital fossa); (69) Exoccipital fused with opisthotic in adult; (70) apex of neural spine expanded in dorsal view (viz. -spine tables' present); (71) Parasaggital osteoderm rows; (72) short lateral interclavicle processes (possible diagnostic at node 3); (73) calcaneal tuber posteriorly directed (possible diagnostic at node II or 3).

Benton and Clark (1988) Node 5
DEFINITION: taxa included are Crocodylotarsi and Ornithosuchia **(crown-group archosaurs)**

DIAGNOSED BY: (74) parietals send posterior processes into the occiput which meet the supraoccipital; (75) discrete postparietal and exoccipitals absent beyond juvenile stages of development; (76) pterygoids meet medially in the palate; (77) palatal teeth absent.

Sereno (1991b) Node 5
DEFINITION: taxa included are Crurotarsi and Ornithodira (**Archosauria**, Gauthier 1986 excluding *Euparkeria* ; crown-group of Benton).

DIAGNOSED BY: (77 palatal teeth on pterygoid, palatine, and vomer absent); (78) calcaneal tuber directed more than 45 degrees posterolaterally; (79) calcaneum with contiguous articular surfaces for fibula and distal tarsal 4.

Gauthier (1986) Node 5
Pseudosuchia. DEFINITION: taxa included are: Parasuchia, Aetosauria, Rauisuchia and Crocodylomorpha).

DIAGNOSED BY: (77) (also in ornithosuchians aside from *Euparkeria*); (80) crocodile normal crurotarsal ankle joint, in which the peg is on the astragalus and socket on the calcaneum; (81) calcanear tubercle enlarged (also in Ornithosuchidae); (82) cervical ribs short and stout; (83) discrete postparietal confined to early juvenile or prehatching ontogenetic stages (also in ornithosuchians aside from *Euparkeria*).

Benton and Clark (1988) Node 6
Crocodylotarsi. DEFINITION: taxa included are Phytosauridae, *Gracilisuchus*, Pseudosuchia sensu Benton (=Stagonolepididae, *Ticinosuchus* and *Saurosuchus*), *Postosuchus*, *Terrestrisuchus*, *Protosuchus* and Crocodylia.

DIAGNOSED BY: (80); (81); (82); (84) deltopectoral crest extends less than one quarter of the way down the humerus shaft (reversal of character 31).

Sereno (1991b) Node 6
Crurotarsi. DEFINITION: taxa included are Parasuchia, Ornithosuchidae, *Prestosuchus* and Suchia *sensu* Sereno (=*Gracilisuchus stipanicicorum*, Aetosauria, Rauisuchia Poposauridae and Crocodylomorpha) and all descendants of their common ancestor.

DIAGNOSED BY: (85) proximal humerus strongly arched under inner tuberosity; (86) anterior trochanter of fibula robust and knobshaped; (87) distal end of fibula wider than proximal end; (88) hemicylindrical calcaneal condyle for articulation with fibula; (89) astragalus with flexed tibial articular surface; (90) robust calcaneal tuber with shaft wider than high; (91) calcaneal tuber with flared distal end; (92) ventral astragalocalcaneal articulation larger than dorsal articulation; (93) single paramedian osteoderm pair per cervicodorsal vertebra.

Gauthier (1986) Node 6
Unnamed taxon. DEFINITION: included taxa are Aetosauria, Rauisuchia and Crocodylomorpha.

DIAGNOSED BY: (94) septomaxilla is absent; (95) no separate postparital at any stage in posthatching ontogeny; (96) fusion of second intercentrum and first centrum in juvenile or earlier stages of ontogeny; (97) triradiate pelvis (also in Ornithosuchians); (98) 'screw joint' tibio-astragalar articulation (also in Ornithosuchians); (99) fully developed crocodile-normal crurotarsal joint; (100) osteoderms on ventral surface of tail

Benton and Clark (1988) Node 7
Suchia. DEFINITION: included taxa are *Gracilisuchus*, Pseudosuchia sensu Benton (=Stagonolepididae, *Ticinosuchus* and *Saurosuchus*), *Postosuchus*, *Terrestrisuchus*, *Protosuchus* and Crocodylia.

DIAGNOSED BY: (94) (parallelism in Ornithosuchia); (101) lower temporal fenestra is reduced in size and triangular in shape, with a dorsal point; (102) axial diapophysis is reduced or absent; (103) no pubo-ischiadic plate, and much reduced contact between pubis and ischium (parallelism in Ornithosuchia); (104) pubis is long and narrow and subvertically oriented (parallelism in Ornithosuchia); (105a) pubis is longer than ischium (parallelism in Ornithosuchia); (106) proximal head of femur is turned inwards at about 45 degrees (not in Stagonolepis); (107) advanced crocodile-normal tarsus; (108) digit V of the foot is reduced (shorter than I) (parallelism in Ornithosuchia).

Sereno (1991b) Node 7
Unnamed taxon. DEFINITION: taxa included Ornithosuchidae, (Prestosuchus?) and Suchia *sensu* Sereno (=*Gracilisuchus stipanicicorum*, Aetosauria, Rauisuchia, Poposauridae and Crocodylomorpha).

DIAGNOSED BY: (105b – pubis is longer than ischium and at least three times anteroposterior diameter of acetabulum); (109) posterior pubic acetabular margin recessed.

Sereno (1991b) Node 8
Suchia. DEFINITION: taxa included *Gracilisuchus stipanicicorum*, Aetosauria, Rauisuchia, Poposauridae and Crocodylomorpha.

DIAGNOSED BY: (110) postorbital-squamosal temporal bar anteroposteriorly short with subtriangular laterotemporal fenestra.

Benton and Clark (1988) Node 8
Unnamed taxon. DEFINITION: included taxa are Pseudosuchia **sensu** Benton (=Stagonolepididae, *Ticinosuchus* and *Saurosuchus*), *Postosuchus*, *Terrestrisuchus*, *Protosuchus* and Crocodylia.

DIAGNOSED BY: (95 – postparietals are absent in posthatching stages); (96 – atlas centrum and axial intercentrum are fused from the juvenile stage); (100); (111) pit between basioccipital and basispheniod

(=foramen intertympanicum of living crocodilians; Clark 1986); (112) accessory neural spine on caudal vertebrae (not in *Stagonolepis*).

Gauthier (1986) Node 7
Unnamed taxon. DEFINITION: taxa included Rauisuchia and Crocodylomorpha.

DIAGNOSED BY: (113) first (atlantal) intercentrum much longer than wide; (114) axial diapophysis reduced or absent (or corresponding process of axial rib reduced); (115) enlarged, pneumatic, basipterygoid processes; (116) length of pubis exceeds three times width of acetabulum (also in ornithosuchians aside from *Euparkeria*); (117) fewer than four phalanges in pedal digit five.

Benton and Clark (1988) Node 8.1
Benton believed that Rauisuchidae and Stagonolepididae defines a monophyletic taxon, **Pseudosuchia**, diagnosed by: (118) dorsal centra very constricted in ventral view; (119) acetabulum is subhorizontal and faces downwards, giving a 'pillar-like' erect posture of the hindlimb; (120) iliac blade is oriented subhorizontally; (121) iliac blade is low and long; (122) pubis attaches to anteroventral face on the ilium.

Benton and Clark (1988) Node 8.2
Rauisuchidae DEFINITION: taxa included are *Ticinosuchus*, *Luperosuchus*.

Diagnosed by: (123) extra slit-like fenestra between maxilla and premaxilla; (124) movable joint between the maxilla and premaxilla; (125) main antorbital fenestra is low in front; (126) tall orbit with a 'stepped' postorbital/jugal bar behind; (127) lacrimal forms a heavy ridge over the orbit; (128) proximal distance between the ischia is less than that between the pubes; (129) pubis is shorter than the ischium (reversal of character (105a)).

Benton and Clark (1988) Node 9
Unnamed clade. DEFINITION: taxa included are *Postosuchus* and Crocodylomorpha.

DIAGNOSED BY: (115) (Gauthier 1986; in *Poposaurus*, but not in *Postosuchus*); (116) (parallelism in Ornithodira; ?also in *Saurosuchus*); (130) posterior border of lower temporal fenestra is not bowed (reversal of character (11)); (131) short descending process of squamosal and tall quadratojugal that contact the postorbital (this may be a convergence: *Postosuchus* has a second lower temporal fenestra above this contact which is absent in crocodylomorphs, and the latter generally lacks a descending process of the squamosal); (132) maxillary-vomer secondary palate (also in *Chanaresuchus*); (133) reduction or loss of clavicle (parallelism in Dinosauria); (134) forelimb:hindlimb ratio is about 0.5 (parallelism in Ornithosuchia); (135) acetabulum is perforated (parallelism in Ornithosuchia) [more precisely "parallelism in Ornithodira" as Benton listed the character as an apomorphy for this clade and not as an Ornithosuchian synapomorphy]; (136) supra-acetabular crest on ilium (parallelism in Ornithodira; ?also in Saurosuchus); (137) pedal digit V has no phalanges (but not in *Terrestrisuchus*); (138) stance is digitigrade (parallelism in Ornithodira).

Gauthier (1986) Node 8
Ornithosuchia. DEFINITION: taxa included are *Euparkeria*, Ornithosuchidae, *Lagosuchus*, Pterosauridae – including *Scleromochlus*, Herrerasauridae, Ornithischia, Sauropodomorpha, Theropoda – including birds.

DIAGNOSED BY: (139) squamosal reduced and descending ramus gracile (reversed in large-headed carnivorous Ornithosuchians such as Tyrannosaurs); (140) centra steeply inclined in at least the first four postatlantal cervicals; (141) modifications in the hindlimb and girdle correlated with semierect gait (also in pseudosuchians aside from Parasuchia); (142) ventral flange of astragalus absent; (143) crocodile reversed ankle joint, with peg on calcaneum and socket on astragalus (including loss of perforating foramen) (144) pedal digit five with fewer than four phalanges (also in rauisuchian-crocodylomorph group).

Benton and Clark (1988) Node 10
Ornithosuchia. DEFINITION: taxa included are Ornithosuchidae, *Lagosuchus*, Pterosauridae, and Dinosauria (including Aves).

DIAGNOSED BY: (139); (142) (also in *Euparkeria*); (145) digit V of the foot is reduced (shorter than I) (parallelism in Suchia); (146) septomaxilla is absent (parallelism in Suchia); (147) manual digit I is short and equipped with a diverging claw; (148) no pubo-ischiadic plate, and much reduced contact between pubis and ischium (parallelism in Suchia); (149) pubis is long and narrow and subvertically oriented (parallelism in Suchia); (150) pubis is longer than ischium (parallelism in Suchia); (151) possession of a lesser trochanter; (152) fourth trochanter is a sharp flange; (153) shaft of femur is bowed dorsally; (154) prominent cnemial crest on tibia (also in *Gracilisuchus*).

Gauthier (1986) Node 9
DEFINITION: taxa included are Ornithosuchidae, *Lagosuchus*, Pterosauridae – including *Scleromochlus*, Herrerasauridae, Ornithischia, Sauropodomorpha, Theropoda – including birds.

DIAGNOSED BY: (155) discrete postparietals are absent in post-hatching ontogeny (L?; also in pseudosuchians); (156) palatal teeth absent (L?; also in pseudosuchians); (157) coracoid tubercle lies close to glenoid fossa and coracoid foramen; (158) first metacarpal with offset distal condyles, and pollex directed medially and bearing enlarged ungual (L?; Pt?); (159) manus more asymmetrical than in pseudosuchians, with inner digits much larger than outer digits (L?; Pt?); (160) supra-acetabular buttress; (161) Prominent triradiate pelvis with pubis length at least three times width of acetabulum (also in crocodylomorph-rauisuchian group and to a lesser extent aetosaurs); (162) anterior trochanter on femur appears early in post-hatching ontogeny; (163) aliform fourth trochanter; (164) fifth metatarsal gracile.

Ornithodira

Gauthier (1986) Node 10
DEFINITION: taxa included are *Lagosuchus*, Pterosauridae – including *Scleromochlus*, Herrerasauridae, Ornithischia, Sauropodomorpha, Theropoda – including birds.

DIAGNOSED BY: (165) postfrontal absent (L? also in crocodylomorphs); (166) atlantal intercentrum enlarged, completely surrounding odontoid ventrally and laterally and fitting into prominent recessed area below odontoid on axis; (167) axial intercentrum, and then odontoid, fuses to axis at cessation of growth; (168) modification of cervical centra and zygapophyses that combine

to yield an S-shaped neck (compared to dinosaurs, rudimentary in both *Lagosuchus* and in Pterosauria ancestrally; although within pterosaurs the neck may be in some ways more birdlike than is the neck of *Archaeopteryx*;); (169) zygapophysial facets nearly vertically disposed in all but proximal part of the tail (L?); (170) interclavicle absent (L?); (171) clavicle reduced and gracile (L?; enlarged in coelurosaurs); (172) glenoid facet on scapulocoracoid faces posteroventrally (pt?); (173) coracoid small, with subcircular profile, and lying in nearly the same plane as the scapula (Pt?); (174) Forelimbs less than 55% of hindlimb length (Pt?), and hindlimb very long relative to length of trunk; (175) apex of deltopectoral crest placed distally on humerus (Pt?); (176) less than five phalanges in manual digit four and less than three phalanges in manal digit five (L?); (177) at least three vertebrae involved in sacrum (L?; also in Ornithosuchidae?); (178) brevis shelf appears on ventral surface of postacetabular portion of ilium (Pt?); (179) birdlike distal end of femur prominent, anterior and posterior intercondylar grooves, with the latter constricted by prominent external tibial condyle, and appearance of a discrete fibular groove and condyle; (180) tibia as long or longer than femur (reversed in all dinosaurs over a few meters in length, or larger in the case of theropods); (181) fibula thin and strongly tapered distally and calcaneum reduced; (182) astragalus tranversely widened; (183) astragalus and calaneum with smooth rollerlike articular surfaces abutting against depressed distal tarsals; (184) metatarsals elongate and closely appressed; (185) pes digitigrade; (186) pes functionally tridactyl (Pt?); (187) pedal digit five reduced, does not exceed length of metatarsal IV (Pt?), and composed of no more than two phalanges; (188) parasagittal rows of osteoderms absent.

Benton and Clark (1988) Node 11

DEFINITION: taxa included are: *Lagosuchus*, Pterosauria and Dinosauria.

DIAGNOSED BY: (161 – pubis length is more than three times the width of acetabulum; (170 – ?also in *Postosuchus*); (179 – distal end of femur forms two subterminal condyles); (185 – stance is digitgrade (parallelism in *Gracilisuchus*, *Postosuchus* and Crocodylomorpha)) (186 – metatarsals II-IV are elongated and the foot is functionally tridactyl); (189) presacral vertebral column is divided into three regions (cervical, cervical-thoracic, lumbar); (190) centra are steeply inclined in at least cervicals 3-6; (191) zygapophyses of the middle and posterior caudals are inclined posteroventrally; (192) acetabulum is perforated (parallelism in Postosuchus and Crocodylomorpha); (193) supraacetabular crest on ilium (parallelism in *Saurosuchus*, *Postosuchus* and Crocodylomorpha); (194) fourth trochanter is a wing -like process; (195) fourth trochanter runs down one third to one-half the length of the femur shaft (parallelism in Erythrosuchus and *Chanaresuchus*); (196) knee particulates at 90°; (197) mesotarsal ankle joint with astragalus and calcanum fused to tibia, (198) calcaneum with no tuber at all; (199) ascending process of astragalus fits between tibia and fibula; (200) metatarsals II-IV are closely bunched as a unit.

Sereno (1991b) Node 8

DEFINITON: taxa included are Pterosauria, *Scleromochlus*, Dinosauromorpha (including birds) and all descendants of their common ancestor.

DIAGNOSED BY: (170); (180); (188 – dorsal body armour absent); (200 – compact metatarsus with proximal third of metatarsals 1-4 shafts closely appressed); (201) anterior cervical centrum length longer than mid-dorsal length; (202) clavicles rudimentary or absent; (203) subrectangular deltopectoral crest; (204) femoral shaft bowed anteriorly along at least 80 percent of femoral length; (205) posterior groove on astragalus absent; (206) calcaneal tuber rudimentary or absent; (207) distal tarsal 4 subequal in transverse width to distal tarsal 3; (208) metatarsal 2-4 elongate with metatarsal 3 more than 50 percent of tibial length.

From hereon all references to nodes are made with respect to the cladogram of Dinosauromorpha (see below).

Node D1

Dinosauromorpha

Sereno (1991b)

DEFINITION: taxa included are *Lagerpeton chanarensis*, *Lagosuchus talampayensis*, *Pseudolagosuchus major*, Dinosauria (inc. Aves) and all descendants of their common ancestor.

DIAGNOSED BY: (209) cervical column following strong sigmoid curve with dorsal offset of the anterior face of the centrum present as far posteriorly as the ninth or tenth presacral; (210) forelimb 50 percent or less of hindlimb length; (211) astragalus with acute anteromedial corner; (212) distal articular surface of calcaneum with transverse width 35 percent or less that of astragalus; (213) distal tarsal 4 with articular surface for metatarsal 5 limited to half of its lateral surface; (214) metatarsal 5 with articular surface for distal 4 oriented parallel to shaft axis – 'hooked' proximal end absent; (215) mid-shaft diameters of metatarsals 1 and 5 less than those of metatarsals 2-4.

Node D2

Dinosauriformes

Novas (1992)

DEFINITION: taxa included are *Lagosuchus*, *Pseudolagosuchus* and Dinosauria.

DIAGNOSED BY: (154 – tibia with prominent cnemial crest); (162 – anterior trochanter on femur); (203 – subrectangular, distally projected deltopectoral crest on humerus); (216) presence of a trochanteric shelf on the lateroproximal surface of the femur; (217) distal tibia with lateral longitudinal groove.

Node D3

Novas (1992)
Unnamed clade

DEFINITION: taxa included are *Pseudolagosuchus* and Dinosauria.

DIAGNOSED BY: (218) elongated pubis, nearly as long as the femur; (219) presence of a pyramidal-shaped ascending process of the astragalus, with a posterior, subvertical facet and presence of an elliptical depression behind the process.

Benton (1990a) listed the following apomorphies uniting Pterosauria and Dinosauria(=**Ornithotarsi**); (not shared by *Lagosuchus*): (165); (220) caudal zygapophyses nearly vertical; (221) no more than four phalanges in manual digit IV; (222) proximal head of femur fully offset.

Node D4

Dinosauria

Gauthier (1986)
DEFINITION: taxa included are Herrerasauridae, Ornithischia, Sauropodomorpha and Theropoda-including birds.

DIAGNOSED BY: (223) vomers enlogate, reaching posteriorly at least to level of antorbital fenestra (also in aetosaurs?); (224) scapula at least three times longer than width at base, and entire scapulacoracoid further inclined posterodorsally (also in pterosaurs aside from *Scleromochlus*); (225) increased asymmetry of hand, with small outer two digits having fewer phalanges (ancestral phalageal formula for: Archosauria=2-3-4-5-3; Ornithodira=2-3-4-4-?; and Dinosauria=2-3-4-3-2); (226) semiperforate acetabulum and prominent supra-acetabular buttress; (227) birdlike femur and antitrochanter: medial rotation about long axis of element of that portion of femur proximal to fourth trochanter (=inturned head of femur), proportional elongation of femoral shaft; fore-and-aft compression of femoral head in proximal view; and femoral head more distinctly set off from the shaft of the femur. Also modifications of the distal end of the femur noted above are more prominent in dinosaurs. These modifications are also accompained by reorientation of the anti-trochanter, which faces mostly dorsally in archosaurs ancestrally, but faces mostly ventrally in dinosaurs; (228) anterior trochanter enlarged; (229) dinosaur tibia: cnemial crest prominent and with weakly crescentic profile in dorsal view (size and shape of cnemial crest varies with size of animal and style of locomotion). Distal end of tibia broadened mediolaterally, thus the element appears twisted nearly 90° with respect to proximal end. And with prominent fossa on anterolateral face of distal end of tibia for reception of ascending process; (230) birdlike ankle: [characters 205, 206 and 207] proximal tarsals fit caplike onto tibia and fibula; crurotarsal joint and calcanear tubercle absent; ascending process of astragalus present (i.e. intermedium moves dorsally)-thus, motion within the ankle confined mainly to a simple, hingelike joint between the rollerlike proximal and the compressed, distal tarsals. (Like the femur, the ankle joint in pterosaurs appears to be more dinosaurlike than that of *Lagosuchus*; these apomorphic similarities suggest a monophyletic pterosaur-dinosaur group (Ornithotarsi n. txn.)); (231) pedal digit five shorter than metatarsal I; the foot is tridactyl in typical dinosaurian condition.

Benton (1990a)
DEFINITION: as by Gauthier.

DIAGNOSED BY: (223(1990)); (232) three or more sacral vertebrae (parallelism in *Postosuchus* and Ornithosuchidae); (233) scapula is long and strap-like without an expanded tip; (234) glenoid faces fully backwards; (235) deltopectoral crest is low and runs one-third or one-half of the way down the shaft; (236) three or fewer phalanges in the fourth digit of the hand; (237(1990)) largely to fully open acetabulum; (238) proximal head of femur is fully offset, with distinct ball and neck; (239) greatly reduced fibula; (240) ascending process of astragalus is well developed.

Novas (1992)
DEFINITION: as by Gauthier.

DIAGNOSED BY: (225); (226 – perforated acetabulum); (238 – femoral head more distinctly set off from shaft of femur); (241) ishium with slender shaft and with ventral -keel' (obturator process) restricted to the proximal third of the bone; (242) tibia overlaps anteroproximally and posteriorly the ascending process of the astragalus (i.e. ascending process inserts beneath the tibia), with consequent ventral projection of the posterior process of the tibia; (243) calcaneum with a concave proximal articular surface, fixed to the distal end of the fibula.

Sereno and Novas (1992)
DEFINITION: as by Gauthier.

DIAGNOSED BY: (154 – cnemial crest on the tibia); (165); (178 – a brevis fossa on the ilium); (232 – addition of a dorsal vertebra to the sacrum); (235 – elongate deltopectoral crest on humerus); (236 – loss of the ungual on the fourth digit of the hand); (240 – ascending process on the astragalus); (244) extension of adductor musculature onto the frontal; (245) lateral exposure of the quadrate head; (246) reduction of the posttemporal opening to a foramen; (247) antitrochanter within the acetabulum that is divided by a notch; (248) subrectangular femoral head; (249) reduction of the medial process of the calcaneum; (250) reduction of the heel on distal tarsal 4.

Node D5

Eudinosauria

Benton (1990a)
DEFINITION:the common ancestor of Saurischia and Ornithischia and all its decendants.

DIAGNOSED BY: (232); (251) lesser trochanter on the femur is a spike or a crest; (252) tranversely expanded distal end of tibia.

Novas (1992)
DEFINITON: as by Benton.

DIAGNOSED BY: (178 – presence of a prominent brevis shelf on the lateroventral side of the postacetabular blade of the ilium); (228 – presence of a prominent anterior (lesser) trochanter on the femur); (232); (253) trochanteric shelf reduced to a slight prominence.

Node D6

Saurischia

Gauthier (1986)
DEFINITION: birds and all dinosaurs that are closer to birds than they are to ornithischians.

DIAGNOSED BY: (244 – temporal musculature extends onto frontal); (254) lateral overlap of the quadratojugal onto the posterior process of the jugal [listed in

addendum]; (255) contact between maxillary process of premaxilla and nasal reduced or absent; (256) posterior cervicals elongate; (257) axial postzygapophyses set lateral to prezygapophyses; (258) epipophyses present on anterior cervical postzygapophyses; (259) hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae (also in some Rauisuchia and Aetosauria); (260) manus more than 45% of length of humerus plus radius; (261) manus markedly asymmetrical {digit two longest digit of hand}; (262) bases of metacarpals IV and V lie on palmar surfaces of manual digits three and four respectively; (263) saurischian pollex {= 1. pollex robust and bearing a large ungual phalanx; 2. Metacarpal I is only half or less the length of metacarpal II and the distal condyles are markedly asymmetrical; 3. First phalanx much longer than metacarpal I; the first phalanx equals or exceeds the length of any other phalanx in the hand}.

Benton (1990a)

DEFINITION: as by Gauthier.

DIAGNOSED BY: (244); (254); (256-262); (263 - heavy pollex with very broad metacarpal).

*Parrish (1992) lists possession of a fourth trochanter (9) as an apomorphy for this taxon.

**Parrish (1992), in agreement with Gauthier, lists the absence of an intertrochanteric fossa (45) as apomorhpic for this taxon.

APPENDIX 2

Characters and character state matrix (20 taxa, 74 characters) used in present analyses.

In the character list plain numbers correspond to the numbering of characters in the matrix and new diagnoses (below); italicised numbers refer to the diagnoses and discussion above. Numbers followed by 'm' indicates that characters have been modified from their original phrasing. Characters (68) and (69) are taken from Gauthier's diagnoses of Tetanurae and Theropoda which are not included in the above review, but see the present character matrix for the distribution of these two characters.

(1, *3*) Antorbital fenestra: absent (0); present (1).

(2, *6*) Laterosphenoid: absent (0); present (1).

(3, *7*) Serrated teeth: absent (0); present (1).

(4, *9/152m*) Fourth trochanter: absent (0), present (1) or present in the form of a sharp flange (2).

(5, *12*) Marginal teeth: conical (0); laterally compressed (1).

(6, *17*) Lateral mandibular fenestra: absent (0); present (1).

(7, *21*) Teeth on transverse process of pterygoid: present (0); absent (1).

(8, *34m*) Anterior process on iliac blade: absent (0); present (1).

(9, *35m*) Pubic tuber: anteroventrally directed (0), or strongly downturned in lateral aspect (1).

(10, *36*) Large posteroventral process on the ischium (the ischium is longer than the iliac blade): absent (0), present (1).

(11, *40*) Parietal foramen: present (0), absent (1).

(12, *45*) Intertrochanteric fossa: present (0), absent (1).

(13, *57m*) Ankle type: 'PM' (0); 'MPM' (1); rotary, crurotarsal (2); 'AM' (3).

(14, *55*) Dorsal body osteoderms: absent (0); present (1)

(15, *93/55m*) Dorsal body osteoderms: absent (0), present as a single median row (1), a paramedian pair per cervicodorsal vertebra (2), or in excess of a paramedian pair per cervicodorsal vertebra (3)

(16, *60*) Postfrontal: present (0); absent (1).

(17, *62*) Antorbital fossa (in connection with the antorbital fenestra): absent (0); present (1).

(18, *67*) Postaxial intercentra: present (0); absent (1).

(19, *68*) Crural facets on astragalus: separated by a non-articular surface (0), or continuous (1).

(20, *70*) -Spine tables' on neural spines: absent (0); present (1).

(21, *75m*) Exoccipitals and opisthotics: discrete (0); fused (1).

(22, *10*, 2m, *75m*) Postparietals: unfused (0), fused (1), or absent (2).

(23, *77*) Palatal teeth: present (0); absent (1).

(24, *78*) Orientation of calcaneal tuber: lateral (0), or deflected more than 45 degrees posterolaterally (1).

(25, *79*) Articular surfaces for fibula and distal tarsal IV on calcaneum: separated by a non-articular surface (0), continuous (1).

(26, *82*) Cervical ribs: slender (0); short and stout (1).

(27, *88*) Hemicylindrical calcaneal condyle: absent (0); present (1).

(28, *89*) Astragalar fibular facet: concave (0); flexed (1).

(29, *90*) Calcaneal tuber shaft proportions: taller than broad (0); broader than tall (1).

(30, *91*) Calcaneal tuber distal end: antero-posteriorly compressed (0), rounded (1), or flared (2).

(31, *101*) Lower temporal fenestra shape: non-triangular (0), or triangular and reduced in size (1).

(32, *105a*) Pubis: shorter than ischium (0); longer than ischium (1).

(33, *108*) Pedal digit V length relative to I: longer (0); shorter (1).

(34, *112*) Accessory neural spine on mid-caudal vertebrae: absent (0); present (1).

(35, *116*) Length of pubis: less than three times width of acetabulum (0); exceeds three times width of acetabulum (1).

(36, *119m*) Acetabulum: laterally oriented (0), ventrally deflected (1), open ventrally (2).

(37, *123*) Subnarial fenestra or foramen between premaxilla and maxilla: absent (0); present (1).

(38, *126*) Postorbital/jugal bar behind orbit: curved or straight (0), or "stepped" (1).

(39, *136*) Supraacetabular crest on ilium: absent (0); present (1).

(40, *137*) Phalanges/phalanx on pedal digit V: present (0); absent (1).

(41, *144*) Pedal digit five with four or more (0), or fewer than four phalanges (1).

(42, *151*) Lesser trochanter on femur: absent (0), weakly developed (1), or a spike or crest (2).

(43, *154*) Prominent cnemial crest on tibia: absent (0); present (1).

(44, *170*) Interclavicle: present (0); absent (1).

(45, *174*) Forelimb/hindlimb length ratio: more than .55 (0); less than .55 (1).

(46, *177m*) Number of sacral vertebrae: two (0), two plus an incipient third (1), or three or more (2).

(47, *178*) Brevis shelf on ilium: absent (0); present (1).

(48, *180*) Tibia/femur ratio: less than 1.0 (0); more than 1.0 (1).

(49, *181*) Fibula non-tapering and calcaneum un-reduced (0), or thin, tapered fibula and reduced calcaneum (1).

(50, *200*) Metatarsus configuration: metatarsals diverging from ankle (0), or compact metatarsus (metatarsals II-IV are closely bunched) (1).

(51, *203*) Deltopectoral crest: rounded (0); subrectangular (1).

(52, *206*) Calcaneal tuber: prominent (0); rudimentary or absent (1).

(53, *207*) Distal tarsal 4 transverse width: broader than (0), or subequal to distal tarsal 3 (1).

(54, *208*) Metatarsal 2-4: less (0), or more (1) than 50 percent of tibial length.

(55, *211*) Anteromedial corner of astragalus: obtuse (0); acute (1).

(56, *212*) Size of distal articular surface of calcaneum: transverse width more (0), or less (1) than 35 percent of that of the astragalus.

(57, *214*) 'Hooked' proximal end of metatarsal V: present (0); absent (1).

(58, *215m*) Relative metatarsal mid-shaft diameters: I and V subequal or greater than II-IV (0), I and V less than II-IV (1), V and IV greater than I-III (2), or V greater than I-IV (3).

(59, *235m*) Elongate deltopectoral crest with apex situated at a point corresponding to less

than 38% (0), or 38% or more (1) down the length of the humerus.

(60, *237m*) Acetabulum: imperforated (0), semi-perforated (1), or largely perforated (2).

(61, *238m*) Femoral head: rounded and not distinctly offset (0), or subrectangular and distinctly offset (1).

(62, *242*) Markedly distally projected posterior process of tibia with receiving depression on dorsal aspect of astragalus: absent (0); present (1).

(63, *243m*) Proximal articular surface of calcaneum: convex or flat (0), or concave (1).

(64, *245*) Head of quadrate in lateral aspect: exposed (0); not visible (1).

(65, *256m*) Length of presacral centrum 8/length of presacral centrum 18: less than (0), or more than 1.0 (1).

(66, *259*) Hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae: absent (0); present (1).

(67, *262*) Bases of metacarpals IV and V: lie more or less in the same plane as the inner metacarpals (0), or lie on palmar surfaces of manual digits three and four respectively (1).

(68; Gauthier, 1986) Pubic foot: absent (0); present (1).

(69m; Gauthier, 1986) Manual digits I-III: comparatively short with relatively blunt unguals on at least digit II and III (0), or long, penultimate with trenchant unguals on digit I-III (1).

(70; Parrish, 1993) Parasphenoid rostrum: rodlike (0), or a dorsoventrally expanded wedge (1).

(71; Parrish, 1993) Pedal digit V phalangeal count: three or more (0), or fewer than three (1).

(72; Parrish, 1993) Dorsoventrally aligned median depression on distal end of tuber calcis: absent (0); present (1).

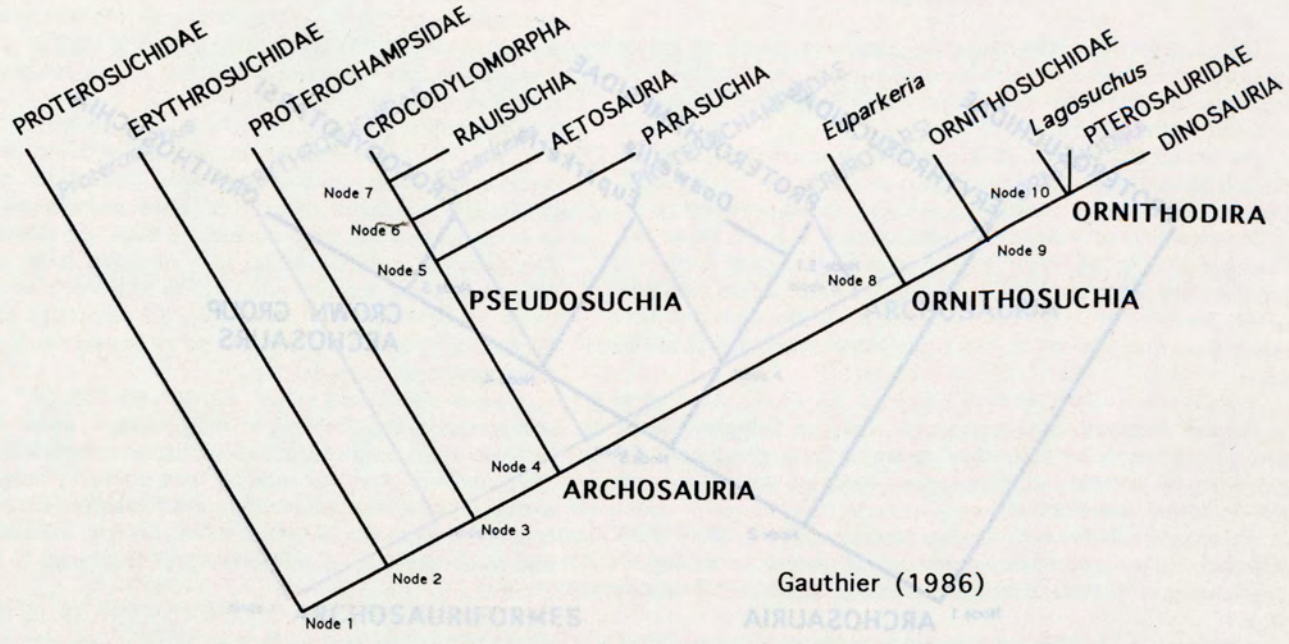
(73; Sereno and Novas, 1994) Intra-mandibular joint: absent or poorly developed (0); well-developed (1).

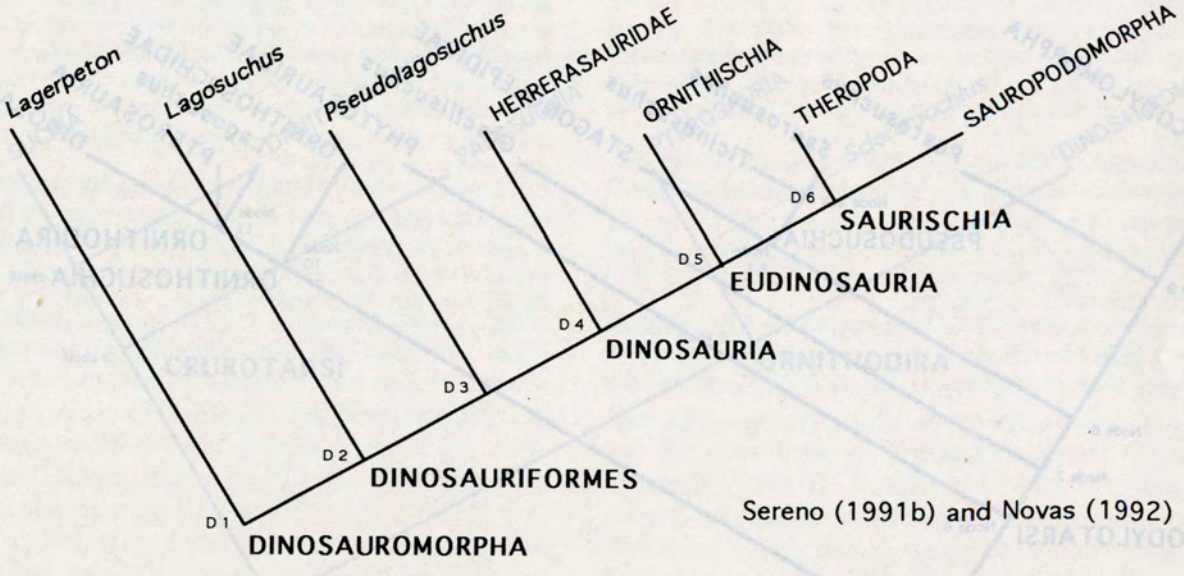
(74; new) Squamosal not overhanging quadratojugal laterally (0), squamosal overhanging quadrate and quadratojugal laterally, and contacting the laterotemporal fenestra dorsally (1), or squamosal overhanging quadrate and quadratojugal laterally, but is excluded from the rim of the laterotemporal fenestra by postorbital and quadratojugal (2).

Character

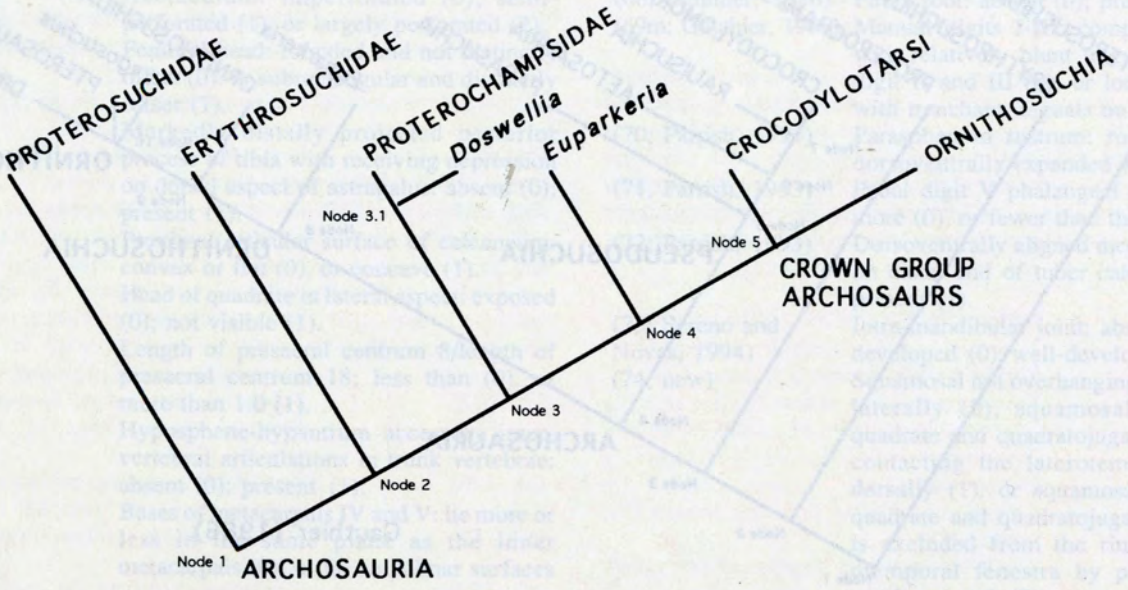
	1		2		3		4		5		6		7		
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	1234
Prolacerta	00001	00010	00000	00000	02000	00000	01000	00000	0000?	00100	00000	0?200	00001	00000	0000
Youngina	00000	0001?	00000	00000	00000	00000	0?0?0	00000	?000?	00?00	000??	01100	00?0?	00000	??00
Rhynchosauria	00000	01010	00000	00100	02000	00000	00000	0?000	00010	00000	00020	00300	0000?	00000	0000
Proterosuchus	11101	10000	00000	00000	01000	00000	00000	01000	?0000	00000	00000	00000	00000	00000	0000
Erythrosuchidae	11111	11111	0001?	00000	?1100	00000	00000	01000	10000	00000	00000	00000	00010	00000	0000
Euparkeria	11111	11111	11112	01001	01000	00000	00000	0?000	10000	00000	00000	00000	00010	00000	0000
Proterochampsidae	1?111	11111	11111	1?110	11000	00000	00100	00001	10000	00000	00000	01000	00010	00000	?000
Parasuchia	11111	11111	11212	01111	12111	11111	00100	00000	00000	00000	00000	00000	00010	00000	0000
Gracilisuchus	1?101	111?1	11213	0111?	11111	1??11	1?10?	00001	10101	00000	00000	01000	00010	000?1	1101
Stagonolepidae	11010	11111	11212	01111	11111	11111	11100	10000	00000	00000	00000	00000	00010	?0000	0100
Prestosuchidae	1?111	11111	11213	01111	11111	11111	0011?	11100	10000	00000	00000	00000	00010	?0000	?100
Postosuchus	11111	11111	112??	01110	12111	11111	11101	21111	10000	20000	00000	00?01	00010	10101	1102
Crocodylomorpha	11111	11111	11212	11110	12111	11111	011?1	00011	10000	00?00	00000	0?001	00010	00001	1101
Ornithosuchidae	1?121	11111	11212	01111	12111	11111	01101	00010	12100	20000	00000	00001	00010	00000	0000
Pterosauria	10001	01111	11300	111?0	121??	00000	00100	000?0	10010	20111	11110	01000	00010	00010	1000
Lagosuchus	1?121	11111	11300	?1110	???11	00000	01100	0?011	110?1	00111	11111	11101	000?0	0?0??	1???
Herrerasaurus	11121	11111	11300	11111	12111	00000	01101	01010	11111	10011	11111	11112	11100	11110	1010
Ornithischia	11121	11111	11300	11110	12111	00000	01101	0001?	12111	21111	11111	11112	11001	00000	1000
Sauropodomorpha	11121	11111	11300	11110	12111	00000	01101	01010	1211?	21011	11111	11112	11101	11000	1000
Ceratosauria + Tetanurae*	11121	11111	11300	11110	12111	00000	01101	0?011	12111	21111	11111	11112	11101	11?10	1010

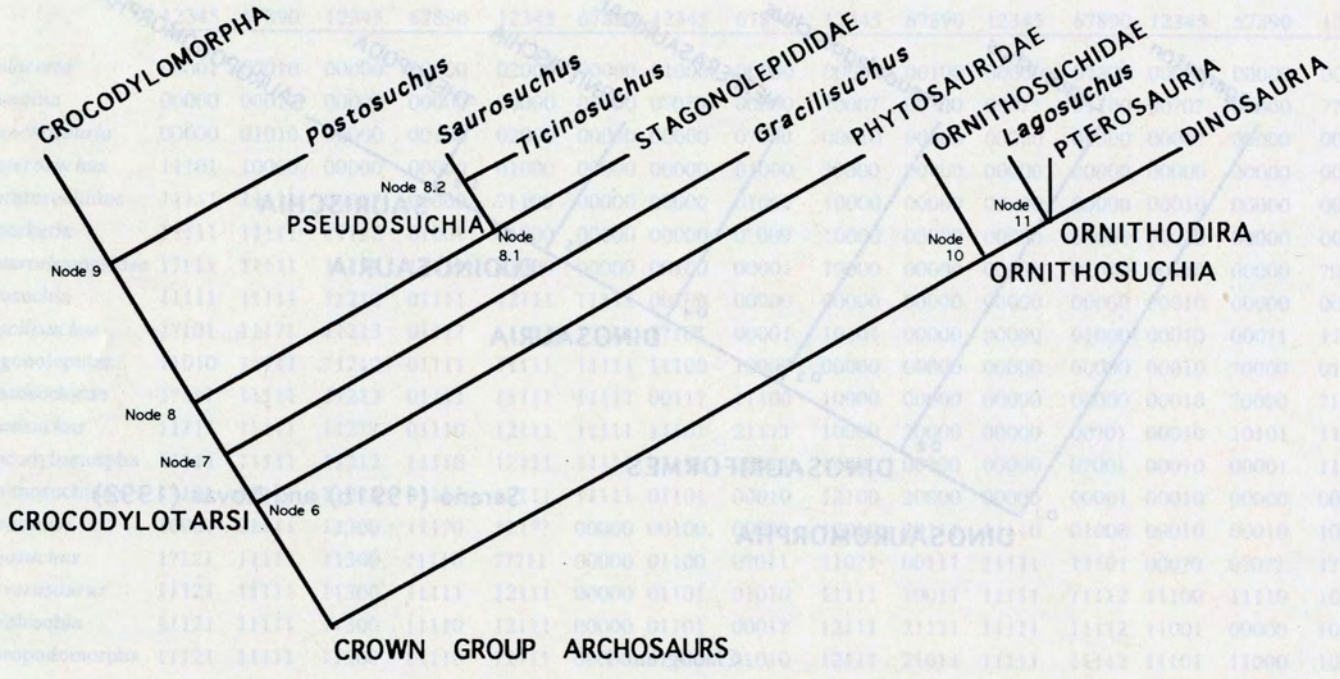
? = not preserved/unknown; * = Theropoda prior to inclusion of *Herrerasaurus* in this taxon by Sereno and Novas (1992)


PROTEROSUCHIDAE
ERYTHROSUCHIDAE
PROTEROCHAMPSIDAE
CROCODYLOMORPHA
RAUISUCHIA
AETOSAURIA
PARASUCHIA
Euparkeria
ORNITHOSUCHIDAE
Lagosuchus
PTEROSAURIDAE
DINOSAURIA
Node 7
Node 6
Node 5
Node 10
ORNITHODIRA
Node 9
Node 8
PSEUDOSUCHIA
ORNITHOSUCHIA
Node 4
ARCHOSAURIA
Node 3
Node 2
Node 1
Gauthier (1986)


Lagerpeton
Lagosuchus
Pseudolagosuchus
HERRERASAURIDAE
ORNITHISCHIA
THEROPODA
SAUROPODOMORPHA
D6
SAURISCHIA
D5
EUDINOSAURIA
D4
DINOSAURIA
D3
D2
DINOSAURIFORMES
D1
DINOSAUROMORPHA
Sereno (1991b) and Novas (1992)

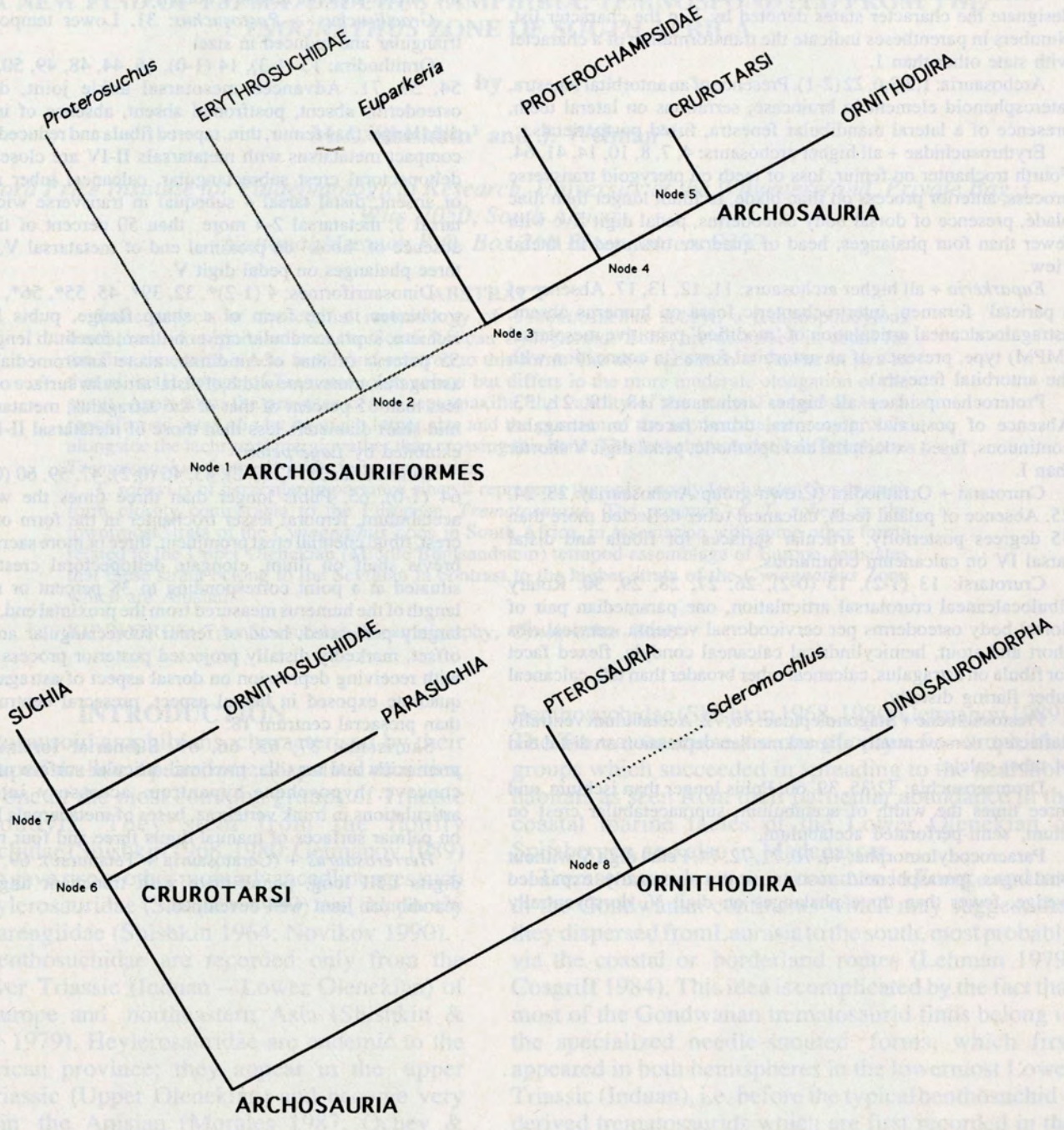
Cladogram 1





Benton and Clark (1988)

Cladogram 2



Sereno (1991b)

Cladogram 3

DIAGNOSES

Unless specified otherwise the character numbers below designate the character states denoted by 1 in the character list. Numbers in parentheses indicate the transformation of a character with state other than 1.

Archosauria: 1,2,3,6, 22 (2-1). Presence of an antorbital fenestra, laterosphenoid element in braincase, serrations on lateral teeth, presence of a lateral mandibular fenestra, fused postparietals.

Erythrosuchidae + all higher archosaurs: 4, 7, 8, 10, 14, 41, 64. Fourth trochanter on femur, loss of teeth on pterygoid transverse process, anterior process on iliac blade, ischium longer than iliac blade, presence of dorsal body osteoderms, pedal digit five with fewer than four phalanges, head of quadrate obscured in lateral view.

Euparkeria + all higher archosaurs: 11, 12, 13, 17. Absence of a parietal foramen, intertrochanteric fossa on humerus absent, astragalocalcaneal articulation of 'modified' primitive mesotarsal (MPM) type, presence of an antorbital fossa (in connection with the antorbital fenestra).

Proterochampsidae+ all higher archosaurs: 18, 19, 21, 33. Absence of postaxial intercentra, crural facets on astragalus continuous, fused exoccipital and opisthotic, pedal digit V shorter than I.

Crurotarsi + Ornithodira (Crown-group Archosauria): 23, 24, 25. Absence of palatal teeth, calcaneal tuber deflected more than 45 degrees posteriorly, articular surfaces for fibula and distal tarsal IV on calcaneum continuous.

Crurotarsi: 13 (1-2), 15 (0-2), 26, 27, 28, 29, 30. Rotary fibulocalcaneal crurotarsal articulation, one paramedian pair of dorsal body osteoderms per cervicodorsal vertebra, cervical ribs short and stout, hemicylindrical calcaneal condyle, flexed facet for fibula on astragalus, calcaneal tuber broader than tall, calcaneal tuber flaring distally.

Prestosuchidae + Stagonolepidae: 36, 72. Acetabulum ventrally deflected, dorsoventrally aligned median depression on distal end of tuber calcis.

Dromaeosuchia: 32/35, 39, 60. Pubis longer than ischium, and three times the width of acetabulum, supraacetabular crest on ilium, semi-perforated acetabulum.

Paracrocodylomorpha: 40, 70, 71, 72, 74. Pedal digit V without phalanges, parasphenoid rostrum a dorsoventrally expanded wedge, fewer than three phalanges on digit V, dorsoventrally aligned median depression on distal end of tuber calcis, squamosal overhanging quadrate and quadratojugal laterally, and contacting the laterotemporal fenestra dorsally.

Gracilisuchus + *Postosuchus*: 31. Lower temporal fenestra triangular and reduced in size.

Ornithodira: 13 (1-3), 14 (1-0), 16, 44, 48, 49, 50, 51, 52, 53, 54, 57, 71. Advanced mesotarsal ankle joint, dorsal body osteoderms absent, postfrontal absent, absence of interclavicle, tibia longer than femur, thin, tapered fibula and reduced calcaneum, compact metatarsus with metatarsals II-IV are closely bunched, deltopectoral crest subrectangular, calcaneal tuber rudimentary or absent, distal tarsal 4 subequal in transverse width to distal tarsal 3, metatarsal 2-4 more than 50 percent of tibial length, absence of 'hook' on proximal end of metatarsal V, fewer than three phalanges on pedal digit V.

Dinosauriformes: 4 (1-2)*, 32, 39*, 45, 55*, 56*, 58*. Fourth trochanter in the form of a sharp flange, pubis longer than ischium, supraacetabular crest on ilium, forelimb length less than 55 percent of that of hindlimb, acute anteromedial corner on astragalus, transverse width of distal articular surface of calcaneum less than 35 percent of that of the astragalus, metatarsal I and V mid-shaft diameters less than those of metatarsal II-IV. (*= also exhibited by *Lagerpeton*)

Dinosauria: 35, 42 (0-2), 43, 46 (0-2), 47, 59, 60 (0-2), 61, 62, 64 (1-0), 65. Pubis longer than three times the width of the acetabulum, femoral lesser trochanter in the form of a spike or crest, tibial cnemial crest prominent, three or more sacral vertebrae, brevis shelf on ilium, elongate deltopectoral crest with apex situated at a point corresponding to 38 percent or more of the length of the humerus measured from the proximal end, acetabulum largely perforated, head of femur subrectangular and distinctly offset, markedly distally projected posterior process of the tibia with receiving depression on dorsal aspect of astragalus, head of quadrate exposed in lateral aspect, presacral centrum 8 longer than presacral centrum 18.

Saurischia: 37, 63, 66, 67. Subnarial foramen between premaxilla and maxilla, proximal articular surface of calcaneum concave, hyposphene-hypantrum accessory intervertebral articulations in trunk vertebrae, bases of metacarpals IV and V lie on palmar surfaces of manual digits three and four respectively.

Herrerasaurus + (Ceratosauria + Tetanurae): 69, 73. Manual digits I-III long, penultimate with trenchant unguals, intramandibular joint well-developed.