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THE PHYLOGENY OF BASAL ARCHOSAURS

by

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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

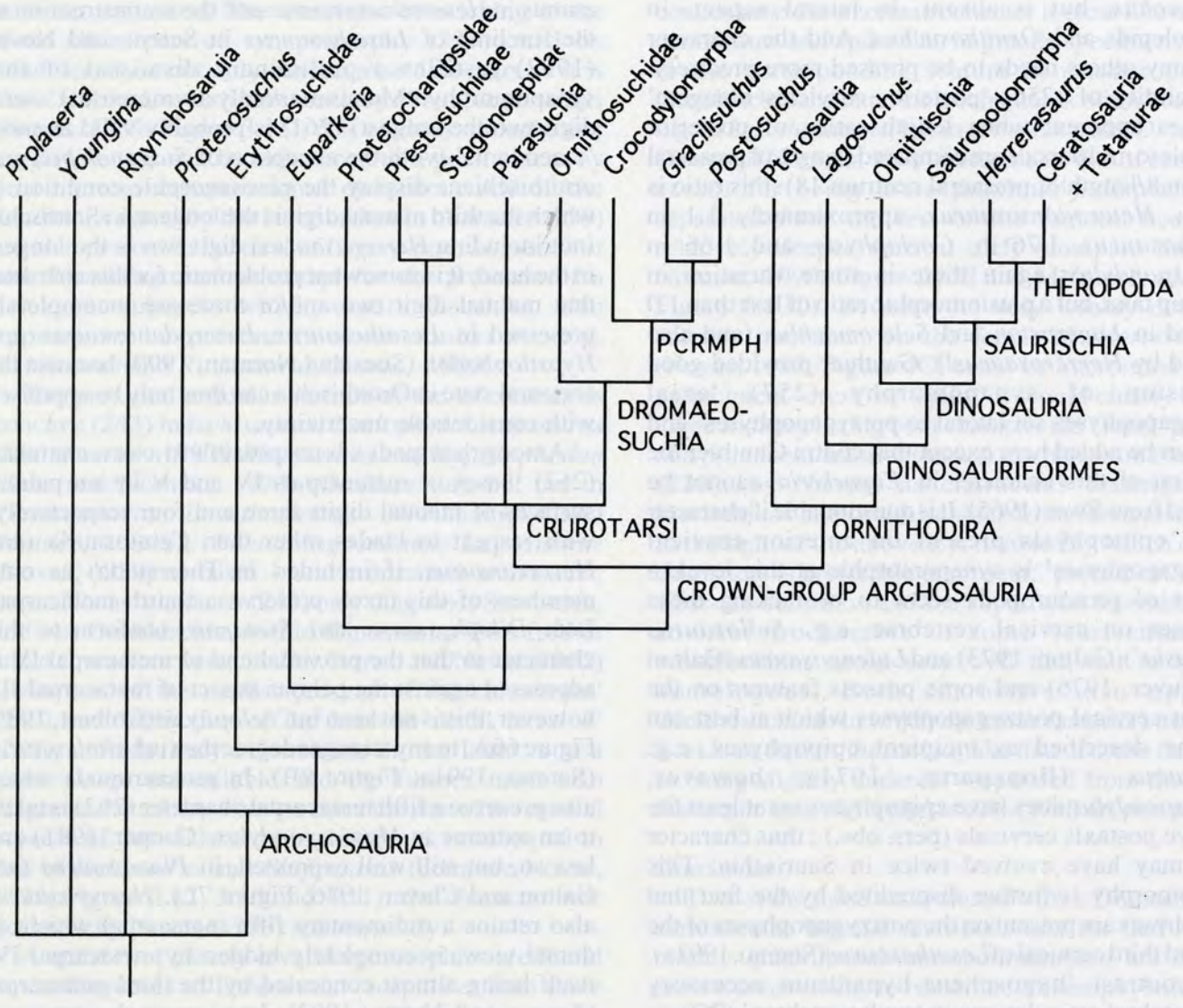


Figure 1. Cladogram resulting from the present analysis of archosaur interrelationships. Characters, character state matrix and diagnoses of the constitutent clades (except terminal taxa) are given in appendix 2. Strict consenus of three trees. The definition of theropoda is here extended to include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

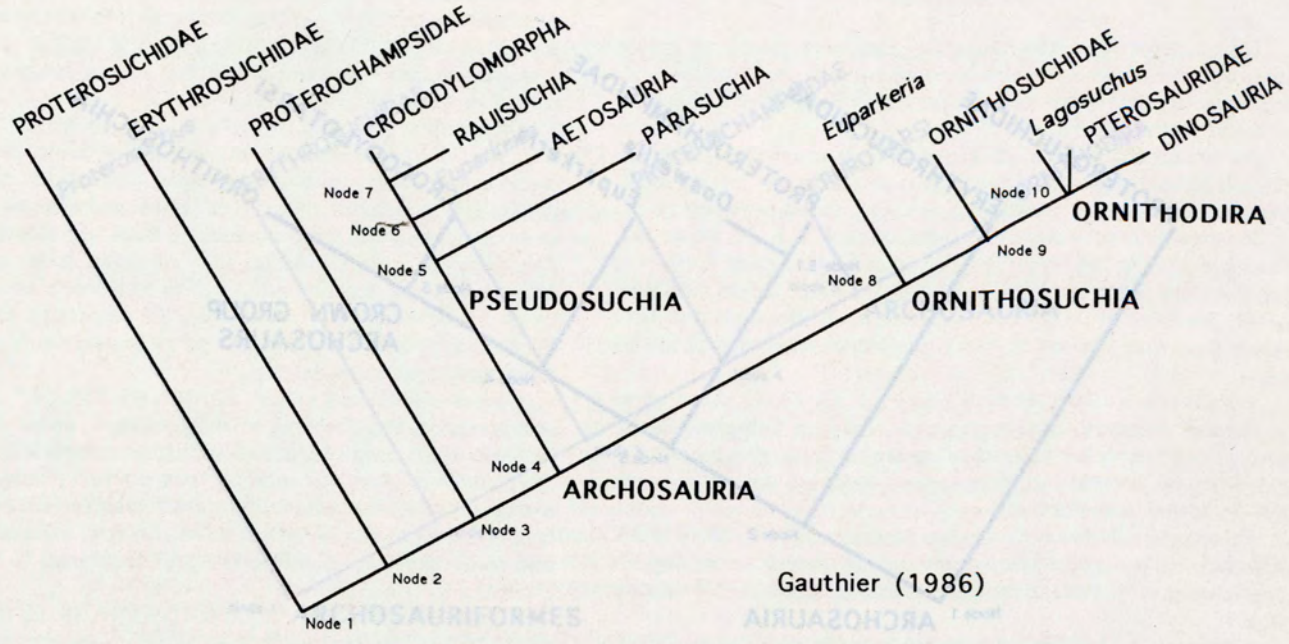
(73; Sereno and Novas, 1994) Intra-mandibular joint: absent or poorly developed (0); well-developed (1).

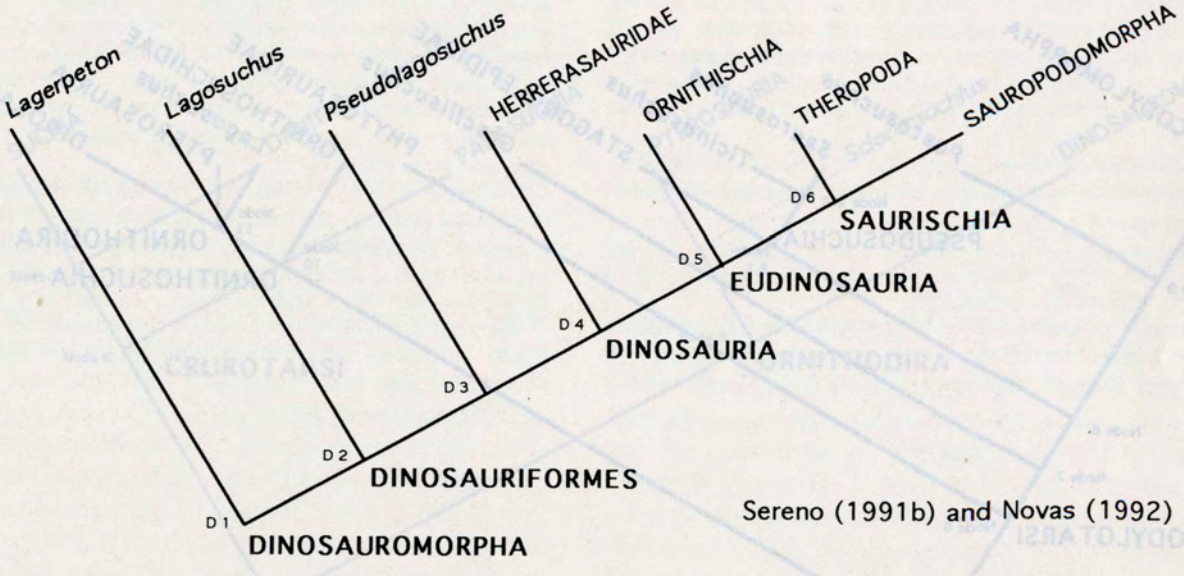
(74; new) Squamosal not overhanging quadratojugal laterally (0), squamosal overhanging quadrate and quadratojugal laterally, and contacting the laterotemporal fenestra dorsally (1), or squamosal overhanging quadrate and quadratojugal laterally, but is excluded from the rim of the laterotemporal fenestra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

Character

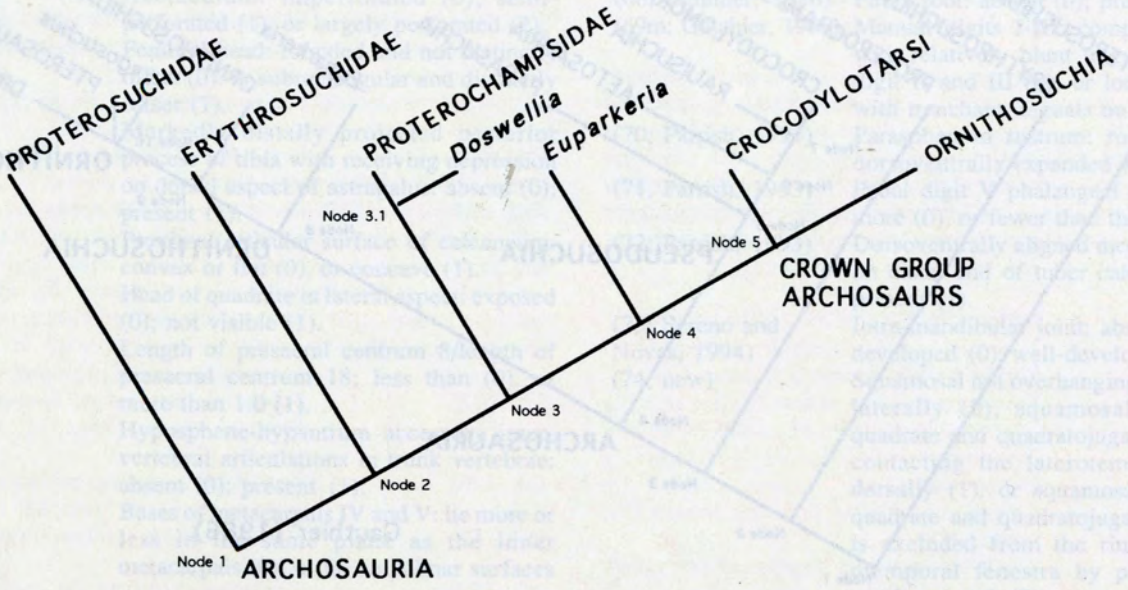
	1		2		3		4		5		6		7		
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	1234
Prolacerta	00001	00010	00000	00000	02000	00000	01000	00000	0000?	00100	00000	0?200	00001	00000	0000
Youngina	00000	0001?	00000	00000	00000	00000	0?0?0	00000	?000?	00?00	000??	01100	00?0?	00000	??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

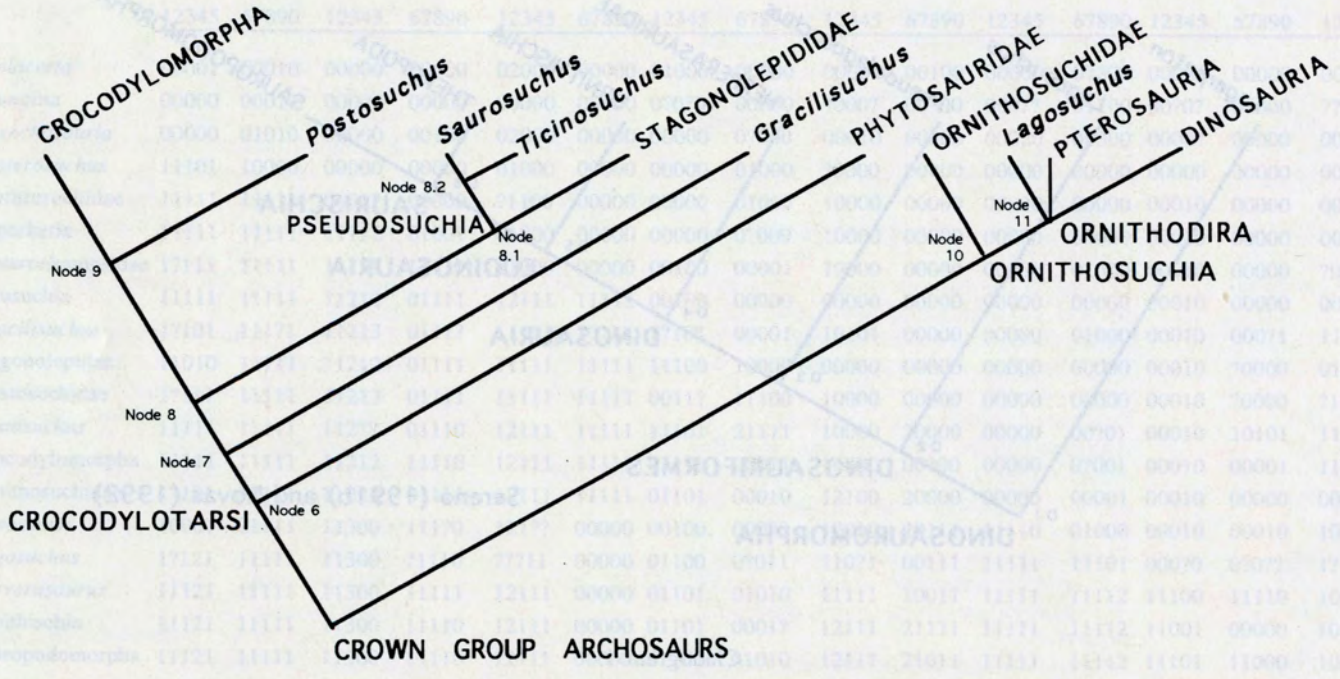
? = not preserved/unknown; * = Theropoda prior to inclusion of *Herrerasaurus* in this taxon by Sereno and Novas (1992)


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)

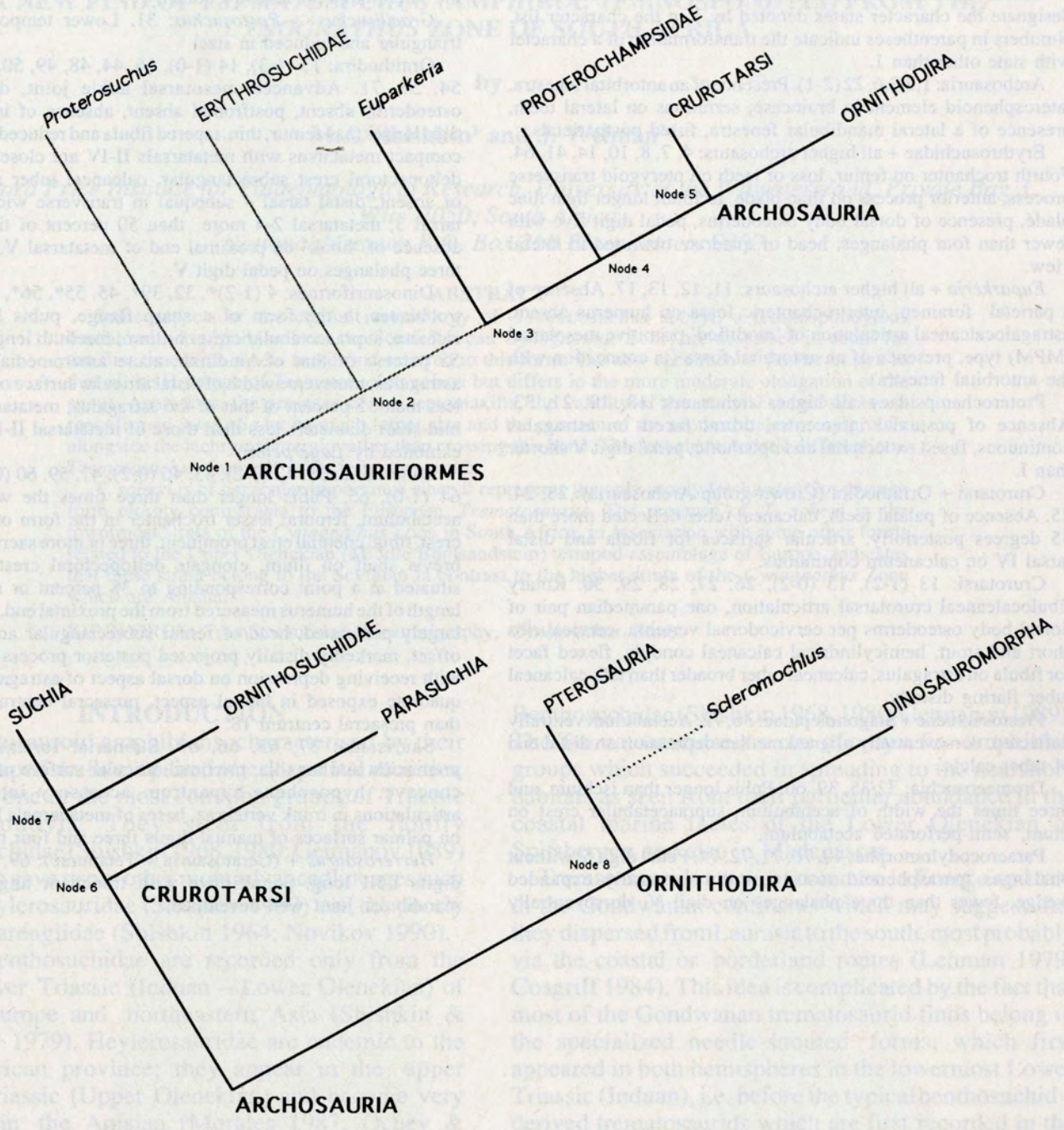
Cladogram 1





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.

Palaeont. afr., **31**, 39-49 (1994)

A NEW FIND OF *TREMATOSUCHUS* (AMPHIBIA, TEMNOSPONDYLI) FROM THE *CYNOGNATHUS* ZONE OF SOUTH AFRICA

by

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ABSTRACT

Some aspects of the cranial morphology of *Trematosuchus sobeyi*, a temnospondylous trematosaurid amphibian from the South African *Cynognathus* Zone, are described in detail for the first time from a new fossil find referred to this form. The new specimen is similar in size to that of the Holotype of *Trematosuchus sobeyi* but differs in the more moderate elongation of the snout. Apart from the presence of the septomaxilla, the validity of the genus *Trematosuchus* is reconfirmed *inter alia* by its much larger size and the position of the supraorbital sensory groove alongside the lachrymal margin rather than crossing this bone. This last characteristic differentiates *Trematosuchus* from all other trematosauroids.

T. sobeyi is of particular importance since it represents the only purely freshwater Gondwanan form closely comparable to the European *Trematosaurus*. The presence of *T. sobeyi* in the lowermost strata of the *Cynognathus* Zone in South Africa, in association with some other forms related to the Upper Olenekian (Middle Buntsandstein) tetrapod assemblage of Europe, indicates that these strata belong to the Scythian in contrast to the higher strata of the *Cynognathus* Zone which are Anisian.

KEYWORDS: Trematosauridae, Biostratigraphy, *Cynognathus* Zone.

INTRODUCTION

Trematosauroid amphibians, characterised by their wedge-shaped skullsand paired anterior palatal vacuities, comprise one of the most common groups of Triassic temnospondyls. They stem from the family Benthosuchidae (Shishkin 1968, 1980; Getmanov 1989) which also gave rise to other more advancedlineages such as the Heylerosauridae (Shishkin 1980) and the poorly known Yarengiidae (Shishkin 1964; Novikov 1990).

The Benthosuchidae are recorded only from the early Lower Triassic (Induan – Lower Olenekian) of eastern Europe and northeastern Asia (Shishkin & Lozovsky 1979). Heylerosauridae are endemic to the Euroamerican province; they appear in the upper Lower Triassic (Upper Olenekian) and become very common in the Anisian (Morales 1987; Ochev & Shishkin 1989; Shishkin & Ochev 1993; Milner 1990). The Yarengiidae are known only from eastern Europe (Upper Olenekian). In contrast, members of the family Trematosauridae are recorded from all the continents except for South America and Antarctica.

The majority of trematosaurids come from the Lower Triassic. Middle Triassic finds reported from North Africa, India (Lehman 1971; Chatterjee & Hotton 1986; Welles 1993) and Canada (Baird 1986) are rare and poorly known. The Upper Triassic trematosaurids are known from a single find from western Europe (Hellrung 1987).

A number of transitional forms from the Lower Olenekian of eastern Europe suggest that Trematosauridae can be derived from the Laurasian Benthosuchidae (Shishkin 1968, 1980; Getmanov 1989). The Trematosauridae are one of only a few amphibian groups which succeeded in spreading to the nearshore habitats as seen from their particular abundance in the coastal marine facies of the Lower Olenekian of Spitsbergen and also in Madagascar.

Trematosaurids are most common in Europe and rare in the Gondwanan continents which may suggest that they dispersed fromLaurasia to the south, most probably via the coastal or borderland routes (Lehman 1979; Cosgriff 1984). This idea is complicated by the fact that most of the Gondwanan trematosaurid finds belong to the specialized needle-snouted forms, which first appeared in both hemispheres in the lowermost Lower Triassic (Induan), i.e. before the typical benthosuchid – derived trematosaurids which are first recorded in the Lower Olenekian (as exemplified by the Spitsbergen assemblage). The earliest Indian long-snouted forms are known from the Panchet Series of India (*Gonioglyptus*, *Panchetosaurus*; Tripathi 1969), the marine Prionolobus Beds of the Salt Range in Pakistan (*Halobatrachus kokeni*; Huene 1920; Hammer 1987) and from the Vokhmian horizon of the Cis-Urals (undescribed form; Shishkin & Ochev 1993). This seems to reinforce the suggestion that theassemblage of forms currently termed Trematosauridae may well prove to be diphyletic in origin (cf. Bystrow and Efremov 1940 p 143; Shishkin 1964). The subdivision of the Trematosauridae into two (or three) subfamilies has been suggested by Efremov (1933) Säve-Söderberg (1935), Hammer (1987) and Welles (1993).

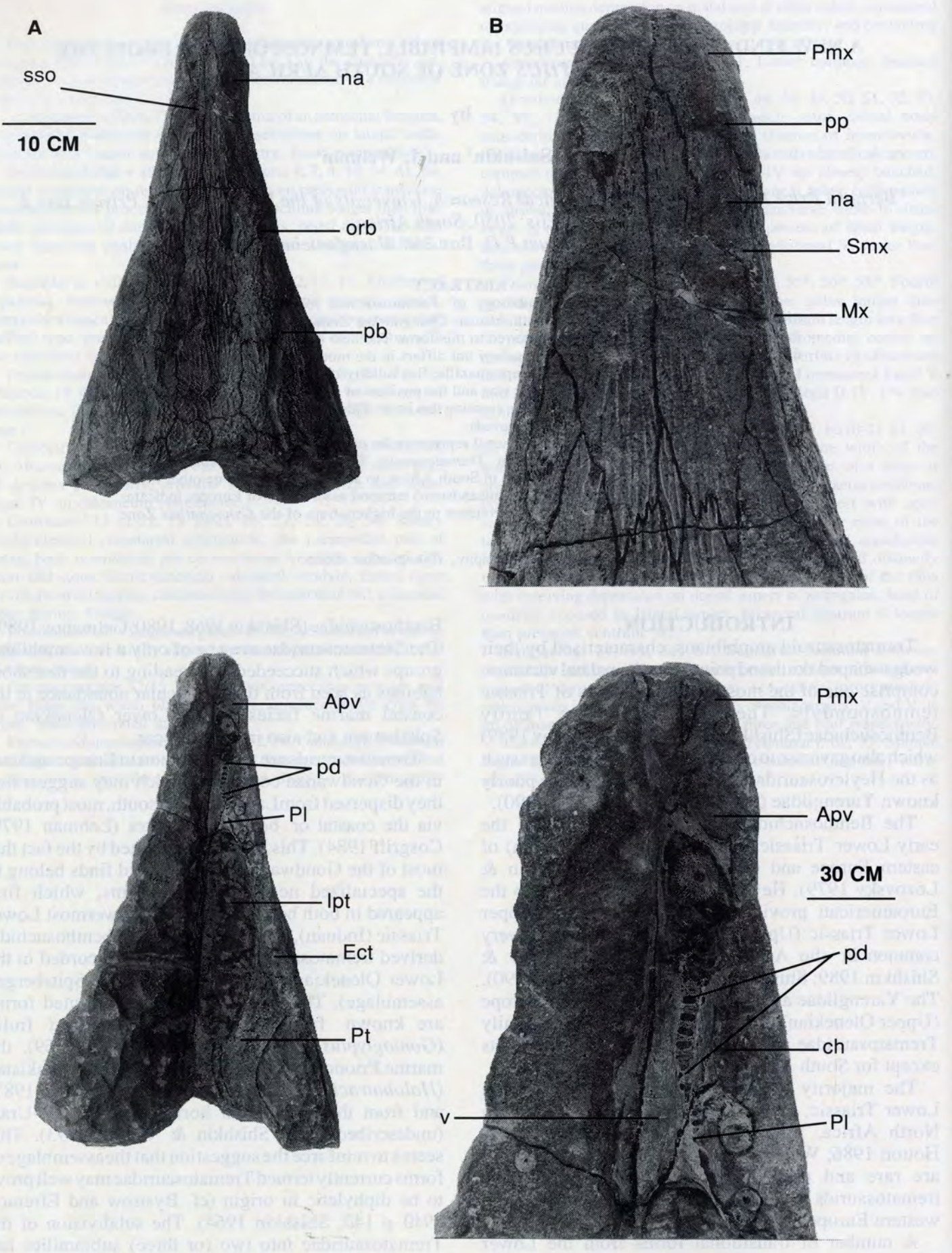


Figure 1. *Trematosuchus sobeyi* SAM 2979 (Holotype) A. Dorsal view of the skull, B. dorsal view of the snout, C. ventral view of the palate, D. ventral view of the anterior part of the palate.

Apart from the finds from Madagascar, India and Pakistan mentioned above, Gondwanan trematosaurids are known only from Australia and South Africa. All the Australian finds belong to the long-snouted forms and include the type of *Erythrobatrachus* from the Blina Shale (Cosgriff & Garbutt 1972) and unidentifiable fragments from the Arcadia Formation and the lower part of the overlying Glenidal Formation (Warren 1985), the former two stratigraphic units being most probably lower Olenekian (Smithian) in age.

In South Africa trematosaurids were first recovered in the early part of this century and are represented by two Triassic forms from the Beaufort Group, *"Trematosaurus" kannemeyeri* and *Trematosuchus sobeyi* (Broom 1909; Haughton 1915, 1925; Huene 1920). The former is a poorly known long-snouted *Aphaneramma*-like form described from a fragment of skull (Broom 1909), the provenance of which is uncertain. Kitching (1978) considers it to come from the *Cynognathus* Zone (Upper Beaufort Group) which is variously considered to be Upper Olenekian (Spathian) to Anisian in age (Ochev & Shishkin 1989).

Trematosuchus sobeyi, is of particular importance since it represents the only instance in Gondwana where a complete trematosaurid skull (Figure 1) is recorded from a purely fresh water environment (fluvial-lacustrine deposits of the Upper Beaufort Group). Furthermore, it is the only Gondwanan form which is comparable with the European *Trematosaurus*.

Both the type (Figure 1) and referred specimen of *T. sobeyi* described by Haughton (1915, 1925) were obtained from a sandstone quarry of the *Cynognathus* Zone in the Queenstown area, Cape Province. According to Kitching (pers. comm.) the fossil-bearing sandstone belongs to the lower part of the *Cynognathus* Zone. No further finds of this genus have been reported until recently when another specimen (Figures 2-5) was recovered in the *Cynognathus* Zone of the northeastern Orange Free State (Welman *et al.* 1991). The new *Trematosuchus* find (NMQR 3263) includes two fragments of the same skull collected at Verdun Farm, Paul Roux district. The narrowness of the snout fragment combined with paired elongated anterior palatal vacuities and strong reduction of the interchoanal tooth row immediately suggest the trematosaurid affinity of the specimen. Although no more fossils were discovered from this site, the faunal assemblage of this stratigraphic unit includes *Cynognathus*, trirachodontid cynodonts, an erythrosuchid thecodontian and *Parotosuchus*-like capitosauroid amphibians (Welman et al. 1991). Hancox *et al.* (in press) show that this faunal complex is distinct from the main faunal assemblage of the *Cynognathus* Zone known from the Cape Province and the southern Orange Free State, and underlies it. This makes the new find of *Trematosuchus* important for biostratigraphic subdivision of the *Cynognathus* Zone.

In addition, the new find provides data on the cranial morphology of *Trematosuchus* which cannot be discerned in the type.

SYSTEMATIC PALAEONTOLOGY

Trematosuchus sobeyi (Haughton 1915)
Trematosaurus sobeyi: Haughton 1915, p.47, pl.VIII, IX
Trematosuchus sobeyi: Watson 1919, p.41
Trematosaurus sobeyi: Huene 1920, p.443
Trematosuchus sobeyi: Haughton 1925, p.250, fig.15

Holotype

SAM 2979, a nearly complete skull; Queenstown, Cape Province, Upper Beaufort (*Cynognathus* Zone). (Figure 1).

Referred specimens under description

NMQR 3263 A & B (two fragments of the same skull) Verdun Farm, Paul Roux District, Orange Free State, *Cynognathus* Zone (Figures 2-5).

Generic and specific diagnosis

Large form (skull about 420mm in midline length); orbits extremely small and round; septomaxilla and interfrontal present; parietals not narrowed anteriorly; supraorbital sensory groove alongside the medial lachrymal margin rather than crossing the lachrymal.

PRESERVATION AND METHODS

NMQR 3263 (Figures 2-5) consists of Block A: the snout broken off obliquely behind the nasochoanal area, and Block B: a part of the right side of the palate immediately in front of the subtemporal fossa, together with the dorsal portion of the jugal.

Both blocks, obviously from a fine-grained grey sandstone lens, were found lying close together on the surface but not in situ.

They exhibit the same type of mineralization and weathering (the surface of the bones being brown and glossy) and are consistent in size. There seems to be no doubt that both fragments belong to the same individual, in spite of the lack of immediate contact between them. The fresh fracture surfaces of the specimen indicate that fragmentation of the skull almost certainly occurred only after it weathered out of the embedding rock. The good preservation of sharp edges on the specimen suggests that the skull was neither transported over any long distance prior to burial nor did it suffer post depositional sedimentary reworking.

NMQR 3263 was mechanically prepared under a stereo microscope with a pneumatic engraver. The engraver was fitted with a sharpened, round tungsten-carbide tip. Exposed bone was covered with a Glyptal cement solution, diluted with lacquer thinners.

MORPHOLOGICAL DESCRIPTION

The fragment comprising block A (Figures 2, 3, 5 A-C) is comparable in size with the corresponding part of the type skull. It includes both premaxillae, septomaxillae, the anterior parts of the nasals and maxillae, a part of the left palatine and both vomers, the right of which lacks most of its parachoanal area.

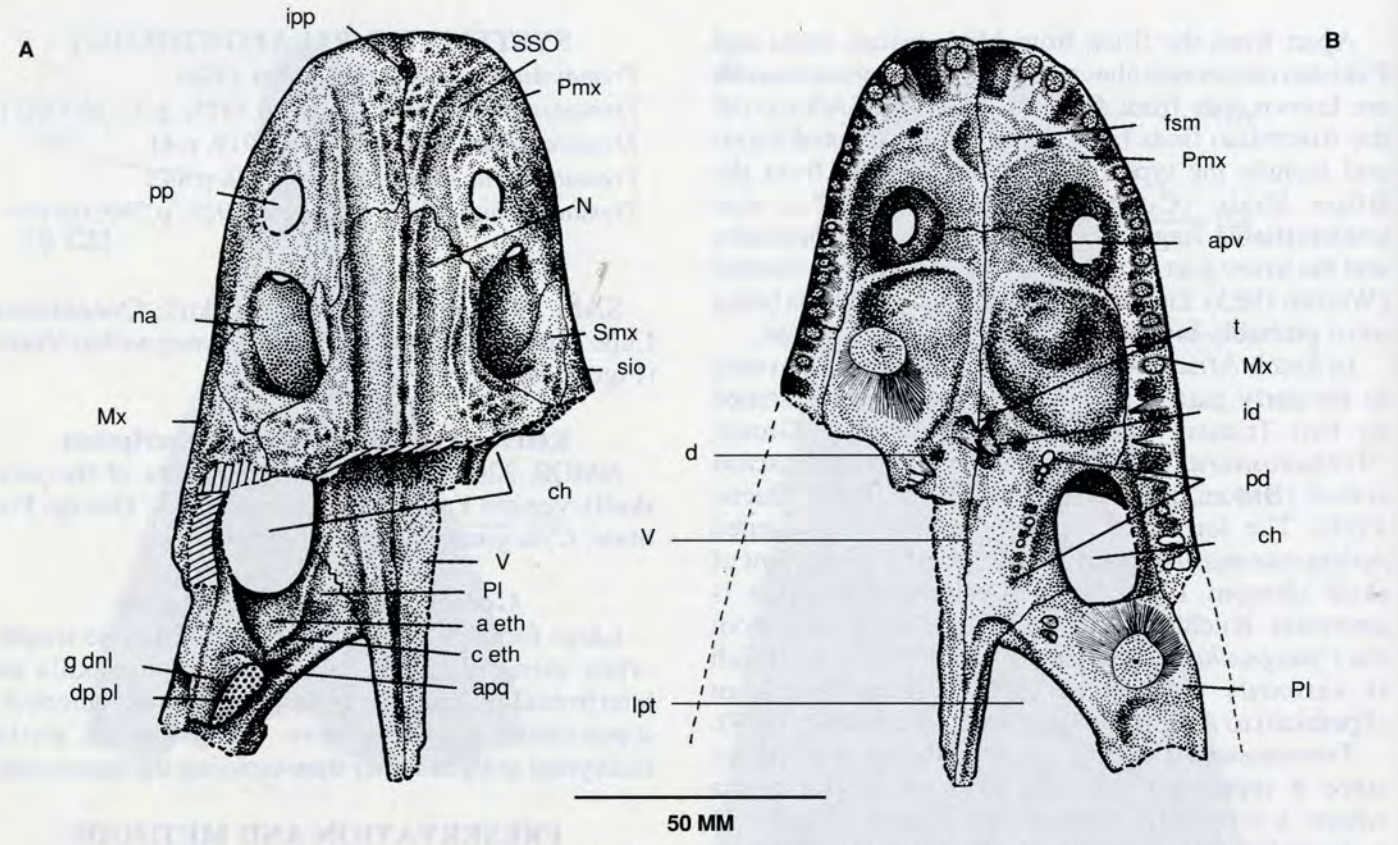


Figure 2. *Trematosuchus sobeyi* NMQR 3263A. Anterior part of the skull. A. dorsal view, B. ventral view.

Skull roof

The snout is narrow, with a blunt end. The nares are elongated and irregular in shape. They differ from those in the type skull (Figure 1A) in their more anterior position and in that they diverge anteriorly rather than being parallel. In front of them, the dermal roof is pierced by paired foramina (Figure 2A; pp) which housed the tips of the symphyseal tusks of the lower jaw. Although their margins are partially damaged it is clear that they were regularly oval. The left foramen is somewhat larger than the right.

It is difficult to decide whether these prenarial perforations are also present in the type skull. The irregular prenarial opening seen on its left side (Figure 1B) is the anterior palatal vacuity exposed dorsally due to erosion of the dorsal surface of the premaxilla. Prenarial perforations similar to those seen in our specimen, are typical for mastodonsaurids (Fraas 1889; Wepfer 1923; Ochev 1972) and may occur in the large individuals of other Triassic temnospondyls, such as cyclotosaurids (Fraas 1913). They were also figured by Zittel for *Trematosaurus* (Woodward 1932, fig. 311).

The right naris and the prenarial foramen as well as the right premaxilla in our specimen are slightly displaced forward relative to their left counterparts. The small foramen in the center of the median premaxillary suture described in the type (Haughton 1915) is not present, but there is a corresponding pit (Figure 2A; ipp) situated more anteriorly in the new material.

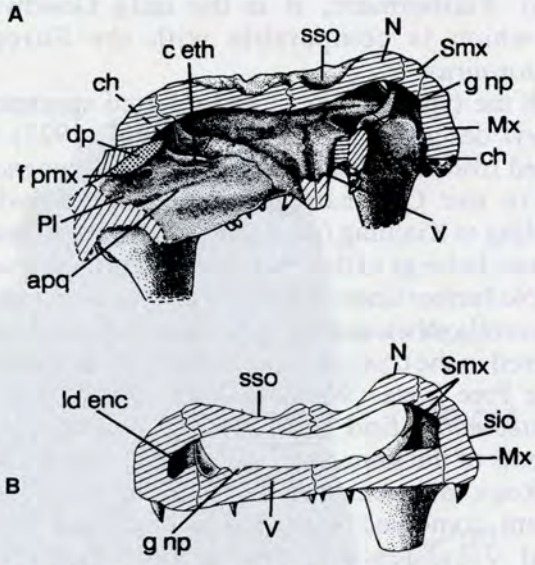


Figure 3. *Trematosuchus sobeyi* NMQR 3263A. A. Anterior part of the skull in posterior view, seen slightly from the top, B. Diagram of transverse section through the anterior end of the choanae in posterior view.

The dermal sculpture is coarsely pitted. On the anterior part of the maxillary and lateral to the prenarial perforation on the premaxilla, the pits are elongated.

The supraorbital sensory grooves (Figures 2A, 3; sso) are very broad, but shallow and run (in the snout area) along the midline of the skull roof towards the anterior end of the snout where they diverge slightly. The ends of the preserved portions of these grooves diverge posteriorly, immediately posterior to the nares.

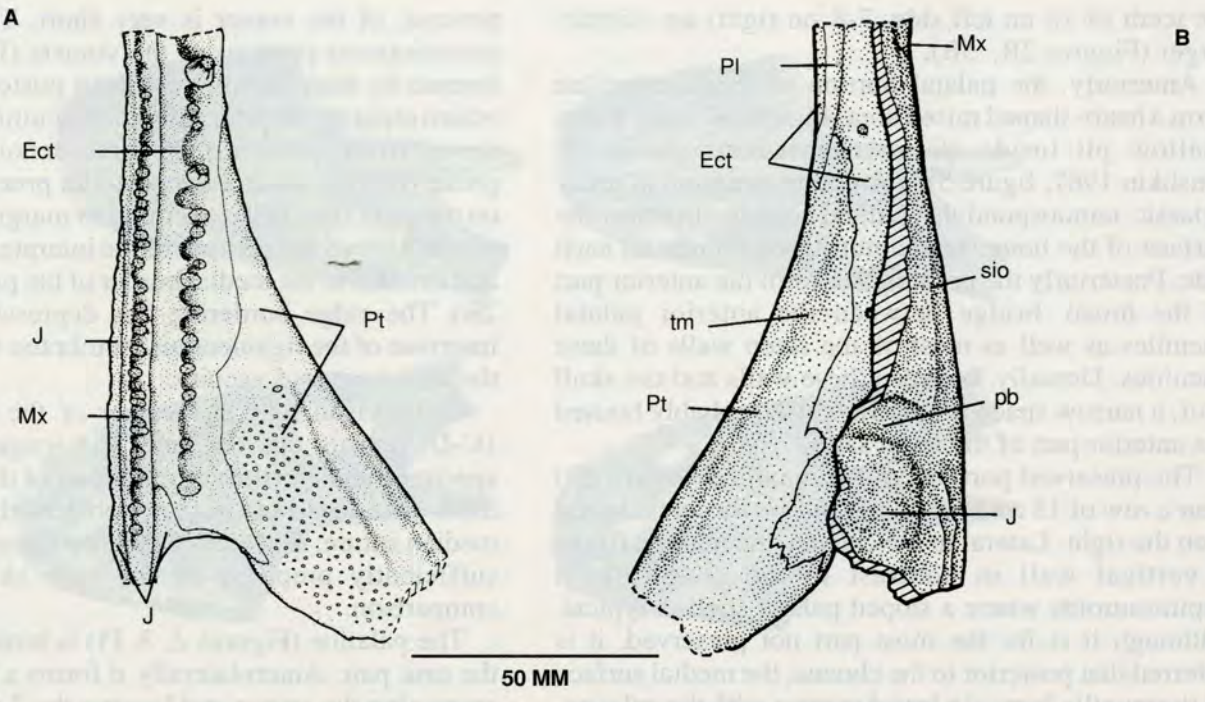


Figure 4. *Trematosuchus sobeyi* NMQR 3263B. Fragment of palate. A. ventral view, B. dorsal view

The anterior parts of the infraorbital grooves (Figures 2A, 3B, 4C; sio) are similarly broad but expressed less markedly as they run along the smooth labial surface of the maxillae. The sensory grooves of the type skull (Figures 1A-B) have the same pattern, but their anterior (snout) segments are poorly preserved except for the postnarial exposure of the supraorbital grooves.

The premaxillae have a long median suture anteriorly. Their posterior parts, separated by an anterior projection of the nasals, are much shorter than the median suture. In contrast, in the type of *Trematosuchus* (Figures 1A-B) the separated posterior parts of the premaxillae exceed the anterior contacting parts in length, and their sutures with the nasals form a sharper angle.

The septomaxilla (Figures 2A, 3B, 5A; Smx) forms the posterolateral rim of the naris and consists of two parts. The dorsal semilunar part belongs to the skull roof and is ornamented. It extends anteriorly along 3/5 of the lateral border of the naris and reaches the premaxilla-maxilla suture. It constitutes a concave smooth plate forming the posterolateral wall of the naris and extending down to the dorsal surface of the vomer (Figure 3B).

The structure and position of the septomaxilla as described is much the same as in the type skull except for the triangular rather than semilunar shape of the dorsal part of the bone in the latter. The figure by Haughton (1915, plate VIII, figure 2) showing the septomaxilla limited to the area behind the naris is inaccurate and at variance with his description (Figures 1a-b).

The maxilla broadens dorsally behind the septomaxilla to contact the nasal and is ornamented in this area (Figure 2A). The labial strip of the bone alongside the tooth margin is smooth. The maxilla-premaxilla contact begins dorsally on the lateral narial border, extends down to the marginal tooth row and crosses it at the level of the anterior vomerine tusk (Figures 2A-B).

Palatal complex

The palatal view of block A exhibits the paired anterior palatal vacuities common in trematosauroids, the left choana and the anteriormost part of the left interpterygoid vacuity (Figures 2B, 5B). The anterior palatal vacuities are very deep with steep walls, and appear to be more widely separated and situated closer to the tip of the snout than in the type skull (Figures 1C-D). Perforations of the skull roof are situated (Figure 2B) immediately dorsal to these vacuities. The choana is clearly shorter and broader than in the type, (Figures 1C-D). The anterior end of the interpterygoid vacuity in our specimen is pointed at the level of the posterior end of the vomer-palatine suture and extends anteriorly far as the posterior border of the choana (Figures 2A-B). In contrast, the anterior end of the interpterygoid vacuity in the type is broadly rounded and situated far posterior to the choana (Figure 1C).

On the ventral side the premaxilla consists of the tooth bearing marginal area and the palatal shelf (Figure 2b). In the tooth row of each premaxilla the anteriormost 3-4 teeth are large and subsequent teeth decrease slightly in size posteriorly. The next posterior set consists of uniformly small teeth, 10-11 in number including the empty tooth pits. Behind these teeth, posterior to the midpoint of the anterior palatal vacuity and extending backwards to the end of the premaxilla,

the teeth (9-10 on left side; 7-8 on right) are slightly larger (Figures 2B, 5B).

Anteriorly, the palatal portion of the premaxillae form a heart-shaped raised area (Figure 2B; fsm) with a shallow pit inside (*fossa subrostralis media* cf. Shishkin 1967, figure 5), a structure common in many Triassic temnospondyls. Lateral to this structure the surface of the bone bears a nutritive foramen on each side. Posteriorly the premaxillae form the anterior part of the broad bridge between the anterior palatal vacuities as well as most of the steep walls of these vacuities. Dorsally, between these walls and the skull roof, a narrow space is present which probably housed the anterior part of the nasal sac.

The preserved portions of the maxillae (Figure 2B) bear a row of 13 teeth and tooth pits on the left side and 5 on the right. Lateral to the choana, the maxilla forms a vertical wall in contrast to the condition in capitosauroids where a sloped palatal shelf is typical. Although it is for the most part not preserved, it is inferred that posterior to the choana, the medial surface of the maxilla formed a broad contact with the palatine. The teeth of the maxilla and premaxilla are moderately compressed at the base and have an almost circular cross-section half-way along their length.

The vomer (Figures 2, 3, 5A-C), although long, is somewhat shorter than in the type (ratio of its width to length, measured between the posterior end of the anterior palatal vacuity and anterior end of interpterygoid vacuity, is 0.36, as compared with 0.33 in the type). The ventral surface of the vomer can be subdivided antero-posteriorly into 4 parts. The anterior part is short and narrow and forms together with its counterpart, the posterior half of the bridge between the anterior palatal vacuities (Figure 2B). The surface of this bridge is transversely convex. The broadest part of the bone is occupied by a large depression which houses the tusk pair. On the left side of the palate the anterior tusk was functional, and is followed posteriorly by the pit for the replacing tusk; on the right side the condition is reversed (Figure 2B).

The interchoanal part of the vomer is narrow, ventrally flattened and wedges anteriorly between the elevated borders of the tusk depressions. Along the median suture of the vomers, the anterior wedged area of this portion bears one small tooth on each side (Figure 2; id) and an associated empty replacement pit. Anterior to these teeth, an unpaired central tuber (Figure 2B; d) is present which may have borne a single tooth. One more small tooth is present on each side lateral to the central group, close to the border of the tusk depression (Figure 2B; d). Lateral to this pair of teeth, just behind the tusk area, the choanal border of the vomer bears a parachoanal tooth row which is preserved only on the left side and consists of 7 teeth and 3 tooth pits (Figure 2B; pd). Posteriorly, the parachoanal tooth row converges slightly toward the median vomerine suture and diverges from the choanal border. It is separated from the palatine continuation of the same row by a broad gap crossed by the vomer-palatine suture. The posterolateral, palatine process, of the vomer is very short. The fourth and posteriormost portions of the vomers (Figure 2B) are formed by their narrow and deep posterior processes which separate the interpterygoid vacuities and underly the cultriform process of the parasphenoid, which is not preserved. The base of the posterior process, preserved on the right side, bears a semilunar marginal depression which follows the contour of the interpterygoid vacuity and extends to the medial border of the palatine (Figure 2B). The ridge bordering this depression marks the insertion of the ligamentous membrane which covered the interpterygoid vacuity.

Comparison with the vomer of the type (Figures 1C-D) reveals that the latter is longer than in our specimen and that the vomerine part of the parachoanal tooth row does not converge posteriorly towards the median suture. The area of the interchoanal teeth is not sufficiently prepared on the type skull to enable comparison.

The palatine (Figures 2, 3; Pl) is broken off behind the tusk pair. Anterolaterally it forms a broad process contacting the vomer and bearing the 2 posterior teeth of the parachoanal tooth row, referred to above. Anteriorly, the palatine sends off a small plate-like vertical process which forms part of the lateral wall of the choana. The palatine is markedly different from that of the type (Figure 1C-D) in having a shorter and much more transversely positioned suture with the vomer, whereas the anterolateral process is narrower. In accordance with this, the choana and the interpterygoid vacuity are closer to each other than in the type.

The lack of the postnarial part of the skull roof permits examination of the dorsal side of the palatine and the posterior portion of the vomer. In addition, some details of the exoskeletal nasal cavity are seen in posterior view of Block A.

The dorsal surface of the palatine is subdivided into two smooth areas. The medial area extends along the border of the interpterygoid vacuity while the lateral area is more differentiated and bordered laterally by the narrow elevation which contacted the maxilla. These areas are separated by a *processus dorsalis* (Figure 2A; dp pl) which obviously contacted the lachrymal bone as in many other late temnospondyls (cf. Säve-Söderberg 1936; Shishkin 1960, 1968, 1973). Anteriorly, the boundary between the two areas is formed by the narrow ethmoidal ridge (Figures 2A, 3A; c eth) which extends anteromedially from the dorsal process along a curved line toward the posteromedial border of the choana.

The area situated medial to the dorsal process and the ethmoid ridge, was occupied by the anterior sickle-shaped process of the palatoquadrate cartilage (Figure 2A, 3A; apq). It probably reached the posterior wall of the nasal capsule near the vomer-palatine suture where the impression of this cartilage is seen as a shallow groove wedging out anteromedially.

The area situated laterally to the dorsal process and the ethmoid ridge (Figure 2A) consists of two portions separated by a ridge extending from the posterior part of the ethmoid ridge to the posterolateral choanal border.

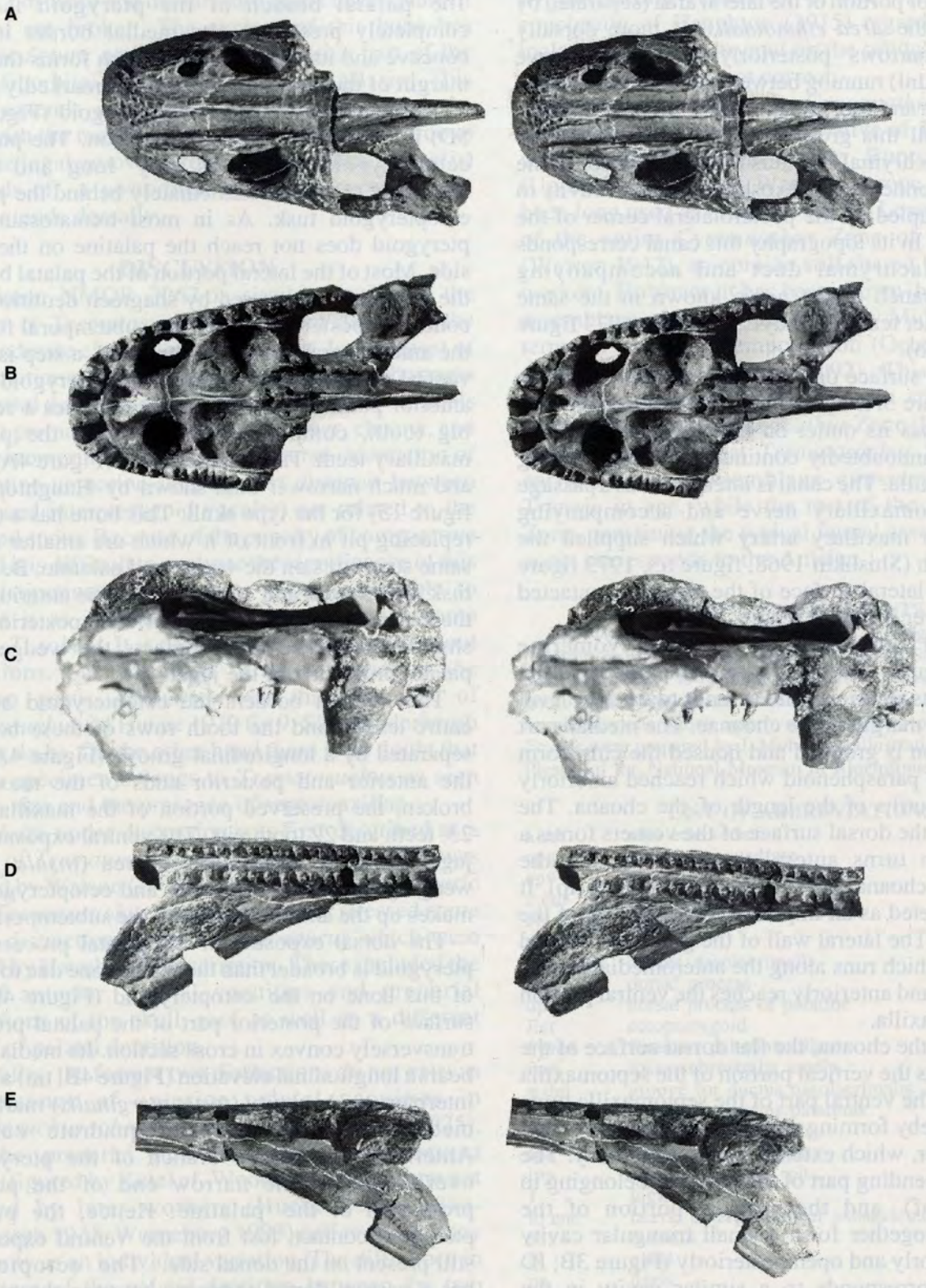


Figure 5. *Trematosuchus sobeyi* NMQR 3263A. Stereo pairs of anterior part of skull A. dorsal view, B. ventral view, C. posterior view. *Trematosuchus sobeyi* NMQR 3263B. Stereo pairs of fragment of the palate D. ventral view, E. dorsal view.

The anteromedial *area ethmoidalis* (Figure 2A; a eth) was occupied by the posterolateral continuation of the floor of the nasal capsule. This structure is comparable to the *planum triangulare* in modern anurans; the corresponding area of the dorsal palatine surface is known in a number of late Permian and Triassic temnospondyls (Shishkin 1968, figure 6B; 1973, figure 22, 60b). In *Trematosuchus* the *area ethmoidalis* differs from that of other trematosauroids in being semilunar rather than triangular, and very steeply sloped toward the choana. The lateral part of this area continues forward along the lateral border of the choana as a narrow groove between the dorsal and palatal divisions of the maxilla.

The posterior portion of the lateral area (separated by a ridge from the *area ethmoidalis*) is more dorsally situated and narrows posteriorly to form a groove (Figure 2A; g dnl) running between the lateral elevation of the palatine and the dorsal process. In a completely preserved skull this groove would be roofed by the maxilla and lachrymal and thus formed the floor of the canal which connected the exoskeletal cranial cavity to the space occupied by the posterolateral corner of the nasal capsule. In its topography this canal corresponds to the nasolachrymal duct and accompanying infraorbital branch of the nerve known in the same position in other temnospondyls (Shishkin 1973 figure 22, 48, 50, 60b).

The medial surface of the dorsal process exhibits a foramen (Figure 3A; f pmx) leading into a transverse canal which has its outlet on the lateral side of the palatine and undoubtedly continued into the missing part of the maxilla. The canal is interpreted as a passage for the palatomaxillary nerve and accompanying branch of the maxillary artery which supplied the maxillary teeth (Shishkin 1968, figure 63, 1973 figure 22, 60b). The lateral surface of the palatine contacted the maxilla over its entire length.

The dorsal surface of the posterior vomerine processes (Figures 2A, 3A) forms a median elevation which broadens anteriorly and extends toward the level of the anterior margin of the choanae. The median part of the elevation is grooved and housed the cultriform process of the parasphenoid which reached anteriorly up to three fourths of the length of the choana. The lateral part of the dorsal surface of the vomers forms a groove which turns anterolaterally following the outline of the choanal border (Figures 3A-B; g np). It can be interpreted as an impression of a branch of the palatal nerve. The lateral wall of the groove is formed by the ridge which runs along the anteromedial border of the choana and anteriorly reaches the ventral portion of the septomaxilla.

Anterior to the choana, the flat dorsal surface of the vomer supports the vertical portion of the septomaxilla (Figure 3B). The ventral part of the septomaxilla turns medially, thereby forming a zone of horizontal contact with the vomer, which extends anteroposteriorly. The vomer, the ascending part of the maxilla (belonging to the skull roof), and the vertical portion of the septomaxilla together form a small triangular cavity pointed anteriorly and open posteriorly (Figure 3B; lD enc) which corresponds to a similar cavity in the brachyopid *Batrachosuchoides* (Shishkin 1967, p. 312). This most probably housed the lateral diverticulum of the nasal sac. There is a notable variation in the structure of this cavity on the two sides of the skull. The right cavity is formed by 3 bones as described, while in the left, the floor and the lateral wall are formed only by the maxilla (Figure 3B).

Most of the ventral exposure of the fragment B (Figures 4A, 5D) belongs to the pterygoid, ectopterygoid and maxilla with a small wedge of jugal intervening from behind between the latter two bones. The palatal branch of the pterygoid is almost completely preserved. Its medial border is gently concave and its lateral border which forms the medial margin of the subtemporal fossa, is markedly convex.

The ventral surface of the pterygoid (Figures 4A, 5D) is concave in transverse section. The pterygoid-ectopterygoid contact is very long and extends anteriorly to a point immediately behind the posterior ectopterygoid tusk. As in most trematosaurids, the pterygoid does not reach the palatine on the ventral side. Most of the lateral portion of the palatal branch of the pterygoid is covered by shagreen dentition which continues posteriorly up to the subtemporal fossa. On the anterolateral margin of this field, a step is formed ventral to the smooth surface of the pterygoid. On the anterior pointed end of the shagreen, lies a relatively big tooth, comparable in size with the posterior maxillary teeth. The ectopterygoid (Figure 4A) is long and much narrower than shown by Haughton (1925, figure 15) for the type skull. This bone has a tusk and replacing pit in front of it which are smaller than the same structures on the vomer and palatine. Behind the tusk are 13 teeth and 12 tooth pits. The anterior part of the ectopterygoid is broken off. The posterior end is slightly broadened and contacts the wedge-shaped palatal projection of the jugal.

The maxilla borders the ectopterygoid along its entire length and the tooth rows of these bones are separated by a longitudinal groove (Figure 4A). Both the anterior and posterior ends of the maxilla are broken, the preserved portion of the maxilla having 23 teeth and 22 tooth pits. The ventral exposure of the jugal forms a small narrow area (*insula jugalis*) wedging between the maxilla and ectopterygoid, and makes up the anterior border of the subtemporal fossa.

The dorsal exposure of the palatal process of the pterygoid is broader than the ventral one due to overlap of this bone on the ectopterygoid (Figure 4B). The surface of the posterior part of the palatal process is transversely convex in cross section. Its medial border bears a longitudinal elevation (Figure 4B; tm) along the interpterygoid vacuity (*torus marginalis*) marking the medial border of the palatoquadrate cartilage. Anteriorly the palatal branch of the pterygoid is overlapped by the narrow end of the posterior projection of the palatine. Hence, the palatine-pterygoid contact, lost from the ventral exposure, is still present on the dorsal side. The ectopterygoid has a narrow dorsal exposure between the pterygoid and the ascending plate of the jugal and reveals a row of nutritive foramina (Figure 4B). The jugal is very thick on the anterior border of the subtemporal fossa and consists of two parts; a narrow palatal portion wedging out anteriorly (Figure 4A) and a deep ascending portion belonging to the skull roof (Figure 4B). The latter faces medially and bears a row of foramina along its base which are similar to those on the ectopterygoid.

In side view fragment B exhibits a narrow labial surface of the maxilla which is smooth and contacted dorsally throughout its length by the jugal. The

anterior, posterior and dorsal sides of the cheek plate of the jugal are broken. The surface of this bone has dermal sculpture and shows the posterior part of the broad infraorbital sensory groove (Figure 4B; sio). This groove extends along, and immediately above the suture with the maxilla. Posteriorly, where this groove meets the jugal groove, it forms a step (*flexura jugalis*) and sends off a postorbital branch (Figure 4B; pb) which extends dorsally.

DISCUSSION

Specimen NMQR 3263 is similar in size to the holotype of *Trematosuchus sobeyi* but differs in the more moderate elongation of the snout. In fact most of the distinctions of our specimen noted above (shortness of prenarial distance; more limited projection of nasals between premaxillae; shortness of vomer, choana, and palatine-vomerine suture; subtransverse orientation of the palatine-vomerine suture; short distance between choana and interpterygoid vacuity) are related to the shortened snout. Because of the paucity of comparative material it is difficult to evaluate the significance of this main distinction, but it seems most reasonable to interpret it as individual variation within the same species, *T. sobeyi*. It is of interest that as regards snout proportions, our specimen is much closer to the European genus *Trematosaurus*, than the type of *Trematosuchus* (cf Huene 1920 fig 9; Säve-Söderbergh 1937 fig 4a,b). On the other hand there is no doubt that the new specimen belongs to *Trematosuchus* as seen from its size and the presence of septomaxillae.

The form under discussion was first described as a species of *Trematosaurus* (Haughton 1915). This was opposed by Watson (1919) who proposed a new generic name, *Trematosuchus*, for this form and stressed some alleged distinctions from *Trematosaurus* which were implied by Haughton's description. These included the lack of anterior palatal vacuities and prenarial perforations of the skull roof as well as a different pattern of palatal dentition.

In reality, the former two distinctions do not exist as the presence of anterior palatal vacuities in *Trematosuchus sobeyi* was shown by Haughton (1925), while the prenarial perforations in *Trematosaurus brauni* (figured by Zittel cf. Woodward 1932) were not reported by later workers (Huene 1920; Säve-Söderbergh 1935, Werneburg 1993) and probably may occur only as an individual variation. The difference in the pattern of the palatal dentition between the two forms discussed is also questionable. Nevertheless, the validity of the genus *Trematosuchus* can be substantiated on the basis of some other characters. These include its much larger size; the extremely small and round orbits; the presence of a septomaxilla and interfrontal; the lack of an anterior narrowing of parietals; and the position of the supraorbital sensory groove alongside the lachrymal margin rather than crossing this bone. This last peculiarity found by us in the type specimen, differentiates *Trematosuchus* from all other trematosauroids and is possibly accounted for by the strong reduction of the lachrymal. The conclusion of Haughton (1915) regarding the broad inclusion of the lachrymal on the orbital margin in the type of *T. sobeyi* is not correct.

Trematosuchus from the *Cynognathus* Zone can be characterised as the closest relative of *Trematosaurus* which comes form the middle Buntsandstein zone (Upper Olenekian) of Western Europe. This fact has been long used as evidence for the Lower Triassic age of the entire *Cynognathus* Zone of South Africa (Watson 1942), an opinion still shared by most recent workers. However, it has been shown that the reptilian assemblage of this zone is typically Middle Triassic in terms of its group compositition (Ochev & Shishkin 1989; Shishkin & Ochev 1992). This contradiction appears to be resolved by a recent study on faunal changes within the *Cynognathus* Zone (Hancox *et al.* in press) suggesting that *Trematosuchus* belongs to the earliest faunal assemblage considered as Lower Triassic in age, while the rest of the *Cynognathus*-Zone, containing the typical faunal assemblage of this zone, corresponds to the Anisian.

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LIST OF ABBREVIATIONS

a eth	area ethmoidalis
apq	area palatoquadrata
apv	anterior palatal vacuity
c eth	crista ethmoidalis
ch	choana
d	tooth pit
dnl	ductus nasolacrimalis
dp	dorsal process
dp pl	dorsal process of palatine
Ect	ectopterygoid
f pmx	foramen palatomaxillare
fsm	fossa subrostralis media
g dnl	groove for ductus nasolacrimalis
g np	groove for nervus palatinus
id	interchoanal dentition
Ipt	Interpterygoid vacuity
ipp	interpremaxillary pit
J	jugal
ld enc	lateral diverticulum of exoskeletal nasal cavity
Mx	maxilla
N	nasal
na	naris
orb	orbit
pb	postorbital branch (groove)
pd	parachoanal dentition
Pl	palatine
Pmx	premaxilla
pp	prenarial perforations
pqa	palatoquadrate area
Pt	pterygoid
sio	sulcus infraorbitalis
Smx	septomaxilla
sso	sulcus supraorbitalis
t	tuberosity
tm	torus marginalis
V	vomer

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NEW FIND OF *DIARTHROGNATHUS* (THERAPSIDA: CYNODONTIA) AFTER SEVENTY YEARS.

by

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ABSTRACT

Diarthrognathus is arguably South Africa's most famous therapsid fossil. Since its discovery seventy years ago no new material had come to light until now. This paper records the recovery, from the Elliot Formation of South Africa, of a partial left lower dentary with most of its dentition preserved.

KEY WORDS: Therapsida, Ictidosauria, Tritheledontidae.

INTRODUCTION

Mammals are descended from a group of fossil mammal-like reptiles known as cynodonts which are well represented in the rocks of the Karoo. Perhaps the most famous cynodont is *Diarthrognathus broomi* (Crompton 1958), one of a group of cynodonts known as ictidosaurs or tritheledontids. The name means "two joint jaw": reptiles and mammals have entirely different jaw suspensions, so it has long been realised that at some stage a mammalian ancestor must have existed in which both types of joint were present. *Diarthrognathus* was considered by Crompton to represent that stage, but such is not the case (Gow 1981). The honours belong instead to the very earliest mammals, such as *Morganucodon*.

The type of *Diarthrognathus*, a partial skull and fairly complete skeleton, and a second specimen, a partial skull and some postcranial elements, came from a sandstone quarry in the Clarens Formation near Ladybrand in 1924. Until now no new material of *Diarthrognathus* has come to light, in spite of much intensive collecting. In fact some have doubted the validity of *Diarthrognathus* (Hopson & Kitching 1972, Kitching & Raath 1984), believing it to be a junior synonym of the closely related, and more common form *Pachygenelus monus* (Watson 1913), usually found as rather small juvenile skulls and lower jaws. Gow (1980) described the dentitions of both taxa, showing that they are similar but clearly different.

Fossils are generally scarce in the rocks of the Stormberg (Elliot and Clarens Formations; formerly Redbeds and Cave Sandstone respectively), but as they represent crucial stages in the evolution of both mammals and dinosaurs the incentive to keep looking is great. An exception to the scarcity rule is a lithological horizon within the Elliot Formation, aparently confined to the outcrop in the northeastern Orange Free State, which represents a time of greatly diminished sedimentation (R Smith, pers. com.), dubbed the *Tritylodon* acme zone (Kitching and Raath 1984). This band is relatively fossil rich, though the fossils are not as well preserved as more isolated finds from other parts of the sequence where burial was more rapid – they tend to be broken, crushed and disarticulated and often coated with a thick layer of haematite. This band does however contain representatives of all the elements of the fauna of the Upper Elliot Formation, and so merits careful attention.

The fragment of *Diarthrognathus* jaw described below was collected by J W Kitching from the *Tritylodon* acme zone on the farm Maquatleng in the Clocolan district. Its identity only became apparent during preparation.

DESCRIPTION

It is convenient to compare the *Diarthrognathus* jaw (part of a left ramus) with a similar jaw fragment of *Pachygenelus* (part of a right ramus which is shown reversed in Figure 1 for comparison). Both are dentary fragments with the postdentary bones missing. Both were coated in haematite and have been prepared using the thioglycolic acid technique (Howie 1974).The leading edge of the coronoid process rises more steeply in *Diarthrognathus*, otherwise the two jaws are very similar. The position of the coronoid is clearly evident on the *Pachygenelus* dentary, with an adductor muscle scar behind it. These features are not displayed by the *Diarthrognathus* jaw, possibly due to poorer preservation, as Crompton (1958) illustrates the coronoid quite clearly.

The *Diarthrognathus* jaw contains evidence of nine postcanine teeth, of which the fourth and last four are complete, and the first is a partially errupted replacing tooth. The fifth tooth shows partial root resorption and its partially erupted successor is visible beneath it. Crypts for replacing teeth are present along the groove for the dental lamina (these are obscured by matrix in the *Pachygenelus* specimen).Though considerably smaller, these teeth are identical to the teeth of the type

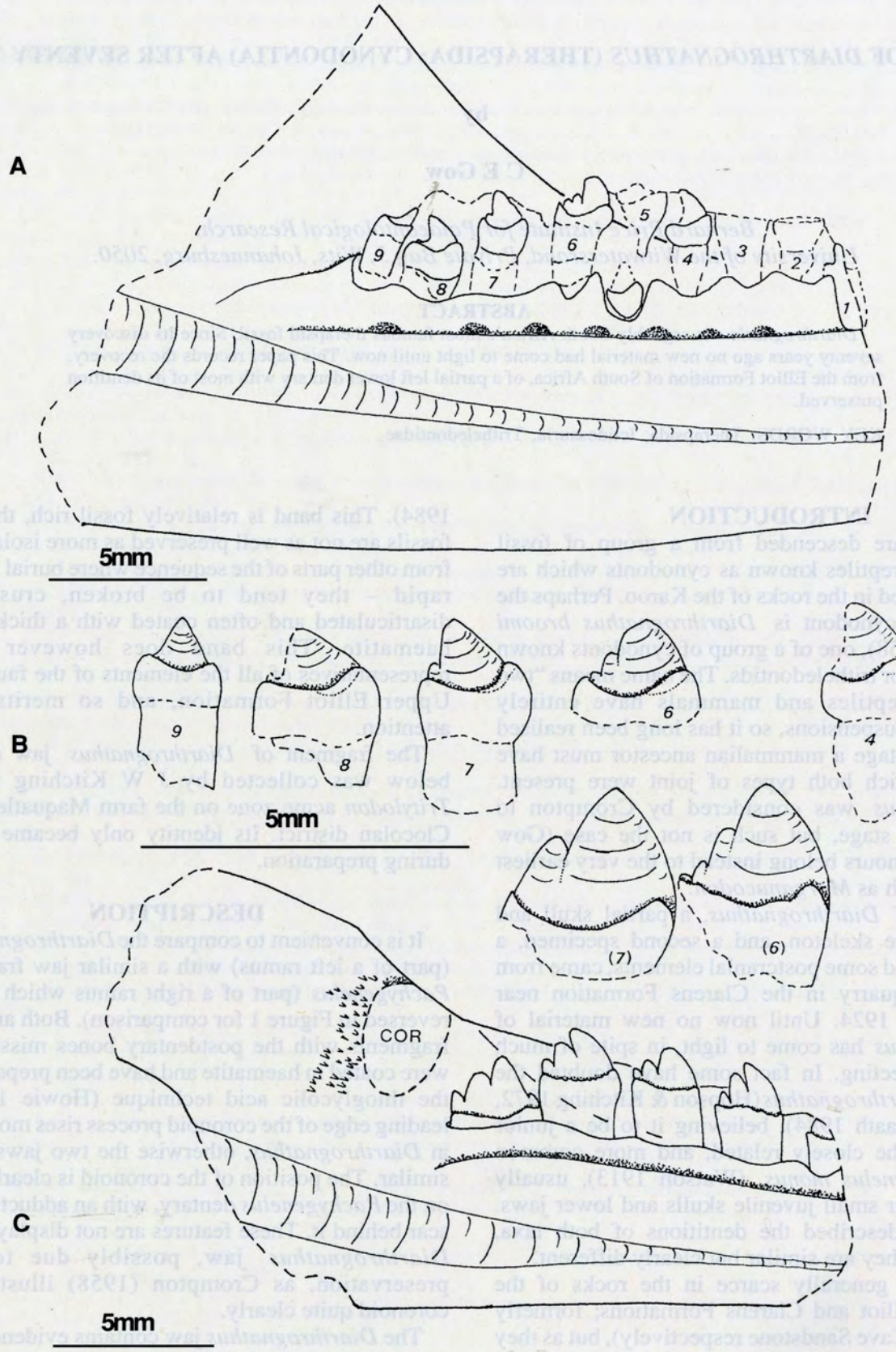


Figure 1. A. *Diarthrognathus* BP/1/4882. Left lower jaw fragment. Matrix between teeth indicated by dashed line. Profile of dentary behind teeth indicated by thick dashes.

B. Enlargement of teeth numbered to correspond with A. Teeth with numbers in brackets belong to the type material of *D. broomi*.

C. *Pachygenelus monus* BP/1/4741. Matrix still present between teeth, outline of dentary indicated by dashed line. COR = position of coronoid, behind this is an adductor muscle insertion scar.
Smaller scale applies to both jaws, larger scale to all teeth.

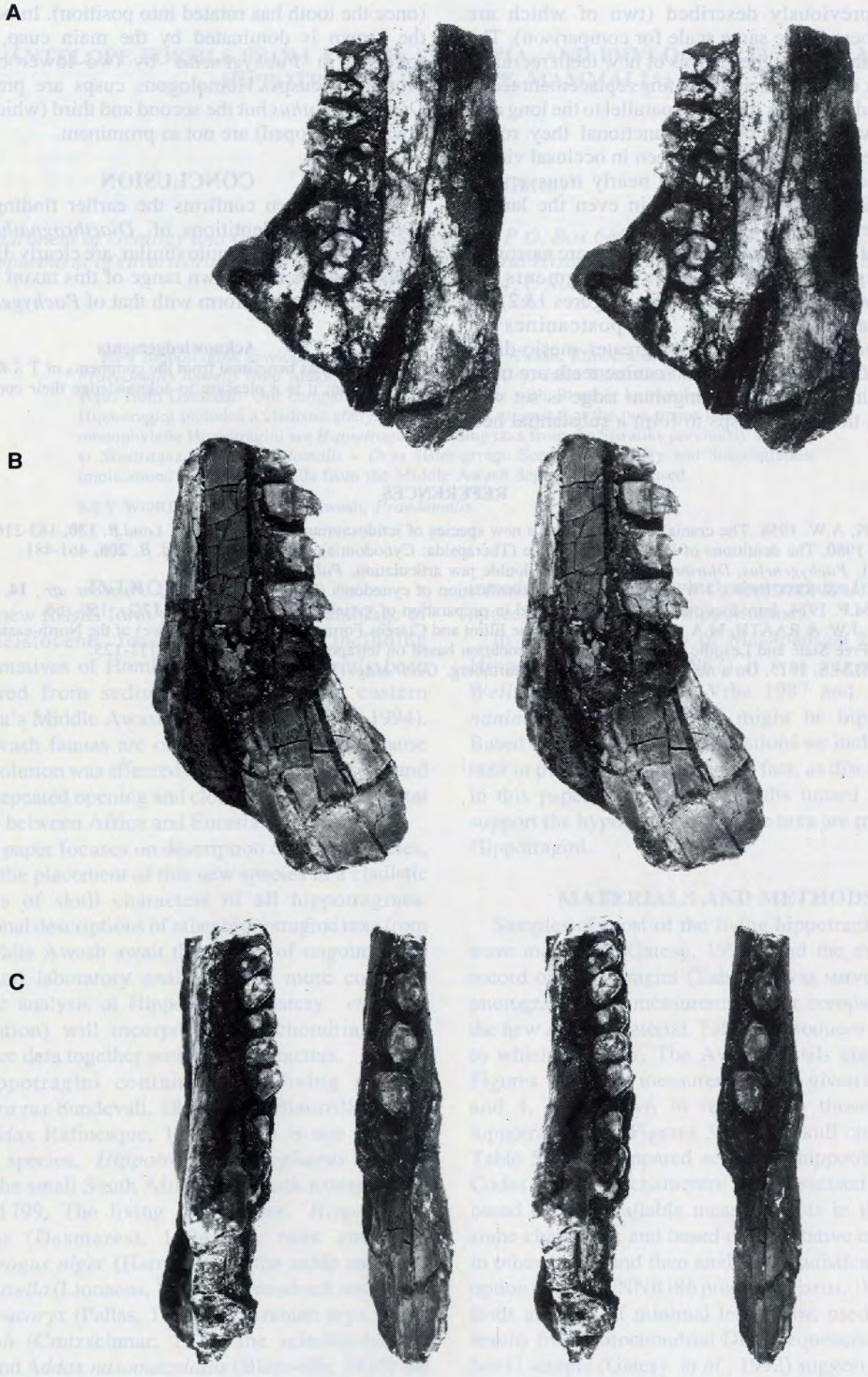


Figure 2 A. *Diarthrognathus* BP\1\4882 medial view, B. *Pachygenelus* BP\1\4741 medial view, C. both jaws in occlusal view with *Diarthrognathus* on the left.

material previously described (two of which are refigured here to the same scale for comparison). The specimen shows that the crowns of new teeth recruited at the back of the row, and erupting replacement teeth, are oriented with their long axes parallel to the long axis of the jaw. As they become functional they rotate (clockwise in the left ramus as seen in occlusal view), until the long axes are arranged nearly transversely. This rotation is far less marked in even the largest *Pachygenelus*.

The post canine teeth of *Pachygenelus* are narrow in bucco-lingual width. The jaw fragments of *Diarthrognathus* and *Pachygenelus* (Figures 1&2) are of comparable size, and the postcanines of *Pachygenelus* have a markedly greater mesio-distal diameter. *Diarthrognathus* post canine teeth are more nearly cylindrical and the cingulum ridge is set well back from the crown cusps to form a substantial heel (once the tooth has rotated into position). In both taxa the crown is dominated by the main cusp, this is followed in *Pachygenelus* by two lower but still prominent cusps. Homologous cusps are present in *Diarthrognathus* but the second and third (which is not always developed) are not as prominent.

CONCLUSION

This specimen confirms the earlier finding (Gow 1980) that the dentitions of *Diarthrognathus* and *Pachygenelus*, while quite similar, are clearly different. It also extends the known range of this taxon into the Upper Elliot, to conform with that of *Pachygenelus*.

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NEW ANTELOPE FOSSILS FROM AWASH, ETHIOPIA, AND PHYLOGENETIC ANALYSIS OF HIPPOTRAGINI (BOVIDAE, MAMMALIA)

by

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ABSTRACT

New hippotragine antelope fossils from the Middle Awash, Ethiopia, include a new species *Praedamalis howelli* from Maka, an early species of *Oryx* from Matabaietu, and *Hippotragus gigas* from Gamedah. Our comparisons of these fossils with all other known fossil and Recent Hippotragini includes a cladistic analysis. The results suggest that the two major lineages in the monophyletic Hippotragini are *Hippotragus* including taxa from the Siwaliks previously ascribed to *Sivatragus*, and a *Praedamalis* – *Oryx* sister-group. Some evolutionary and biogeographic implications of the new fossils from the Middle Awash deposits are discussed.

KEY WORDS: Hippotragini, Awash, *Praedamalis*

INTRODUCTION

The new fossils form part of a large assemblage of Plio-Pleistocene fossil vertebrates, including representatives of Hominidae, that has recently been recovered from sedimentary deposits in eastern Ethiopia's Middle Awash Valley (White *et al.*, 1994). The Awash faunas are of particular interest because their evolution was affected by pervasive tectonism and by the repeated opening and closing of land and habitat bridges between Africa and Eurasia.

This paper focuses on description of a new species, and on the placement of this new species in a cladistic analysis of skull characters of all hippotragines. Additional descriptions of other hippotragine taxa from the Middle Awash await the results of ongoing field work and laboratory analyses. Our more complete cladistic analysis of Hippotragini (Gatesy *et al.*, in preparation) will incorporate mitochondrial DNA sequence data together with skull characters.

Hippotragini contains three living genera: *Hippotragus* Sundevall, 1846; *Oryx* Blainville, 1816; and *Addax* Rafinesque, 1815. There is one recently extinct species, *Hippotragus leucophaeus* (Pallas, 1766) the small South African bluebuck exterminated about 1799. The living species are: *Hippotragus equinus* (Desmarest, 1804) the roan antelope; *Hippotragus niger* (Harris, 1838) the sable antelope; *Oryx gazella* (Linnaeus, 1758) the gemsbuck and beisa; *Oryx leucoryx* (Pallas, 1777) the Arabian oryx; *Oryx dammah* (Cretzschmar, 1826) the scimitar-horned oryx; and *Addax nasomaculatus* (Blainville, 1816) the addax of the Sahara. The extinct taxa in our analysis are introduced in Table 1, which also contains first and last appearance data for all hippotragines.

In a previous survey of Makapansgat Limeworks Hippotragini (Vrba, 1987) it was suggested that *Wellsiana torticornuta* Vrba 1987 and *Brabovus nanincisivus* Gentry 1987 might be hippotragine. Based on these tentative suggestions we included these taxa in the cladistic analysis. In fact, as discussed later in this paper, our cladistic results turned out not to support the hypotheses that these taxa are members of Hippotragini.

MATERIALS AND METHODS

Samples of most of the living hippotragine species were measured (Gatesy, 1993), and the entire fossil record of Hippotragini (Table 1) was surveyed using photographs and measurements for comparison with the new Awash material. Table 2 introduces fossil sites to which we refer. The Awash fossils are shown in Figures 1-4. Their measurements are given in Tables 3 and 4, and shown in relation to those of other hippotragines in Figures 5-9. The skull characters in Table 5 were compared across all hippotragine taxa. Codes for these characters were assessed (Table 6) based on the available measurements in the case of some characters, and based on qualitative comparison in other cases, and then analyzed cladistically. The ie option of the HENNIG86 program (Farris, 1988) which finds all trees of minimal length was used. Cladistic results from mitochondrial DNA sequences of a large bovid sample (Gatesy *et al.*, 1992) suggest that living hippotragines are monophyletic and that Caprini and

TABLE 1.

Living and extinct Hippotragine and Related Taxa.

First and last appearance data (FAD and LAD, given as first and last entries per taxon) and the taxon codes used in figures and Table 3 are given. Selected other fossil sites are cited in some cases. Dates follow Vrba's (in press) review. Literature citations numbered in brackets are: (1) Gentry (1987), (2) Vrba (1987), (3) Vrba (1974, 1976), (4) Klein and Cruz-Uribe (1991), (5) Gentry (1985), (6) Gentry and Gentry (1978), (7) Pilgrim (1939), (8) Lehmann and Thomas (1987), (9) Geraads (1987), Arambourg (1979), (10) Harris (1991), (11) Geraads (1981), (12) Gentry (1981); (13) Smart (1974), personal observation of undescribed fossils including specimen LT188. Millions of years = m.y.; L = Locality; M = Member. LPlio = Late Pliocene. Note on *Hippotragus gigas*: the FAD of this species could be near 2.7 m.y. from Chiwondo, Malawi (Coryndon, 1966; Kaufulu et al., 1981). Concerning its LAD, the tentative Late Pleistocene record for Florisbad by Gentry and Gentry (1978) is not followed here because later studies cast doubt on it (Brink, 1986, 1987). Note on *H. cookei*: the tentative assignment of dentitions from Sterkfontein M4 to this taxon is not reflected here. Note on the date '5.5 m.y. or Late Pliocene' for *H. sp. nov.* from Sahabi: This refers to Geraads's (1989) argument that some of the Sahabi fossils may be datable to the Late Pliocene, which we suspect may be true of this species, and not to the Late Miocene.

Taxon	Site of FAD Site of LAD	FAD date LAD date m.y.	Extinct = † Common name	Taxon code
Taxa possibly related to Hippotragini :				
Brabovus				
nanincisivus	Laetoli (1)	3.6	†	bra
	Laetoli (1)	3.6		
Wellsiana				
torticornuta	Makapansgat M3 (2)	2.7	†	w
	Makapansgat M3 (2)	2.7		
Hippotragini :				
Addax				
nasomaculatus	no fossil record		addax	a
Hippotragus				
equinus	Sterkfontein M4 (3)	2.5	roan antelope	e
niger	Swartkrans M3 (3)	0.7	sable antelope	n
leucophaeus	Elandsfontein (4)	0.6	†, bluebuck	l
	Cape Province	1799 AD		
gigas: all	Shungura C8 (5)	2.6	†	g1
except from	Gamedah L1, Awash	2.5		
Elandsfontein	Olduvai Bed III JK2 (6)	1.0		
gigas: from Elandsfontein	Elandsfontein (4)	0.6	†	g2
cookei	Makapansgat M3 (2)	2.8 - 2.6	†	c
	Makapansgat M3 (2)	2.8 - 2.6		
bohlini	Siwaliks, Pinjor (7, 6)	2.6 - 1.6	†	bo
(*Sivatragus*)	Siwaliks, Pinjor (7, 6)	2.6 - 1.6		
brevicornis	Siwaliks, Tatrot (7, 6)	3.1 - 2.6	†	bre
(*Sivatragus*)	Siwaliks, Tatrot (7, 6)	3.1 - 2.6		
sp. nov.	Sahabi (8)	5.5 or LPlio	†	s
	Sahabi (8)	5.5 or LPlio		
Oryx				
gazella	Ain Hanech (9)	1.8 - 1.7	beisa, gemsbuck	og
sp. nov. 1	Shungura C9 (5)	2.6	†	o1
	Matabaietu L4, Awash	2.5		
sp. nov. 2	Olduvai Bed I (6)	1.8	†	o2
	Koobi Fora, KBS (10)	1.7		
sp. from Ternifine *O. gazella*?	Ternifine (11)	0.7		o3
sivalensis	Siwaliks, Pinjor (7, 6)	2.6 - 1.6	†	os
(*Sivoryx*)	Siwaliks, Pinjor (7, 6)	2.6 - 1.6		
Praedamalis				
deturi	Laetoli (1)	3.6	†	d
	Hadar, Denen Dora (12)	3.2		
	Upper Ndolanya (1)	2.6		
howelli sp. nov.	Awash, Maka L1	3.5	†	ho
	Awash, Maka L1	3.5		
Gen. indet.				
sp. nov.	Lothagam I (13)	6.5	†	lo
	Lothagam I (13)	6.5		

TABLE 2

Fossil Sites. The table gives only those fossil sites and their stratigraphic subunits that are referred to in this paper. The stratigraphic subunits are arranged from latest at the top to earliest at the bottom. Table 2 cites sources for the antelope occurrences at these sites, and Vrba (in press) reviews their chronology.

Site	Country	Time period
Ain Hanech	Algeria	Early Pleistocene
Awash, Middle	Ethiopia	Plio-Pleistocene
Gamedah Locality 1		Late Pliocene
Matabaietu Locality 5		Late Pliocene
Maka Locality 1		Middle Pliocene
Chiwondo	Malawi	Plio-Pleistocene
Mwenirondo		Late Pliocene
Elandsfontein	South Africa	Middle Pleistocene
Florisbad	South Africa	Late Pleistocene
Hadar Formation	Ethiopia	Middle Pliocene
Denen Dora Member		
Kanjera	Kenya	Early Pleistocene
Koobi Fora Formation	Kenya	Plio-Pleistocene
KBS Member		
Upper Burgi Member		
Laetoli Beds	Tanzania	Early Middle Pliocene
Lothagam Unit 1	Kenya	Late Miocene
Makapansgat Limeworks	South Africa	Late Pliocene
Member 3		
Nachukui Formation	Kenya	Plio-Pleistocene
Upper Lomekwi Member		
Nelson Bay Cave	South Africa	Late Pleistocene
Olduvai Gorge	Tanzania	Pleistocene
Beds I-IV		
Sahabi	Lybia	Late Miocene
Shungura Formation	Ethiopia	Plio-Pleistocene
Members B to J		
Siwaliks formations	India and Pakistan	Mio-Pleistocene
Pinjor		Late Pliocene to Early Pleistocene
Tatrot	Early-Middle Pliocene	
Swartklip	South Africa	Late Pleistocene
Swartkrans Formation	South Africa	Lower Pleistocene
Members 1 to 3		
Sterkfontein Formation	South Africa	Late Pliocene
Member 4		
Ternifine	Algeria	Middle Pleistocene
Upper Ndolanya Beds	Tanzania	Late Pliocene

Alcelaphini are sequential outgroups of Hippotragini. We used these results together with the cladistic results for skull characters in Vrba (1979) and Gatesy (1993), to hypothesize the general states for the characters in Table 5 and used these as the states in the hypothetical outgroup of the present taxa. The outgroup rooting option of HENNIG86 was then employed. The NELSEN option of HENNIG86 was used to construct a consensus tree. The multistate characters were ordered on the basis of ontogenetic progression and similarity between adjacent states (see Lipscomb, 1992). The nature of these particular characters suggests that ordering is appropriate. Both the genetic and the empirical bases of allometric evolution (e.g., Atchley *et al.*, 1984) suggest change through adjacent states rather than leaps between extreme states at one splitting event.

SYSTEMATIC RESULTS

The cladistic results are represented by the consensus tree in Figure 10. In terms of these results, we suggest that Hippotragini is the monophyletic group from node 1 in Figure 10. That is, Hippotragini includes all living and extinct taxa previously assigned to hippotragines together with a new Lothagam species, and excludes *Brabovus nanincisivus* and *Wellsiana torticornuta* (*contra* Vrba, 1987). Living and fossil species previously assigned to *Oryx*, and including *Addax*, form a monophyletic group which is the sister-taxon of *Praedamalis*. In terms of these results *Addax* should be synonymized with *Oryx*. The Siwaliks taxa that Pilgrim (1939) called *Sivatragus bohlini* and *S. brevicornis* form parts of a monophyletic group with all living and fossil taxa previously

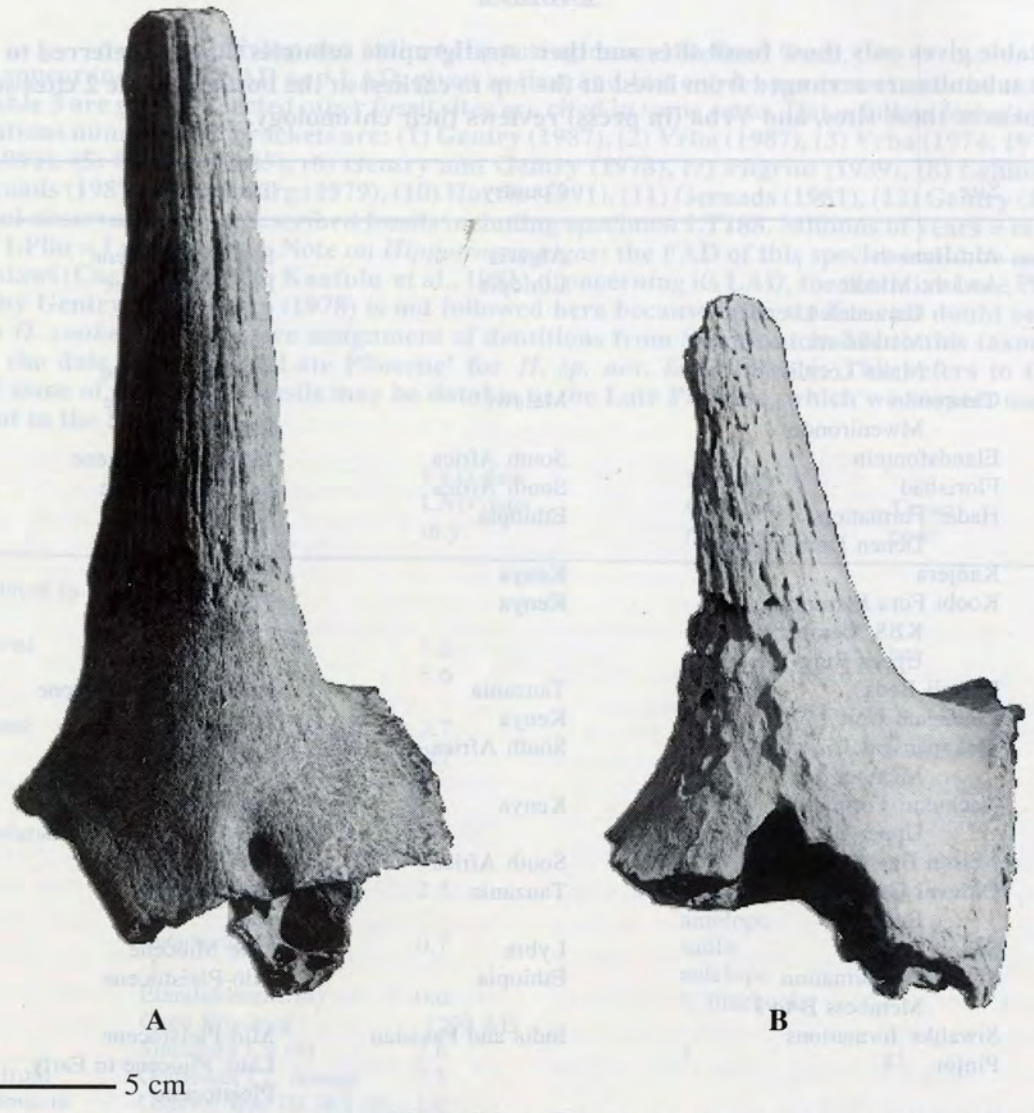


Figure 1. **A**. Holotype right horncore and frontlet MAK-VP-1/24 of *Praedamalis howelli*, **B**. right horncore and frontlet MAK-VP-1/113, both in anterior view.

assigned to *Hippotragus*, although the species *brevicornis* could be assigned to a new genus as the sister-taxon of *Hippotragus*. In the diagnoses and descriptions that follow we will refer both to the characters in this cladistic result, by citing Figure 10, as well as to additional characters.

Tribe Hippotragini

Hippotragini are characterized by horncores that are long and of large basal area relative to skull size, by moderately to well-developed basal sinuses in their horn pedicels and extending into the basal horncore, and by bulbous, lingually-extending metaconids on their P_4's (synapomorphies in Figure 10). Their horacores are unkeeled, little divergent, and generally without transverse ridges, and their postcornual fossae are shallow or absent. In terms of the present cladogram, Hippotragini have plesiomorphously retained long braincases which became secondarily reduced in parallel in oryxes and in the clade that includes *Hippotragus bohlini* and *H. gigas*. Hippotragine teeth are large relative to jaw size and have basal pillars on upper and lower molars and goat folds anteriorly on lower molars. Extant hippotragines are large antelopes that mostly graze, and both sexes have horns. Their mastoids appear to face mainly backwards on the occipital surface from early on in ontogeny. Gentry and Gentry (1978) suggested that additional hippotragine characters are a midfrontal suture that is moderately complicated, a straight and moderately complicated parietofrontal suture, temporal lines not approaching very closely, infraorbital foramen high over the P^2-P^3 junction, premaxillae with a short contact along the sides of the nasals, nasals without lateral flanges anteriorly, median indentation at the back of the palate more or less level with the lateral ones, and mastoid exposures that are moderate to large.

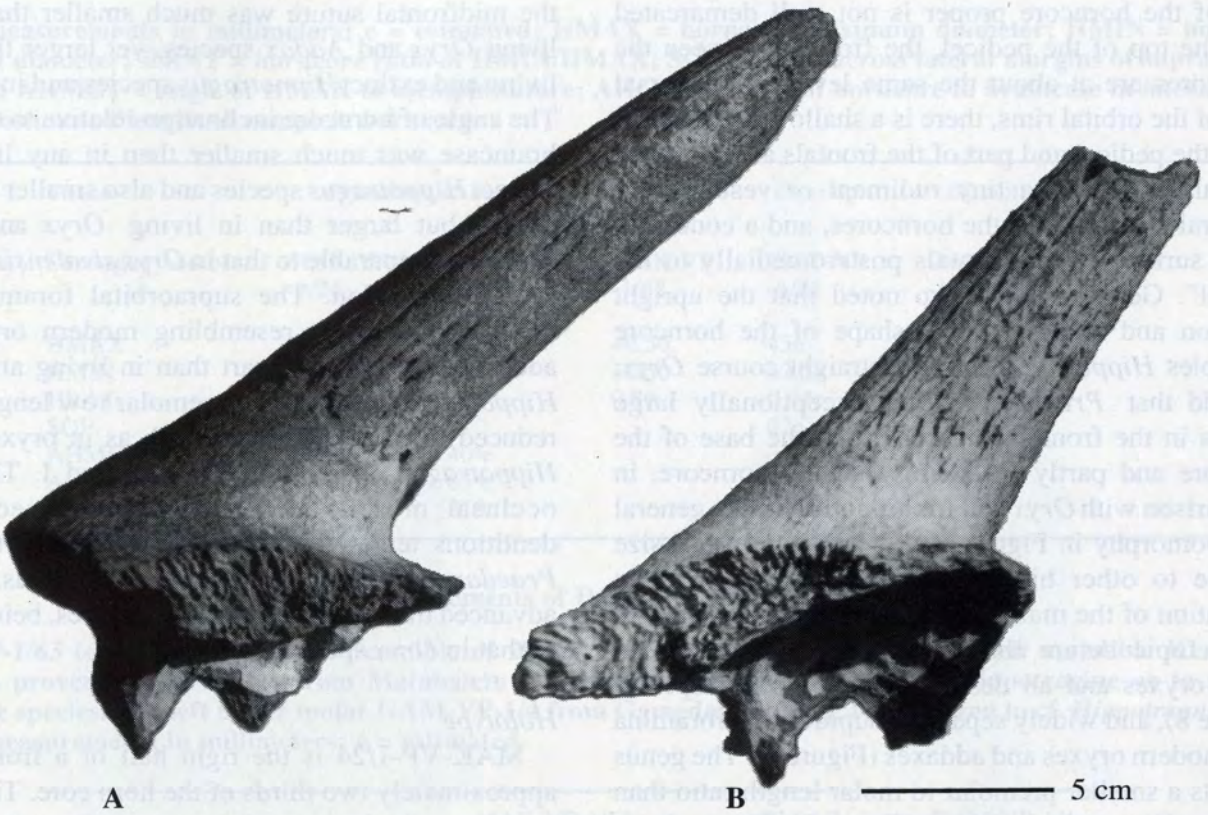


Figure 2. **A**. Holotype right horncore and frontlet MAK-VP-1/24 of *Praedamalis howelli*. **B**. Juvenile right horncore and frontlet MAK-VP-1/113, both in medial view.

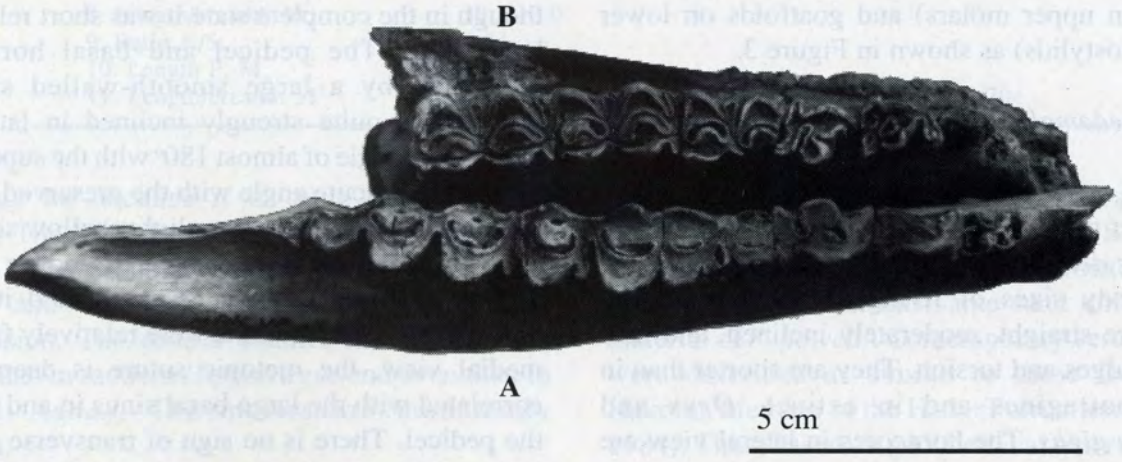


Figure 3 **A** Paratype right mandible MAK-VP-1/63 of *Praedamalis howelli* from Maka Locality 1, Middle Pliocene. **B.** Left mandible KL64-2, possibly referable to late Pliocene Matabaietu Locality 5 (T. White, pers. comm.), which may belong to a small hippotragine species but could be reduncine.

Genus *Praedamalis* Dietrich 1950:30.
Type species *Praedamalis deturi* Dietrich 1950.

Generic diagnosis

Gentry (1987) gave a diagnosis for this genus based directly on the only included species *P. deturi* known at that time from Hadar, the Laetoli Beds and the Upper Ndolanya Beds. We augment this diagnosis in the light of the new Awash species. Gentry (1987, p. 387) considered *Praedamalis* to have "long horncores with some mediolateral compression, no flattening of the lateral or medial surface, no keels or transverse ridges, and hardly any backward curvature. The insertions are rather upright above the back of the orbits, not very wide apart and little divergent. The greatest transverse width of the horncores lies near or

slightly behind the anteroposterior mid-point. The base of the horncore proper is not well demarcated from the top of the pedicel, the frontals between the horn cores are at about the same level as the dorsal parts of the orbital rims, there is a shallow postcornual fossa, the pedicel and part of the frontals are hollowed internally, there is a tiny rudiment or vestige of a temporal ridge behind the horncores, and a concavity in the surface of the frontals posteromedially to the pedicel". Gentry (1987) also noted that the upright insertion and cross-sectional shape of the horncore resembles *Hippotragus* and the straight course *Oryx*. We add that *Praedamalis* has exceptionally large sinuses in the frontals and pedicel at the base of the horncore and partly extending into the horncore, in comparison with *Oryx* and for hippotragines in general (synapomorphy in Figure 10). It had small skull size relative to other hippotragines, horncores with an angulation of the maximum basal diameter relative to the metopic suture that was intermediate between living oryxes and all described *Hippotragus* species (Figure 8), and widely separated supraorbital foramina as in modern oryxes and addaxes (Figure 6). The genus exhibits a smaller premolar to molar length ratio than in living *Hippotragus* species (Figure 9). The teeth are primitive in being buccolingually narrow relative to antero-posterior length, in their lack of constricted molar lobes and complex central enamel cavities, and in that there are poorly developed basal pillars on upper and lower molars (the ectostylids on lower and entostyles on upper molars) and goatfolds on lower molars (protostylids) as shown in Figure 3.

Species *Praedamalis howelli* sp. nov.

Diagnosis

An extinct species that was averagely smaller than *Praedamalis deturi*, and also at the low extreme of the range of body sizes of living hippotragines. The horncores are straight, moderately inclined, and lack transverse ridges and torsion. They are shorter than in living hippotragines and in extinct *Oryx* and *Hippotragus gigas*. The horncores in lateral view are straighter than in *P. deturi* and comparable to some specimens of *Oryx*. The sinuses in the pedicel are exceptionally large, partly extending into the horncore, and surrounded by relatively thin frontal bone in comparison with *Oryx* and hippotragines in general. In this respect the new species is even more extreme than *P. deturi* although the resemblance to *P. deturi* is closer than to other Hippotragini. The horncores were more compressed than in modern and extinct members of *Oryx*, with the exception of *Oryx sivalensis*, and less compressed than in living *Hippotragus* and in *P. deturi* as known from Laetoli, although they show overlap with this species from the Hadar Denen Dora Member. The angle of the maximum basal horncore diameter to the midfrontal suture was much smaller than in any living *Oryx* and *Addax* species, yet larger than in all living and extinct *Hippotragus* species and in *P. deturi*. The angle of horncore inclination relative to the dorsal braincase was much smaller than in any living and extinct *Hippotragus* species and also smaller than in *P. deturi*, but larger than in living *Oryx* and *Addax* species, comparable to that in *Oryx sivalensis* from the Pinjor Formation. The supraorbital foramina were relatively far apart resembling modern oryxes and addaxes, and further apart than in living and extinct *Hippotragus* species. The premolar row length was as reduced relative to molar length as in oryxes and in *Hippotragus gigas* from Olduvai Bed I. The dental occlusal morphology is more advanced that in dentitions tentatively assigned by Gentry (1987) to *Praedamalis deturi* from the Laetoli Beds, yet less advanced than in all living hippotragines, being closest to that in *Oryx* species.

Holotype

MAK-VP-1/24 is the right half of a frontlet with approximately two thirds of the horn core. The frontal anterior to the horncore is preserved from the anterior orbital rim to the metopic suture including the supraorbital pit and foramen (Figures 1a and 2a). The pedicel is moderately long with sloping sides, and it is not well demarcated from the basal horncore margin. The horncore tapers fairly rapidly towards the tip as though in the complete state it was short relative to its basal size. The pedicel and basal horncore are excavated by a large smooth-walled sinus. The horncore is quite strongly inclined in lateral view, forming an angle of almost 180° with the superior facial plane and an acute angle with the preserved part of the dorsal braincase. There is a slight shallow supraorbital pit with a shallow wide groove extending anteriorly. The supraorbital foramen is small, and its position indicates that the foramina were relatively far apart. In medial view, the metopic suture is deep which is correlated with the large basal sinus in and anterior to the pedicel. There is no sign of transverse ridges and little of longitudinal grooving. The orbit is not prominent. There is a slight indication of the depression in the frontal postero-medially to each horncore found in *Praedamalis deturi*.

Paratype

Partial right mandible MAK-VP-1/63 with P_3-M_3 in medium adult wear (Figure 3a). The socket and roots of a relatively reduced P_2 are also preserved. There is a large laterally-directed metastylid, a small basal pillar and a slim anterior goatfold on the M_3. The M_2 has a moderately developed basal pillar protruding from the posterior lobe of the tooth. No goatfold is evident on M_2

TABLE 3: Measurements of Hippotragine Frontlets from the Middle Awash

Length measurements in millimeters; e = estimated; HMAX = horncore maximum diameter; HMIN = horncore minimum diameter; HRAT = horncore ratio of HMIN/HMAX; SOF = width across lateral margins of supraorbital foramina; AHMET = angle of HMAX to metopic suture; AHCBR = angle of horncore to braincase in lateral view; HLEN = estimated length of complete horncore.

Taxon	*Praedamalis howelli*			*Oryx* sp.	*Hippotragus gigas*
Catalogue number	MAK-VP -1/24	MAK-VP -1/113	MAK-VP -1/62	MAT-VP -4/21	GAM-VP -1/14
HMAX	39.80	39.50	40.50	45e	72.80
HMIN	31.83		32.50	42.5e	55.80
HRAT	0.80		0.80	0.94e	0.77
SOF	64e			82e	
AHMET	38°e	40°e			15°e
AHCBR	65°e	65°e			
HLEN	270e	210e			

TABLE 4. Measurements of Dentitions from Middle Awash.

MAK-VP-1/63 is the paratype right mandible of *Praedamalis howelli* from Maka. The left mandible KL64-2 of unknown provenence, probably from Matabaietu Locality 5, may belong to a small hippotragine or to a large reduncine species. The left upper molar GAM-VP-1/4 from Gamedah Locality 1 is referred to cf. *Hippotragus gigas*. Length measurements in millimeters; e = estimated.

	MAK-VP-1/63	KL64-2	GAM-VP-1/4
1. Length P_{2-4}	36e	32.3	
2. Length/breadth P_2	7.8/5.8		
3. Length/breadth P_3	12.9/8.0	12.0/9.6	
4. Length/breadth P_4	14.9/10.0	12.5e/9.9	
5. Length M_{1-3}	66.5e		
6. Length/breadth M_1	16.3e/12.4e	14e/10.5e	
7. Length/breadth M_2	21.4/13.2	17.6/11.4	
8. Length/breadth M_3	30.3/13.0		
9. Ratio 1./5.	0.54		
10. Length P_2-M_3	104e		
11. Length/breadth M^2			31.02/20e

which may be because it is quite heavily worn anteriorly. The M_1 is broken anteriorly. The P_4 has a markedly bulbous and projecting metaconid, and its paraconid and metaconid are touching but without enamel fusion. The central enamel cavities are less complex than in modern *Hippotragus* and even than in *Oryx* and *Addax*. The molars are moderately hypsodont.

Horizon

The holotype and paratype were collected as surface finds associated with a fossiliferous sand unit, the Maka sands at Maka Locality 1, and without doubt derive from the Maka sands.

In this paper each specimen is referred to by its field and locality number, which for Maka Locality 1 is MAK-VP-1/number. White *et al.* (1994) report that within these sands is the tuff MA 90-16 for which no direct age estimate is available to date, but which correlates in several chemical aspects with the SHT tuff at the base of the Hadar Formation and with the Tulu Bor beta tuff in the Turkana Basin with age estimates very close to 3.4 million years (m.y.) (Brown *et al.*, 1992). The first hominid fossil from Maka, a proximal femur, derived from this same sand unit as the type material of *P. howelli*. Contemporary vertebrate fossils were described as similar to those from the Sidi Hakoma Member of the Hadar Formation (Clark *et al.*, 1984). Thus, based on geochemical and radiometric as well as biochronological and stratigraphic data, the fossils from Maka Locality 1 are about 3.4 m.y. old (White *et al.*, 1994).

Name

The new species is named after F. Clark Howell in recognition of his great contributions to mammal palaeontology.

Measurements

Measurements on the holotype and paratype are given in Tables 3 and 4.

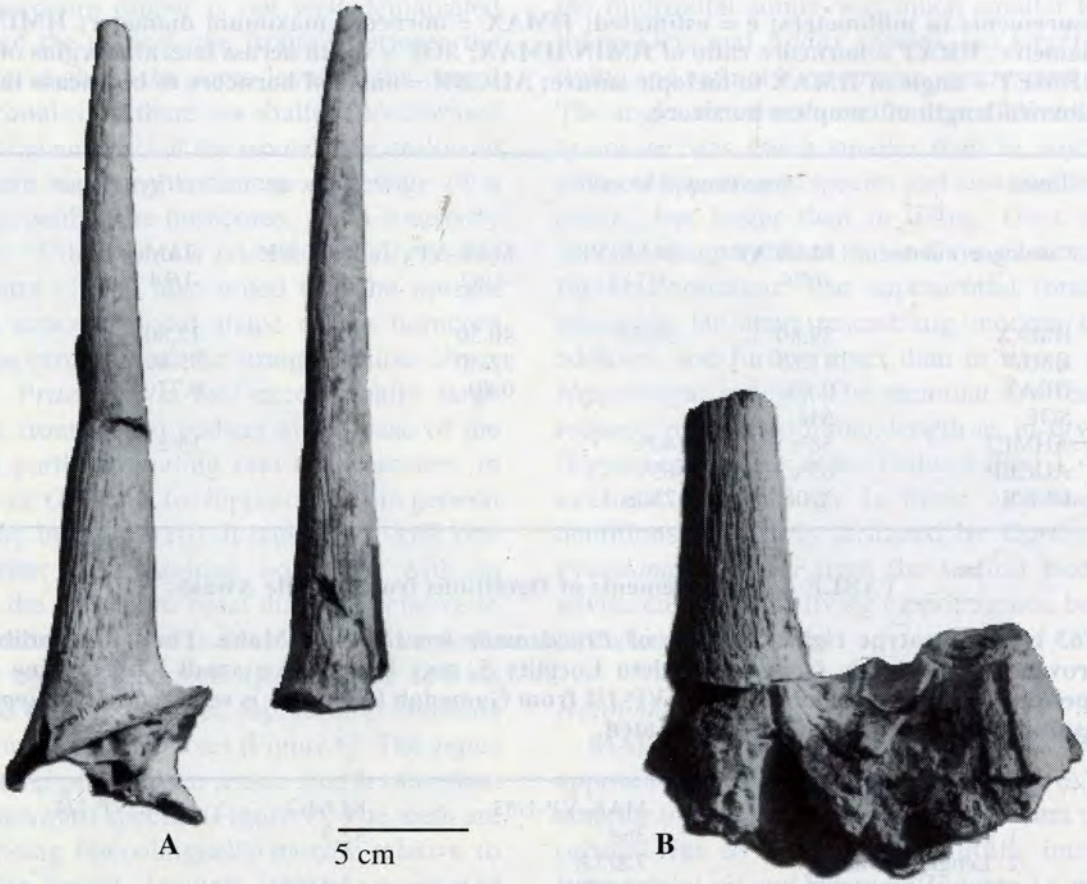


Figure 4. **A**.Right and left horncores MAK-VP-1/62a of *Praedamalis howelli* from Maka unit 1, Middle Pliocene. **B**. Frontlet MAT-VP-4/21 of *Oryx* sp. from Matabaietu Locality 5, Late Pliocene. Both are shown in anterior view.

Referred specimens

Two additional skull fragments were also found in the Maka Locality 1: the right horncore and frontlet MAK-VP-1/113 (Figures 1b and 2b), and the frontlet with both separated horncores and other associated fragments MAK-VP-1/62a and b (Figure 4). Table 3 gives measurements for these fossils. MAK-VP-1/113 differs from the holotype by relatively shorter horncores and higher basal horncore separation. These differences are consistent with subadult status of this specimen. MAK-VP-1/62 is slightly larger than the holotype individual, with horncores that are closer to the orbital margin and have a slightly lower diminution rate from the base upwards. Fragments associated with this specimen include a damaged, abraded basioccipital. It shows anterior narrowing of the somewhat flat surface between the posterior tuberosities, about 32 mm wide, and the anterior tuberosities that measure about 20.5 mm across. Both MAK-VP-1/113 and MAK-VP-1/62 have the same large sinus in the pedicel and horncore base, surrounded by relatively thin bone, that is present in the holotype. Both specimens are very comparable with the holotype in other visible respects.

Comparisons

The new species is clearly closely related to *Praedamalis deturi* from Laetoli and Hadar. However, our result that *deturi* and *howelli* form a sister-group (Figure 10) depends on the current hypothesis that these taxa share a more extensive sinus in the frontal, pedicel and basal horncore than have other hippotragines. If this character is omitted from the analysis, then in several of the most parsimonious trees *howelli* is positioned as the next branch after *P. deturi* and before the diversification of the clade that is here called *Oryx*. The chief differences of *howelli* from *deturi* are the relatively less backbent horncores in the Maka form, its higher angle between the maximum horncore diameter and the midfrontal suture (Figure 8), its less upright (Figure 8) and probably less divergent horncores, and the lesser expression in *howelli* of the depression on the frontal postero-medially to the horncores. The main difference from all oryxes are *howelli*'s shorter horncores relative to skull size (although this character could not be assessed on *O. sivalensis*), the averagely more compressed horncores, and the greater angle between the forehead and the dorsal cranium. Differences between the new

Maka species and *Hippotragus* species are much more far-reaching and numerous (see Figure 10).

We compared the paratype mandible with hippotragine fragmentary dentitions from Shungura Member C unit 6, Member E unit 3, and Member G unit 5, and with dentitions that Gentry (1987) attributed tentatively to *P. deturi* from Laetoli. The Maka specimen is a little smaller than the Shungura dentitions, and less advanced in the degree of outbowing of the lingual molar walls and pinching of the buccal molar lobes, but quite comparable in the low degree of development of basal pillars and goatfolds relative to later hippotragines. As it is not clear to which taxon the Shungura specimens belong, we will not pursue this comparison further. Several of the Laetoli *P. deturi* dentitions look very comparable in the mentioned respects to the Maka paratype, while others are more primitive.

Genus *Oryx* Blainville 1816
Type species *Oryx gazella* (Linnaeus) 1758.

Generic diagnosis

We here construe *Oryx* in terms of the outcome of our cladistic analysis to include *Addax* and the fossil taxa cited under *Oryx* in Table 2. The genus is characterized unambiguously by relatively long horncores and a reduced angle between the face and the dorsal braincase, and ambiguously by reduced braincase length (Figure 10). The genus also shares with *Praedamalis* and *Hippotragus gigas* a reduced premolar/molar ratio (Figure 9), and shares with *Praedamalis* reduced backbending of the horncore, horncore insertion further posteriorly than directly above the orbit, reduced degree of basal horncore compression, and increased distance between the supraorbital foramina.

Oryx sp. from Matabaietu, Middle Awash

The deposits at Matabaietu have yielded abundant and diverse vertebrate fossils including hominids (White, pers. comm.). Matabaietu Localities 1 to 6 (MAT-VP-1 to MAT-VP-6) are associated with tuff MA 90-42 dated 2.52 m.y., with MAT-VP-1 and MAT-VP-2 above this tuff and MAT-VP-3 to MAT-VP-6 below it (White, pers. comm.). Thus, this new *Oryx* sp. from Matabaietu Locality 4 is slightly older than 2.5 m.y..

A broken frontlet, MAT-VP-4/21, apparently belonged to an adult (Figure 4; measurements in Table 3). It includes the basal part of the right horncore and the pedicel of the left horncore. It belonged to an oryx about the size of larger individuals of *O. gazella* and larger than the new species *P. howelli*. The horncores were only slightly compressed (Figure 5). The right horncore base suggests that they were relatively longer than in either of the *Praedamalis* species yet shorter than in living oryxes (Figure 4). The frontal anterior to the horncores is damaged, but the remaining pieces suggest that the supraorbital foramina were far apart as is typical of oryxes, the addax, and the new species *P. howelli* (Figure 6).

In oryx evolution, the horncore length has increased. Also, in the less advanced condition the basal horncore separation was lower and the pedicels and basal horncores were less parallel-sided with a greater tendency for their medial surfaces to slope basally towards the mid-plane and towards each other. The Matabaietu specimen shares this less advanced condition with *Oryx sivalensis* of the Pinjor stage in the Siwaliks, and is more plesiomorphic in this respect than is the juvenile *Oryx* frontlet, Omo 78 69-2731G from upper member G in the Shungura Formation (Gentry, 1985: Plate VII: Figure 4). A relatively high basal horncore separation is characteristic of earlier ontogenetic stages in antelopes, and the very high separation in the Shungura specimen is undoubtedly partly due to its juvenile status. However, the combination of this feature together with longer horncores already in the juvenile state is advanced in the Shungura *Oryx* species relative to that from Matabaietu. Similarly, the *Oryx* sp. reported by Harris (1991) from the KBS and Upper Burgi Members in the Koobi Fora Formation, Kenya, appears to more advanced in this combination of features than the Siwaliks and Matabaietu forms.

The single *Oryx* horncore from Shungura Member C8 (Gentry, 1985) may be a juvenile of the same species as the Matabaietu form. In the cladistic analysis they are treated as such and referred to as *Oryx* sp. 1. The more advanced forms from upper member G in the Shungura Formation (Gentry, 1985), from Olduvai Bed I (Gentry and Gentry, 1978), and the *Oryx* sp. reported by Harris (1991) from the KBS and Upper Burgi Members in the Koobi Fora Formation, and from the Upper Lomekwi Member in the Nachukui Formation (Harris *et al.*, 1988) are tentatively suggested to belong to the same species, called *Oryx* sp. 2 in our cladistic analysis. The *Oryx* from Ternifine, Algeria (Geraads, 1981) is included as *Oryx* sp. 3. On the few available characters, *Oryx* sp. 1 from Matabaietu is less advanced than the later species, and most closely comparable to *Oryx sivalensis* from the Siwaliks. Thus, no difference between them is reflected in our conservative cladistic coding (Table 5). Among possible more subtle differences are that the Matabaietu oryx is larger with less compressed horncores.

A horncore midpiece KL234-48 belongs to an oryx, and a left mandible KL64-2 (Figure 3, Table 3) might

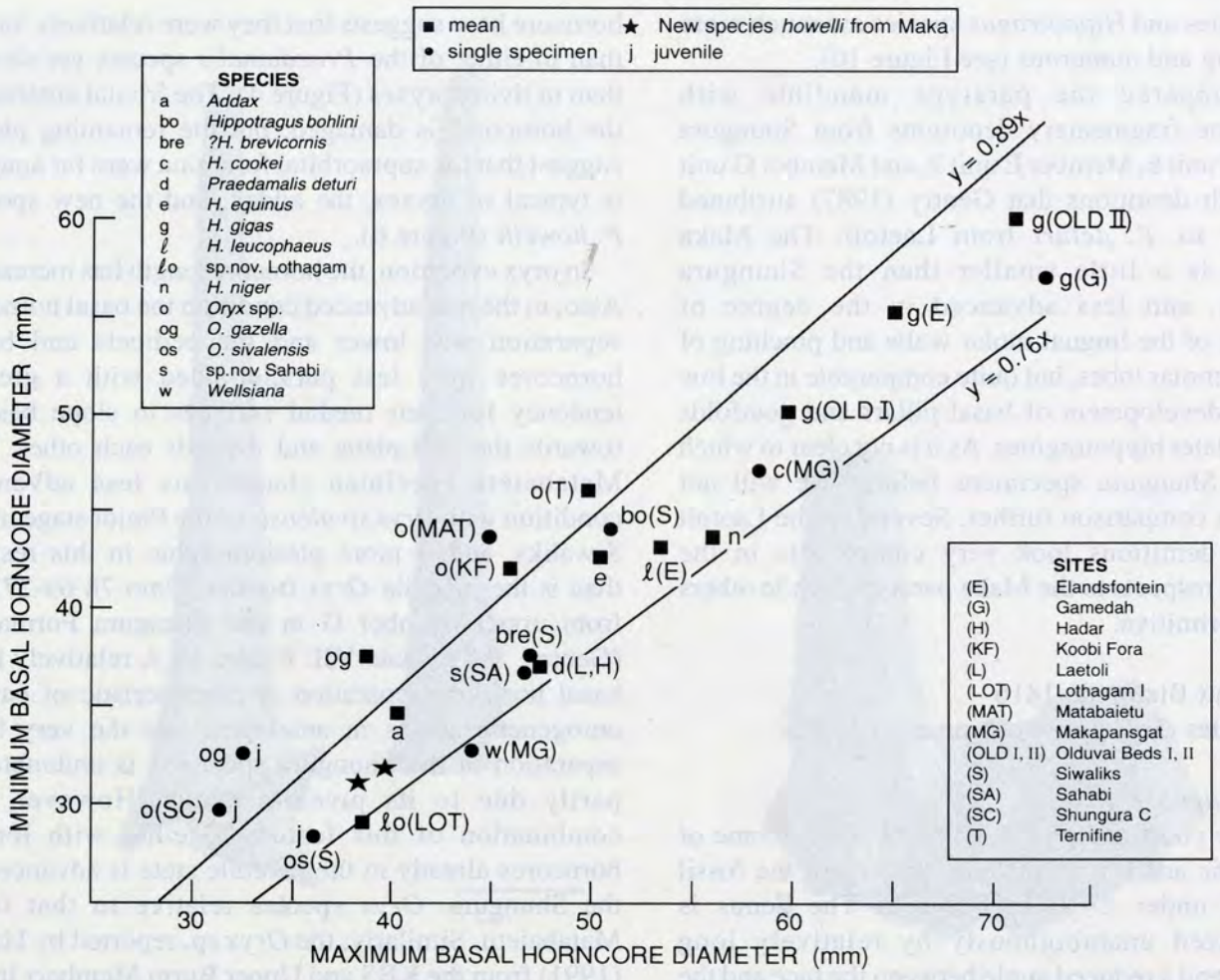


Figure 5. Minimum and maximum basal horncore diameters in some recent and fossil hippotragine taxa. The following sources for measurements apply to Figures 5-9. We have also seen and measured all these specimens ourselves. Numbers in brackets are sample sizes greater than one. Fossil taxa: **solid star** = *Praedamalis howelli* from Awash Maka Locality 1 (Table 3); **d(L)** = *P. deturi* from the Laetoli Beds (Gentry, 1987); **d(H)** = *P. deturi* from Hadar (Gentry, 1981); **d(L, H)** = mean of 4 Laetoli and 2 Hadar *P deturi*, (6); **o(MAT)** = *Oryx* sp. from Awash Matabaietu Locality 4 (Table 3); **o(SC)** = *Oryx* sp. 1 from Shungura Member C (Gentry, 1985); **o(KF)** = *Oryx* sp. 2 from the Upper Burgi and KBS Members, Koobi Fora Formation (Harris, 1991), (5); **o(OLD I)** = *Oryx* sp. 2 from Olduvai Bed I (Gentry and Gentry, 1978), (2); **o(T)** = *Oryx* sp. 3 (cf. *gazella*) from Ternifine (Geraads, 1981), (3); **os(S)** = *Oryx sivalensis* from the Siwaliks Pinjor stage (Pilgrim, 1939); **g(E)** = *Hippotragus gigas* from Elandsfontein (Klein, 1974), (3); **g(OLD I, II)** = *H. gigas* from Olduvai Bed I (3) and Bed II (8) (Gentry and Gentry, 1978), (3); **g(G)** = *H. gigas* from Awash Gamedah Locality 1; **c(MG)** = *H. cookei* from Makapansgat Member 3 (Vrba, 1986); **s(SA)** = *Hippotragus* sp. nov. from Sahabi (Gentry and Gentry, 1978; Lehmann and Thomas, 1987); **bo(S)** = *H. bohlini* from the Siwaliks Pinjor stage (Pilgrim, 1939); **bre(S)** = ?*H. brevicornis* from the Siwaliks Tatrot stage (Pilgrim, 1939); **l(E)** = *H. leucophaeus* from Elandsfontein (Klein, 1974), (7); **w(MG)** = *Wellsiana torticornuta* from Makapansgat Member 3 (Vrba, 1986); **bra(L)** = *Brabovus nanincisivus* from the Laetoli Beds (Gentry, 1987); **lo(LOT)** = nov. sp. from Lothagam (measurements by us; see also Smart, 1976) (4); Extant taxa: **a** = *Addax nasomaculatus*, (3, sex unknown); **g** = *Oryx gazella*, (2, sex unknown); *H. niger* and *H. equinus* after Klein (1974) who gives sample size (N), mean (m), and standard deviation (s), for each sample: **n** = pooled mean for *Hippotragus niger* (♂anteroposterior diameter, ♀apd: N = 11, m = 68.11, s = 8.76; apd: N = 17, m = 48.11, s = 4.77; ♂mediolateral diameter, mld: N = 11, m = 49.42, s = 5.15; ♀mld: N = 17, m = 39.64, s = 3.85); **e** = *H. equinus*, (♂apd: N = 4, m = 59.38, s = 8.96; ♀apd: N = 6, m = 44.40, s = 4.32; ♂mld: N = 4, m = 49.05, s = 5.61; ♀ mld: N = 6, m = 38.35, s = 3.04).

do although it could also belong to a large reduncine. Both are of unknown provenience but possibly referable to Matabaietu Localities 3 and 5 respectively (T. White, pers. comm.). The mandible shows a projecting metaconid on P_4 as found in hippotragines, but less so than in the *P. howelli* paratype mandible (Figure 3), and more extensive development of the goatfolds and basal pillars than in *Praedamalis*.

Genus *Hippotragus* Sundevall 1846
Type species *Hippotragus leucophaeus* (Pallas) 1766

Generic diagnosis

We here construe *Hippotragus* in terms of the outcome of our cladistic analysis to include *Sivatragus* (Pilgrim, 1939). The genus is characterized unambiguously by

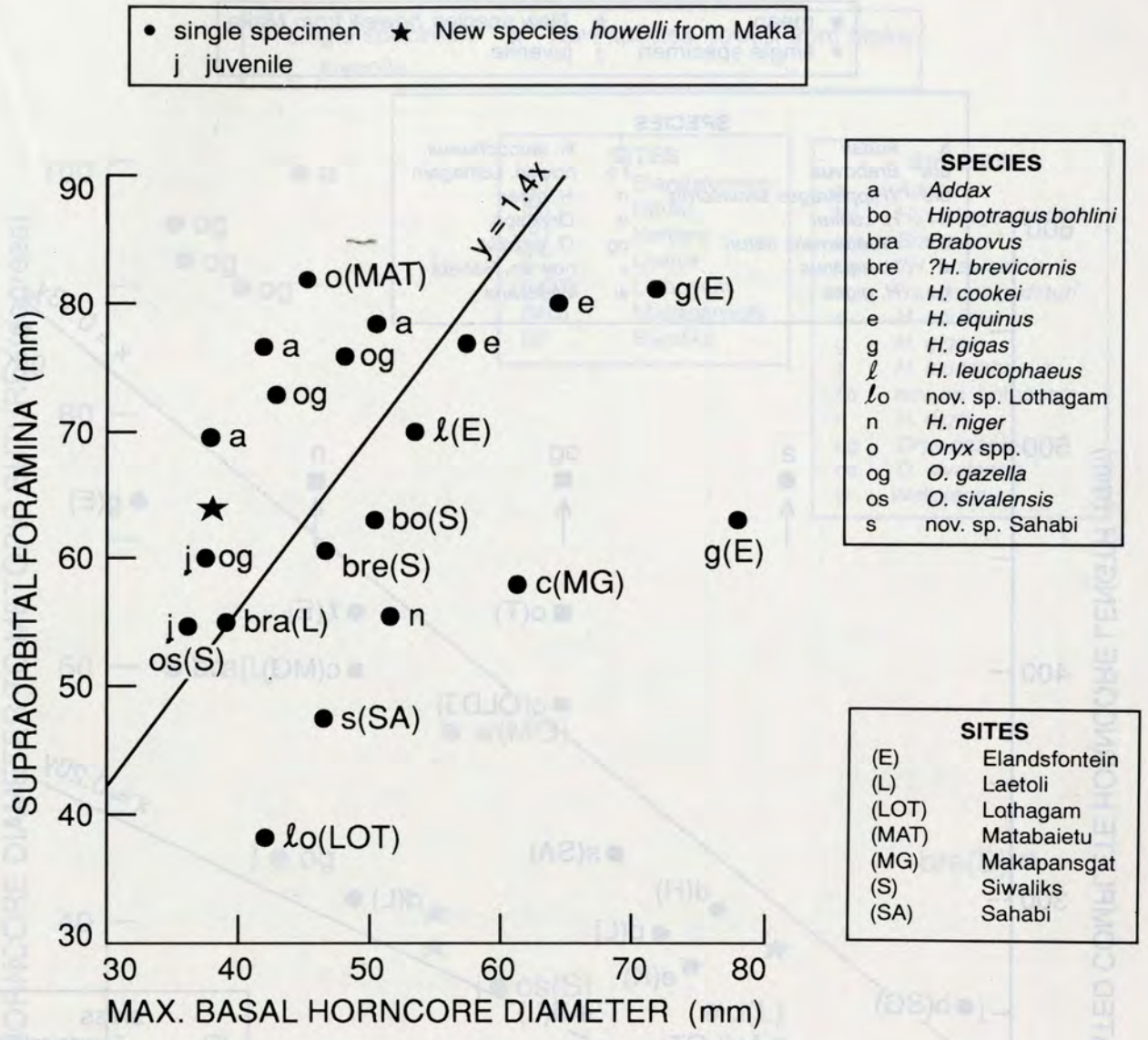


Figure 6. Maximum separation of supraorbital foramina relative to maximum basal horncore diameter in hippotragine taxa. For *Brabovus* see Gentry (1987). See Figure 5 for other sources.

prominently jutting dorsal orbital rims, and by very upright horncores that form a large angle with the dorsal braincase and are inserted right above the orbit and close together. Characters that could characterize the entire clade but that are not preserved on all component species, include relatively narrow premaxillae, an ethmoidal fissure that is largely or totally occluded by bone from the inside or by extension of the frontal, more developed goatfolds on lower molars than in *Oryx*, and relatively compressed horncores. Additional diagnostic features mentioned by Gentry and Gentry (1978) are nasals that are more domed than in *Oryx*, and stronger longitudinal ridges behind the anterior tuberosities of the basioccipital than in *Oryx*.

Hippotragus gigas from Gamedah, Middle Awash

The Gamedah Locality 1 (GAM-VP-1) is not yet directly associated with physical dates. However, according to White (pers. comm.), the Matabaietu Localities 1 to 6 (MAT-VP-1 to MAT-VP-6), associated with tuff MA 90-42 dated 2.52 m.y., on stratigraphic grounds represent the same part of the column as GAM-VP-1. These Matabaietu fossil assemblages share many species with those from GAM-VP-1. Thus, the Gamedah Locality 1 fossils are estimated to be about 2.5 m.y. old although it remains possible that they will turn out to be closer to 2.0 m.y. than to 2.5 m.y..

GAM-VP-1/14 is a right horncore of preserved length 290 mm. The original length was near 560 mm. Additional measurements are given in Table 3. It belonged to a large animal, as large as the *Hippotragus gigas* from Olduvai Bed II, Kanjera and Elandsfontein, and larger than means for *H. gigas* from Olduvai Bed I (Figure 5). Its basal horncore compression is low relative to means from the other assemblages of this species (Figure 5). It had only very slight flattening of the lateral horncore surface, very low horncore separation,

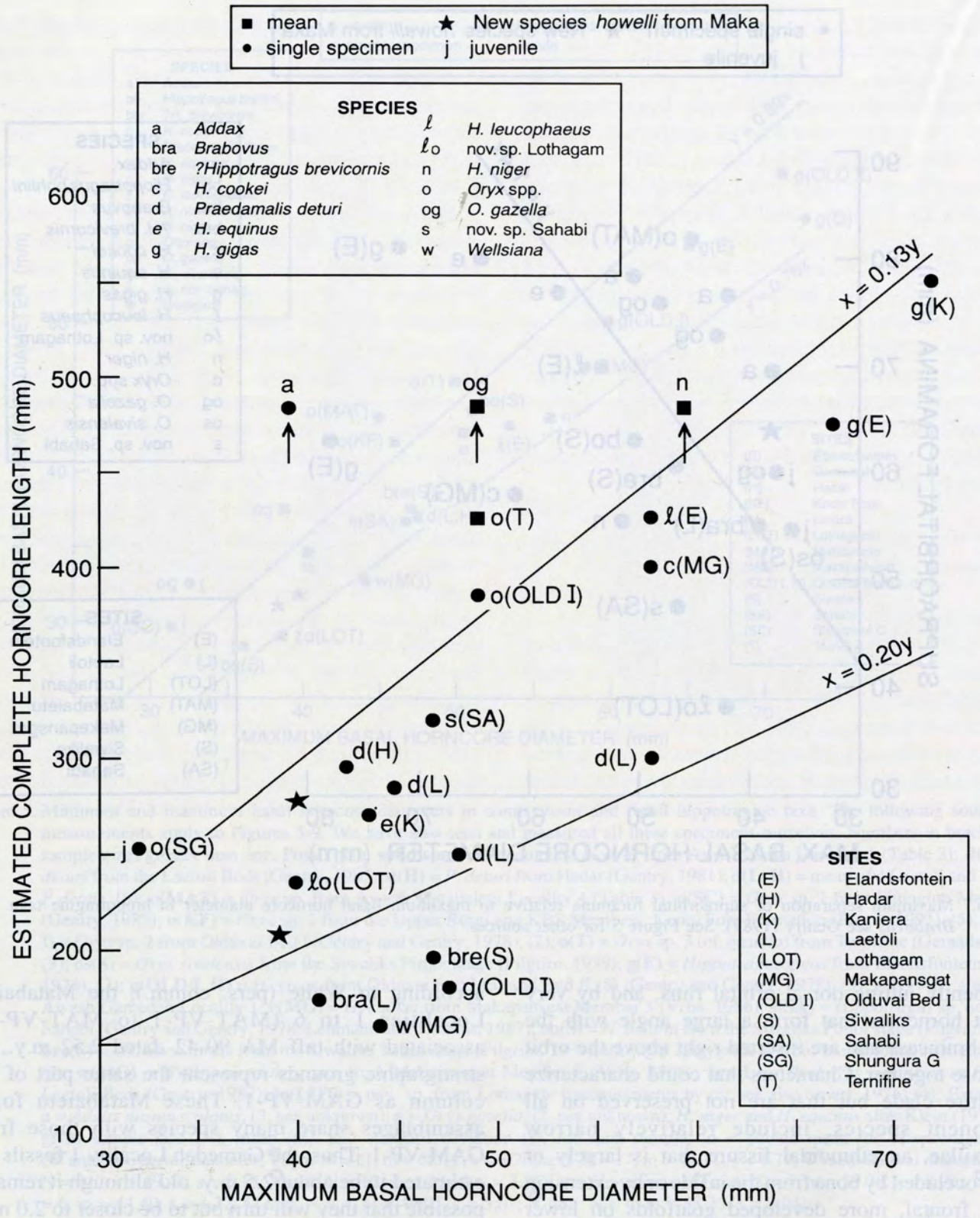


Figure 7. Estimated complete horncore length relative to maximum basal horncore diameter in hippotragine taxa. See Figures 5 and 6 for sources.

a very short pedicel, and a large basal sinus extending into the horncore base. In these respects, as also in size, strong backbending in lateral view, and lack of transverse ridges, the Gamedah horncore is typical of other *H. gigas* specimens, and there is little doubt that it belongs to this taxon. A right upper second molar, GAM-VP-1/4 (Table 4), also belongs to this species.

CONCLUSIONS

The main systematic conclusion is that the new species *howelli* is closely related to taxa previously assigned to *Praedamalis* and *Oryx*. Our assignation of the new species to *Praedamalis* is tentative and awaits additional fossil finds. However, the conclusion that *Praedamalis* and *Oryx* are more closely related to each

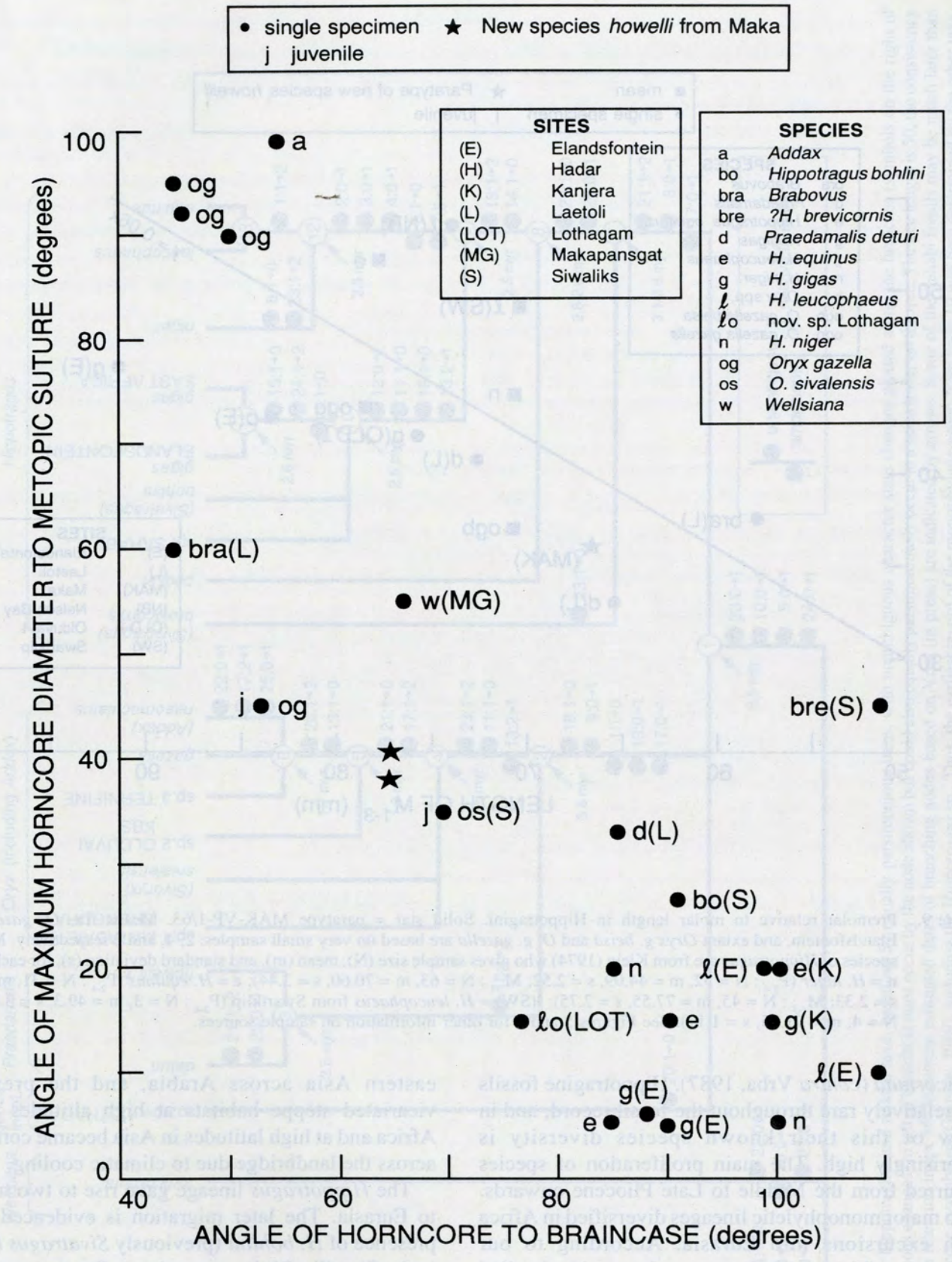


Figure 8. Angle of the maximum basal horncore diameter to the metopic (midfrontal) suture relative to the angle between the basal horncore and the dorsal braincase in lateral view in hippotragine taxa. See Figures 5 and 6 for sources.

other than either is to any taxon previously assigned to *Hippotragus*, and that the new species *P. howelli* belongs in this *Praedamalis-Oryx* clade, is firmly based in terms of our cladogram of skull characters.

In terms of the present cladistic results, we suggest that Hippotragini is the monophyletic group from node 1 in Figure 10, including all living and extinct taxa previously assigned to hippotragines together with the undescribed taxon from Lothagam (Table 1), and excluding *Brabovus nanincisivus* and *Wellsiana*

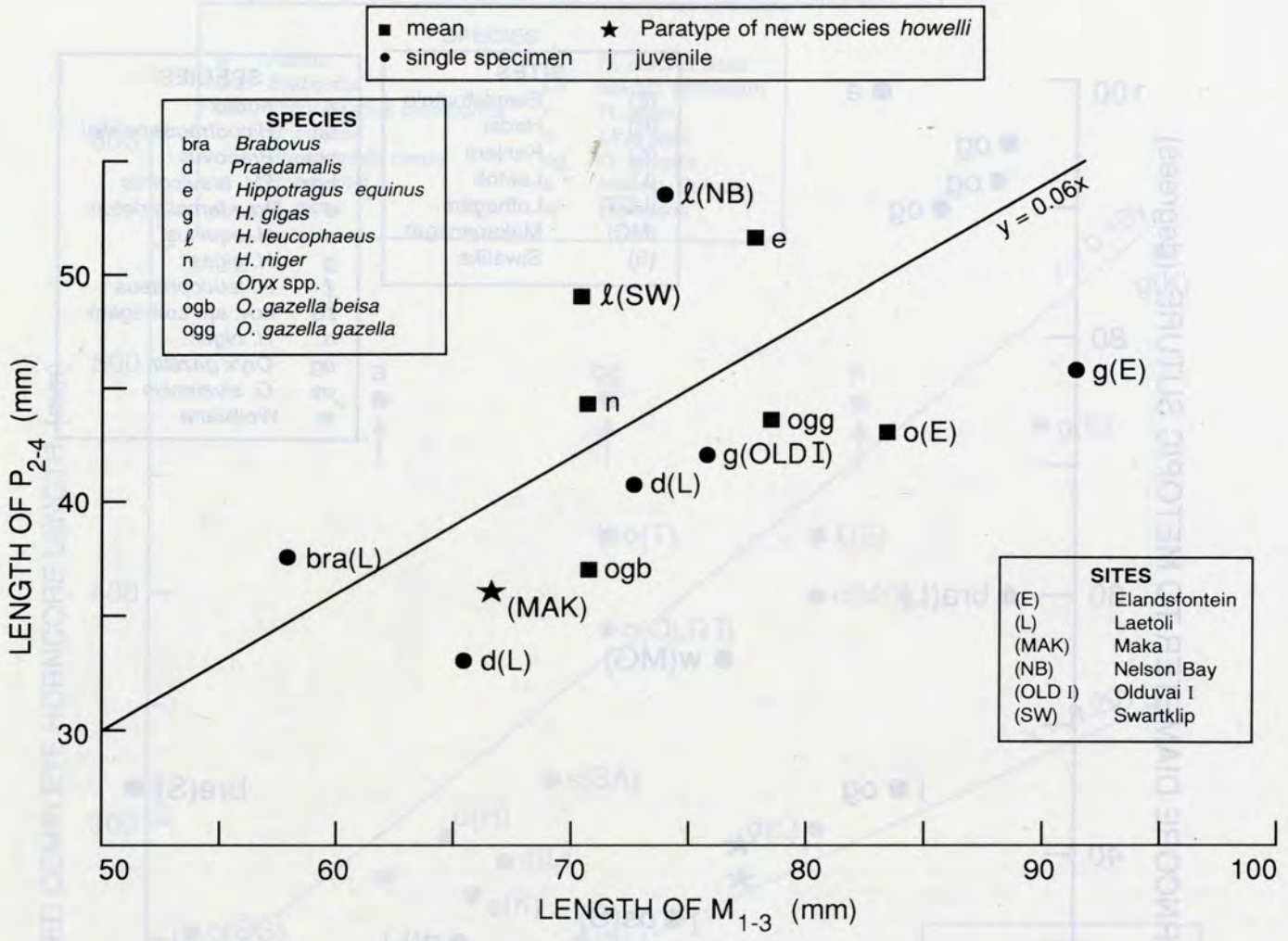


Figure 9. Premolar relative to molar length in Hippotragini. Solid star = paratype MAK-VP-1/63. Means for *O. gazella* from Elandsfontein, and extant *Oryx g. beisa* and *O. g. gazella* are based on very small samples: 2, 4, and 2 respectively. Means for species of *Hippotragus* are from Klein (1974) who gives sample size (N), mean (m), and standard deviation (s), for each sample: **n** = *H. niger* (P_{2-4} : N = 52, m = 44.09, s = 2.52; M_{1-3} : N = 63, m = 70.60, s = 3.44); **e** = *H. equinus* (P_{2-4} : N = 31, m = 51.02, s = 2.33; M_{1-3} : N = 45, m = 77.55, s = 2.75); **l**(SW) = *H. leucophaeus* from Swartklip (P_{2-4} : N = 3, m = 49.3, s = 3.53; M_{1-3} : N = 4, m = 71.15, s = 1.17). See Figures 5 and 6 for other information on sample sources.

torticornuta (*contra* Vrba, 1987). Hippotragine fossils are relatively rare throughout the fossil record, and in view of this their known species diversity is surprisingly high. The main proliferation of species occurred from the Middle to Late Pliocene onwards. Two major monophyletic lineages diversified in Africa with excursions into Eurasia. According to our cladogram (Figure 10) in comparison with detailed chronological information on all the taxa (Vrba, in press), the *Praedamalis-Oryx* lineage diversified and remained in Africa until between 2.7 and 2.0 m.y. ago when an early *Oryx* species, *O. sivalensis*, appeared in the Siwaliks Pinjor stage. Vrba (in press) suggested that this excursion dates to a period close after 2.7 m.y. ago when two conditions coincided: due to sea-level lowering, a landbridge was present between Africa and eastern Asia across Arabia, and the previously vicariated steppe habitats at high altitudes in East Africa and at high latitudes in Asia became continuous across the landbridge due to climatic cooling.

The *Hippotragus* lineage gave rise to two migrants to Eurasia. The later migration is evidenced by the presence of *H. bohlini* (previously *Sivatragus bohlini*) in the Siwaliks Pinjor stage. According to our data this emigration from Africa also occurred close to 2.7 million years ago. (We here took note of Geraads's, 1989, argument that some of the Sahabi fossils may not be datable to the Late Miocene but to the Late Pliocene. Thus, we let the minimum date of the divergence node 10 in Figure 10 be determined only by *Hippotragus gigas* and *H. bohlini*.) This was possibly coeval with the emigration of *Oryx* that culminated in *O. sivalensis*,

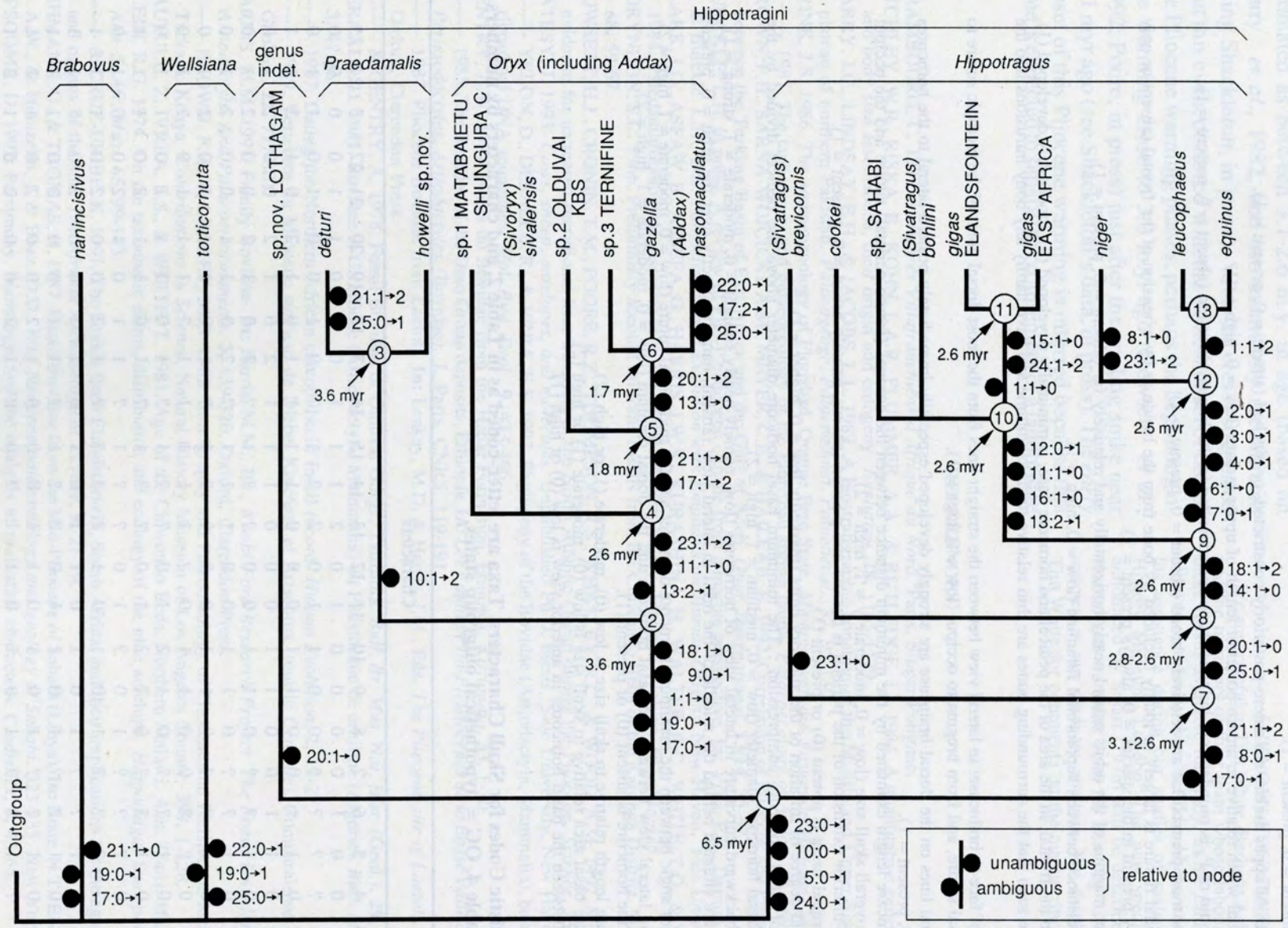


Figure 10. Consensus tree for hippotragine and related taxa, based on 54 equally parsimonious trees, with unambiguous character state changes plotted along the branches (symbols on the right of branches). Ambiguous changes (to left of branches) must occur by the node shown but could also equally parsimoniously occur at a node lower on the tree. The tree length is 50, the consistency index is 68 and the retention index 86. Minimum estimated dates of branching nodes based on Vrba (in press) are indicated by arrows. Some of the Sahabi fossils may be much later than the main Late Miocene assemblage (Geraads, 1989), including the *Hippotragus* sp.. Thus, the earliest record of the monophyletic group from node 10 was here determined by the other taxa. For character numbers see Table 5.

TABLE 5.

Skull Characters. For anatomical terms and diagrams see Sisson and Grossman (1975).

1 The P_{2-4}: M_{1-3} ratio; that is, the maximum lingual length of the lower premolars divided by the maximum lingual length of the lower molars (low = 0, medium = 1, high = 2).

2: Basal pillars (prominent ectostylids on lower and entostyles on upper molars) strongly developed so as to form a Y-shaped structure (absent = 0, present = 1).

3 Medial lobes of upper molars are antero-posteriorly constricted, or pinched (absent = 0, present = 1).

4 Bucco-lingual width relative to antero-posterior length of upper molars (low = 0, high = 1).

5 The metaconid of P_4 is rounded into bulbous shape and extended in the lingual direction (absent = 0, present = 1).

6 The anterior-most premaxillae are relatively broad (absent = 0, present = 1).

7 The ethmoidal fissure is largely or totally occluded by bone from the inside or by extension of the frontal (absent or only occasionally present in the species = 0, always present = 1).

8 The superior margins of the orbits extend nearly horizontally and relatively far (absent = 0, present = 1).

9 Maximum distance between supraorbital foramina (low = 0, high = 1).

10 The sinus in the frontal, in the area of the pedicel and horncore base, is minimally developed (0), moderately developed (1), or extensive such that the surrounding bones are thin relative to sinus volume and have hardly any bony intrusions into the sinus (2).

11 The angle of face to braincase: in lateral view between the straight lines from the most dorsal point of the metopic suture to the internasal suture, and from bregma to occiput (low = 0, high = 1).

12 The temporal lines on the dorsal braincase are strongly developed especially immediately postero-lateral to the horncores (absent = 0, present = 1).

13 Dorsal braincase length estimated by the minimum distance between the coronal (fronto-parietal) suture and the occiput relative to overall skull size (low = 0, moderately = 1, high = 2).

14 The antero-inferior extension of the parietal is narrow and pointed (absent, namely broad = 0, present = 1).

15 The postcornual fossa is absent (0) or present (1).

16 The size and degree of inflation of the auditory bulla (markedly low = 0, higher = 1).

17 The ratio of basal horncore compression : The minimum basal horncore diameter above the pedicel divided by the maximum basal horncore diameter (low = 0, medium = 1, high = 2).

18 Degree of backward curvature in lateral view of horncores (low, namely nearly straight = 0, moderate = 1, strong = 1).

19 Horncores are situated behind the middle of the orbit in lateral view (absent, namely directly over the orbit = 0, present = 1).

20 The posterior angle between the maximum horncore diameter and the midfrontal suture (low = 0, moderate = 1, high = 2).

21 The angle in lateral view between the basal horncore and the dorsal cranium (low = 0, moderate = 1, high = 2).

22 Torsion of the horncore is absent (0) or present (1).

23 The horncore length relative to skull size is low (0), moderate (1) or high (2).

24 The horncore basal area relative to skull size is low (0), moderate (1) or high (2).

25 The angle between the basal horncores in anterior view is low (0) or high (1).

TABLE 6. Cladistic Codes for Skull Characters. Taxa are letter-coded as in Table 2, and characters by numbers as in Table 4. OG = hypothetical outgroup states.

Taxa	Characters																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	3	24	25
OG	1	0	0	0	0	1	0	0	0	0	1	0	2	1	1	1	0	1	0	1	1	0	0	0	0
lo	?	?	?	?	?	?	?	0	0	1	1	0	2	?	1	?	0	1	0	0	1	0	1	1	0
a	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	1	0	1	2	0	1	2	1	1
og	0	0	0	0	1	1	0	0	1	1	0	0	0	1	1	1	2	0	1	2	0	0	2	1	0
o3	?	?	?	0	1	?	?	0	1	1	0	0	?	?	1	?	2	0	1	2	0	0	2	1	0
o2	?	?	?	0	1	?	?	0	1	1	0	0	1	1	1	?	2	0	1	1	0	0	2	1	0
o1	?	?	?	0	1	?	?	0	1	1	0	0	?	?	1	?	1	0	1	1	1	0	2	1	0
os	?	0	0	0	?	?	0	0	1	1	0	?	1	1	1	1	1	?	1	1	1	0	?	1	0
ho	0	0	0	0	1	?	?	0	1	2	1	0	?	?	1	?	1	0	1	1	1	0	1	1	0
d	0	0	0	0	1	?	?	0	?	2	1	0	?	?	1	?	1	0	1	1	2	0	1	1	1
bre	?	?	?	0	?	?	?	1	0	?	1	0	?	?	1	?	1	1	0	1	2	0	0	1	0
s	?	?	?	?	?	?	?	1	0	1	0	1	?	?	?	?	1	2	0	0	2	0	1	1	1
bo	?	?	?	?	1	?	?	1	0	1	0	1	1	0	1	0	1	?	0	0	2	0	?	1	1
c	?	0	0	0	1	?	?	1	0	1	1	0	?	?	1	?	1	1	0	0	2	0	1	1	1
g2	0	0	0	0	1	?	?	1	0	1	0	1	1	0	0	0	1	2	0	0	2	0	1	2	1
g1	0	?	?	?	1	?	?	1	0	1	0	1	1	?	0	0	1	2	0	0	2	0	1	2	1
e	2	1	1	1	1	0	1	1	0	1	1	0	2	0	1	1	1	2	0	0	2	0	1	1	1
n	1	1	1	1	1	0	1	0	0	1	1	0	2	0	1	1	1	2	0	0	2	0	2	1	1
l	2	1	1	1	1	?	?	1	0	1	1	0	2	?	1	?	1	2	0	0	2	0	1	1	1
w	?	?	?	?	?	?	?	?	?	0	1	0	?	?	?	?	0	1	1	1	1	1	0	0	1
bra	1	0	0	0	0	1	0	0	0	0	1	0	2	?	1	?	1	1	1	1	0	0	0	0	0

and also with emigration of one species of Alcelaphini and two of Reduncini (Vrba, in press). The earlier Eurasian immigrant from the *Hippotragus* lineage, *H. brevicornis* (previously *Sivatragus brevicornis*), appeared during the Tatrot stage in the Siwaliks estimated as between 3.1-2.6 m.y. in age (based on Barry *et al.*, 1982, and astronomically recalibrated using Shackleton, in press). Vrba (in press) suggested that this event occurred with the earliest onset of one of the Pliocene warming phases, perhaps the beginning of the warming close to 3.0 m.y. ago (Dowsett *et al.*, 1992; Poore, in press) just after the cooling spike near 3.1 myr ago (see Shackleton's data, in press). The *early* onset of this Pliocene warming is inferred because this time is expected to satisfy the requirement of a landbridge that was still available as melting of polar ice had not yet progressed sufficiently to flood the landbridge, and the requirement that the mesic wooded savanna habitats inferred for *Hippotragus* would have already extended to higher latitudes due to global warming.

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CATALOGUE OF FOSSIL SITES AT THE BUXTON LIMEWORKS, TAUNG

by

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ABSTRACT

The Buxton Limeworks, in the Taung district at the southeastern margin of the Kalahari Desert, harbours fossil deposits in the calcareous tufas spanning a time period from the late Pliocene to the present. Many such fossil sites, including the type site of *Australopithecus africanus*, have been exposed by quarrying and noted by various researchers since 1919. As many of the site locations have been lost in the past due to inadequate records and continued quarrying, an effort was made to relocate previously known sites and to discover new sites. There are now 17 preserved and recognized fossil sites in the Buxton Limeworks, the location and nature of which are documented here for future researchers.

KEYWORDS: Taung, Buxton, *Australopithecus*, Pliocene, Pleistocene.

INTRODUCTION

The Taung site is best known for the 1924 discovery of a fossilized child's skull now known to represent an early hominid. Early in 1925, Raymond Dart described the skull as that of an upright, small brained primitive ape-man, and gave it the species name *Australopithecus africanus* (Dart 1925).

Although the scientific community was most enthralled with the early hominid, little scientific endeavour took place at the Buxton Limeworks where the skull had been found during quarry operations. Quarrying that had begun in 1916 started revealing fossil bones in 1919 (Wybergh 1920), but prior to 1925 no site was marked, no detailed records were kept. Clues to the past history of humankind, other animals, and their environment were being blasted away by the continuing quarry operations. The quarry closed in 1977, with most blasting in the Buxton Limeworks having ceased in the mid-1950's when the focus moved South to nearby Thoming. Quarrying had exposed numerous cave sites that can still be found, and undoubtedly destroyed numerous others.

Some historical records do exist from near the time of the first hominid discovery. The approximate position of the *Australopithecus africanus* type site can be reconstructed (McKee 1993a,b; McKee & Tobias 1994) from the few who did go to Taung shortly after the hominid discovery, i.e. Young (1925), Hrdlika (1925), Cipriani (1928), and Broom (1934). It was clear to each visitor that most, if not all, of the type site had been destroyed.

The University of California African Expedition of 1947-1948 (Camp 1948; Peabody 1954) initiated the first concerted effort at studying the palaeontological and geological context of the Taung hominid. A year of field work by Frank Peabody resulted in a reconstruction of the possible locality of the type site, as based on field observations interviews with quarry workers, and a monument stands in that position today. Peabody also discovered a number of other fossil sites in the Buxton Limeworks, some of which were published by Peabody (1954), but many of which remained only in his field notes, untold until Cooke (1990) published a diorama of the sites. Some of these were destroyed by subsequent quarrying or were otherwise not possible to relocate.

Intensive research and excavation at the Buxton Limeworks resumed in 1988 by a University of the Witwatersrand team under the direction of P.V. Tobias (McKee & Tobias 1990, 1994). By 1993, systematic surveys of the Buxton Limeworks involving repeated, close visual inspection of accessible quarry wall exposures revealed the presence of 17 remaining *in situ* fossil sites, including the Dart deposits which are probable remnants of the type site (McKee 1993a,b; McKee & Tobias 1994).

The purpose of this document is to record these sites for posterity so that they will not again be lost. To accompany the maps and descriptions here, photographs of each site are archived in both the Bernard Price Institute for Palaeontological Research and the Department of Anatomy and Human Biology, University of the Witwatersrand, Johannesburg.

FOSSIL SITES OF THE BUXTON LIMEWORKS

The Buxton Limeworks are located at 27° 37'S, 24° 37'E. All of the known fossil sites at the Buxton Limeworks are marked on the contour map in Figure 1. For convenience, descriptions of the sites are categorized by the four major tufa accretions in which they are found (Figure 2). From South to North these are the Thabaseek, Norlim, Oxland and Blue Pool tufas (Peabody 1954). The types of caves in which the

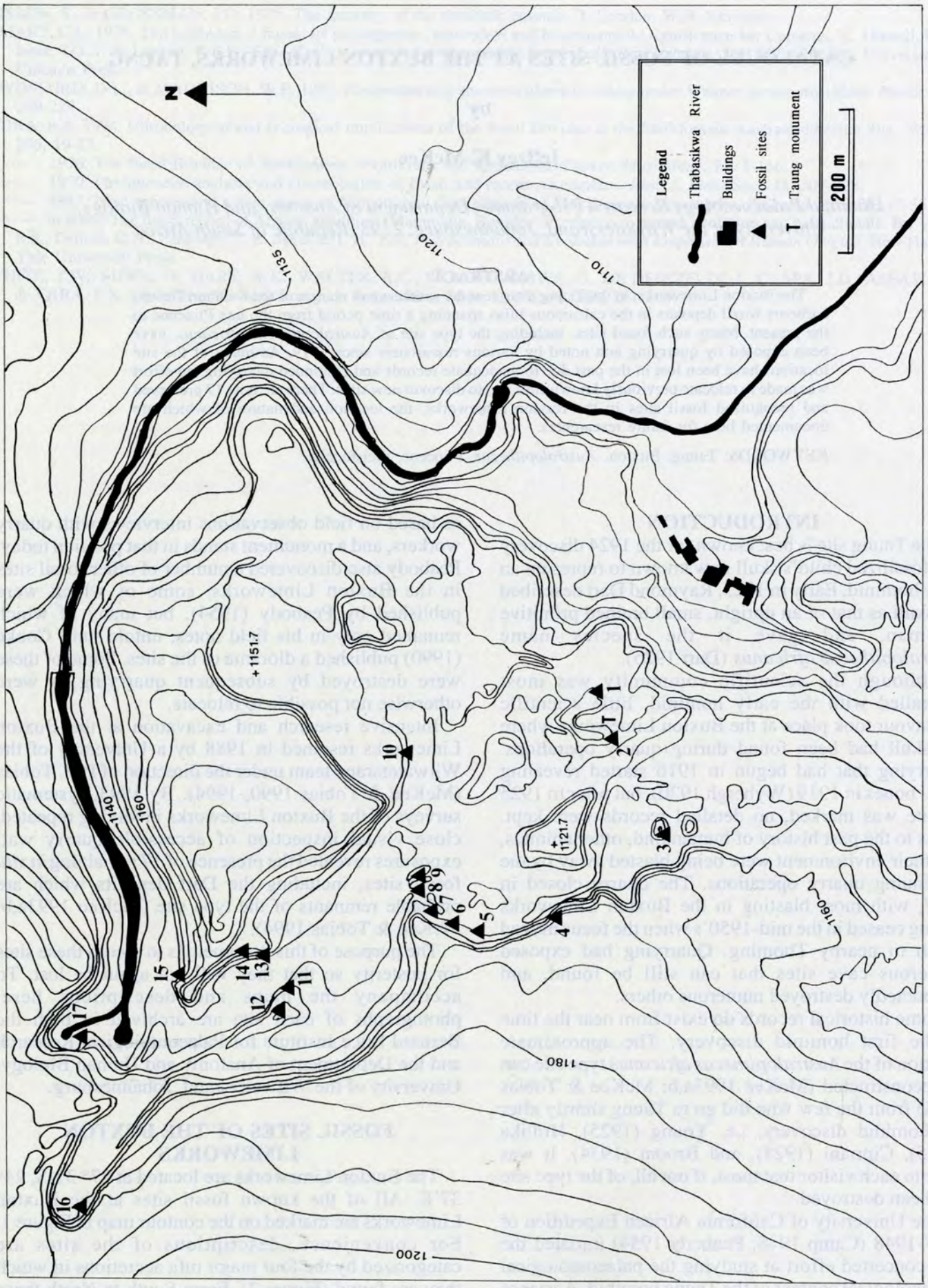


Figure 1. Recognized *in situ* fossil sites of the Buxton Limeworks, indicated by triangles. 1 – Hrdlička deposits; 2 – Dart deposits; 3 – Tobias Pinnacle deposit; 4 – Berger Cave complex; 5 – LSN Cave; 6 – Lucky Moon Cave; 7 – Innominate Cave; 8 – Quinney Cave; 9 – Cut-through Alley; 10 – Black Earth Cave; 11 – Peabody's Equus Site; 12 – Equus Cave; 13 – Blom Cave; 14 – Acacia Cave; 15 – Satan Cave; 16 – Oxland Large Mammal Site; 17 – Alcove Cave.

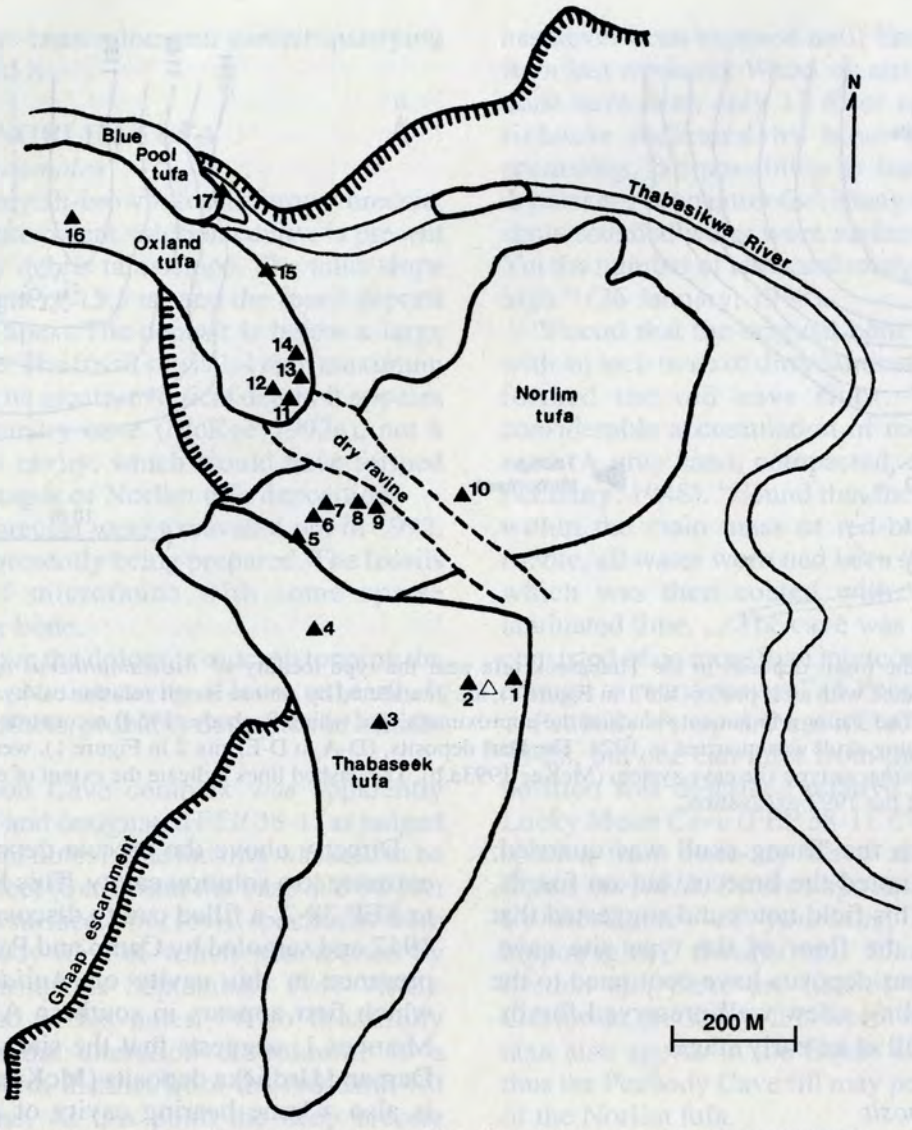


Figure 2. Principle tufa accretions of the Buxton Limeworks. The triangles represent the approximate locations of the 17 sites listed in Figure 1. The hollow triangle represents the position of the Taung Monument. (After Peabody 1954; Partridge 1985; McKee 1993a, b).

deposits accumulated are categorized according to McKee (1993a). Citations to relevant studies are given with each site, where applicable, so that unnecessary repetition of descriptions can be avoided. All of the fossiliferous localities mentioned in Frank Peabody's field notes of 1947-48 are designated by his system; the site numbers not listed here were either archaeological sites or geological sections without fossil material. Unless indicated otherwise, the remaining sites are recorded here for the first time, and were discovered and named between 1988 and 1993. Archaeological sites will be catalogued in a separate publication (Quinney & McKee, in prep.).

Thabaseek Tufa

Hrdlička deposits

Following the discovery of the Taung hominid, Aleš Hrdlička was the first anthropologist to visit the Buxton Limeworks. By the time he arrived in 1925, quarrying had proceeded past the type locality of *Australopithecus africanus* (Hrdlička 1925). He did, however, locate a nearby deposit rich in fossil cercopithecids. This cave system was relocated and named by Peabody (1954), and a portion was excavated. The University of the Witwatersrand excavations focused on the Hrdlička deposits from 1988-1991 (Partridge *et al.* 1991; McKee 1993a,b; Tobias *et al.* 1993). The cave system has at least 5 distinct breccia deposits as well as an intrusive solution cavity with Middle Stone Age (MSA) artefacts. The deposits are illustrated in Figure 3. The fossil fauna known from the deposits are recounted by Cooke (1990) and McKee (1993b).

Dart deposits

In 1991 the University of the Witwatersrand excavation at the Buxton Limeworks uncovered a series of *in situ* fossil deposits in the quarry floor around the southern base of the Dart Pinnacle, a quarry remnant close to the original discovery site of the Taung skull (McKee & Tobias 1994). The nature and location of these deposits are most consistent with that of the historical record of the type site (McKee 1993a,b; McKee & Tobias, 1994), and thus they were dubbed the 'Dart deposits' (Figure 3). The cave system represented by these deposits may be part of the same

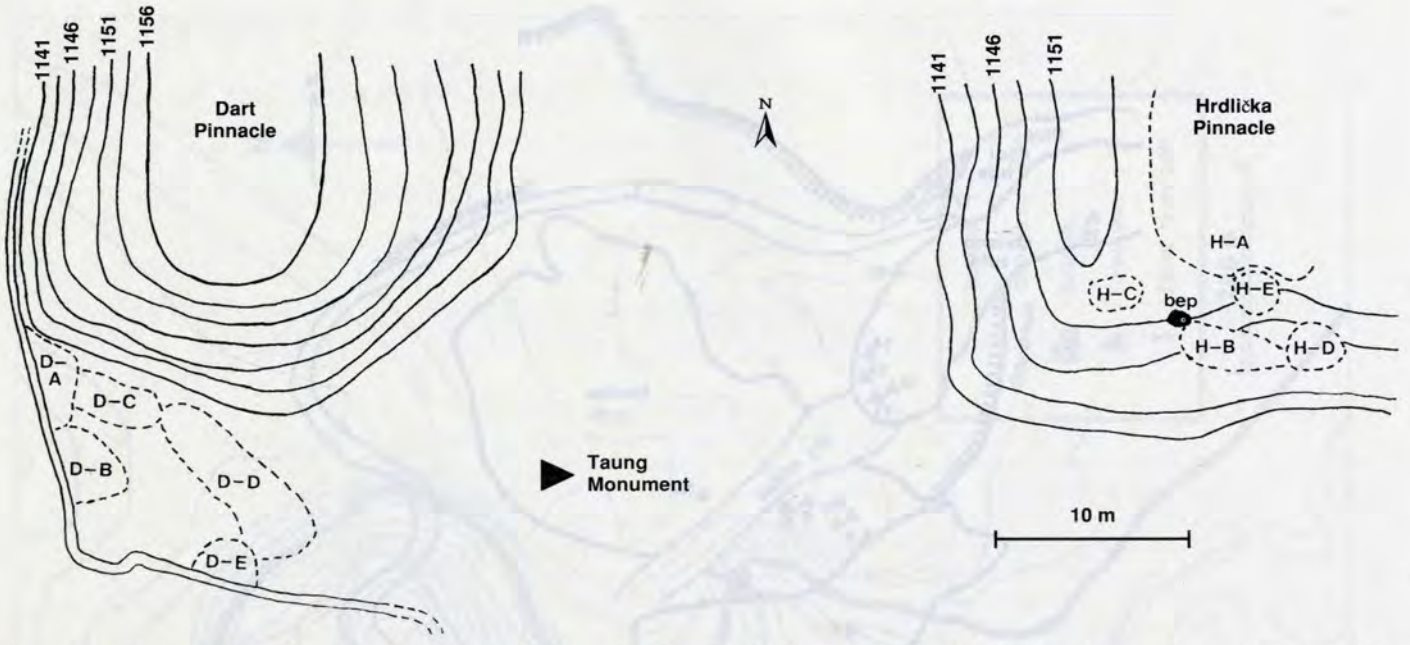


Figure 3. Diagram of the fossil deposits in the Thabaseek tufa near the type locality of *Australopithecus africanus*. The Hrdlička deposits, denoted with an H prefix (site 1 in Figure 1), are intersected by a more recent solution cavity called the "Black Earth Pipe" (bep). The Taung Monument stands at the approximate spot which Peabody (1954) reconstructed as the locality from which the Taung skull was quarried in 1924. The Dart deposits, (D-A to D-E, site 2 in Figure 1), were inferred to be part of the *Australopithecus* type site cave system (McKee 1993a,b). The dashed lines indicate the extent of each deposit as revealed by the end of the 1993 excavation.

labyrinth from which the Taung skull was quarried; Frank Peabody had noted the breccia, but no fossils, from this locality in his field notes and suggested that they may represent the floor of the type site cave. Excavation of the Dart deposits have continued to the present (1994), yielding a few well-preserved fossils, but the analysis is still at an early stage.

Tobias Pinnacle deposit

This is a small lens of brownish-grey breccia. Its current *in situ* exposure, measuring 1 m in horizontal length and 100-150 mm in thickness, is found approximately 7 m up from the level of the quarry floor on the steep southwestern slope of the pinnacle. On the quarry floor in the general vicinity of the pinnacle are *ex situ* blocks of breccia that appear, from breccia colour, texture and content, to be from part of the same deposit. The breccia is dense with microfauna and occasionally has macrofaunal remains, including a distal tibia of a small canid. None of the fauna has yet been identified to species level.

Berger Cave complex

A complex of apparent solution cavities with brownish earth can be found near the top of the eastern face of the quarry wall. At the point marked as site 4 on Figure 1, is a pocket of calcified brown matrix containing fossils that are eroding out (during heavy rains a small waterfall cascades over these deposits). The breccia deposit is approximately 5.5 m down from surface level (6.3 m along the diagonal slope). It is exposed on a horizontal surface jutting out from the quarry wall, covering an area of about 1.1 m. in diameter and reaching to a maximum vertical depth of 0.4 m. A carnivore sacrum has been excavated from this pocket.

Directly above the breccia deposit, up 4 m., is the entrance to a solution cavity. This locality corresponds to FEP 38-2, a filled cavity discovered by Peabody in 1947 and sampled by Camp and Peabody in 1948. The presence in this cavity of *Antidorcas marsupialis*, which first appears in southern Africa at Swartkrans Member 1, suggests that the site would post-date the Dart and Hrdlička deposits (McKee *et al.*, 1994). There is also a bone bearing cavity of uncalcified reddish earth 3.5 m. north and 1 m. above the breccia deposit. It is thus likely that these pockets were all part of one solution cavity system that post-dated the formation of the Thabaseek tufa.

Unnamed Solution Cavities (FEP 38-15, 38-16, 38-25)

These three localities were mentioned in Frank Peabody's field notes and located on the diorama published by Cooke (1990). On the basis of these records it is clear that all were found near the top of the western wall of the quarry; none have produced identified fauna and, despite extensive searching, none have been specifically relocated by our team. The most southern of these solution cavities (38-25) is in an area that our own surveys have found to be void of fossils (no fossils are found south of the Tobias Pinnacle Deposit); Peabody made no notes on this locality other than its position. Peabody notes FEP 38-16 as a red-earth fill carrying many coarsely made artefacts, "25 feet" (7.6 m) down from the top of the quarry. It is recorded to have been just south of the Berger Cave complex, at the apex of where the quarry wall juts out toward the East. Further to the North is FEP 38-15, almost directly above FEP 38-1 (see Norlim section), where Charles Camp located a cemented fill with bone near the top surface. It appears from Peabody's original diorama to be in the Thabaseek

tufa, but has not yet been relocated; further quarrying may have destroyed it.

NORLIM TUFA

Lucky Moon Cave complex

A pocket of greyish-brown fossiliferous breccia, intersected by a more recent solution cavity, is present just above a quarry debris talus slope. The talus slope has an oblique height of 15.5 m, and the fossil deposit is 1.5 m above its apex. The deposit is below a large outcrop of dolomite. The fossil site is 1.4 m in maximum width, and 0.8 m at its greatest vertical depth. It appears to have been a primary cave (McKee 1993a), not a secondary solution cavity, which would have formed during the initial stages of Norlim tufa deposition.

Portions of the breccia were excavated out in 1992, and the fossils are presently being prepared. The fossils consist mostly of microfauna with some sparse fragments of larger bone.

Immediately above the dolomite outcrop topping the breccia deposit is a solution cavity of loose red earth. It contains sparse artefacts, probably dating to the Middle Stone Age.

The Lucky Moon Cave complex was apparently discovered in 1947 and designated FEP 38-1 (as judged from Peabody's field notes). The locality was said to be approximately 10 feet (3 m) from the base and 90 feet (27 m) from the top surface. Four fossil specimens were collected by Peabody (one of which was spotted by Raymond Dart during his September, 1947 visit!). Peabody's recorded in his notes: "Also beautifully demonstrated was the alteration of dolomite to a chocolate brown earth distinct from the red earth fill containing the bone. At this point the deep breccia appears to have been a cave fill resting partly on a floor consisting of dolomite boulder agglomerate." Thus the fossils appear to have come from the upper cave where our team found the stone artefacts in 1992, and the deep breccia may be the brown breccia we called Lucky Moon Cave. This is consistent with Peabody's later note that the deep breccia, "just below and to the right of the pipe", contained bone chips including a vertebra and one rodent incisor. Peabody's sketch of the cave complex does not match the current exposure in detail, but it is apparent that quarrying was still going on in this area and that the quarry wall was blasted back from its 1947 position for a short distance.

The fossils found in the upper cave have been identified in the University of California, Berkeley collection as cf. *Connochaetes* sp., *Gazella* sp., and *Tragelaphus angasi*.

Peabody Cave

Peabody Cave (Cooke 1990) has not been relocated, so it is worth quoting Peabody's field notes in detail concerning this locality, FEP 38-28: "It is a very rich semi-consolidated and semi-cemented, black and red cave deposit outcropping in the very floor of the quarry. It is about 25 ft. from the present face about 30 ft. to the right of the right hand large lower cave and apparently has never been exposed until Erasmus levelled up the floor last weekend. When we arrived last year this spot must have been only 12 ft. or so from the face. The richness indicated by bone lying all around is promising; the possibility is that a fairly large cave deposit has been unroofed. Many of the bone fragments show rounded water worn surfaces and a black polish. Yet the number of teeth and recognizable joint facets is high." (26 January, 1948).

"Found that the original bone deposit was covered with an inch or so of dirty lamination which for a while formed the old cave floor. Then followed the considerable accumulation of red and black clay and sand. A grey sand, compacted, also occurs here." (5 February, 1948). "Found that the main bone level was within the main mass of red-black earth. Bone and rubble, all water worn had been lying free on a surface which was then coated with 1 1/2 inch of dirty laminated lime. ... The cave was not large; it probably consisted of no more than interconnected cells not large enough to rate as caves." (6 February, 1948).

Peabody's map did not include the locality of FEP 38-28, but one can infer from the above notes that its position was described relative to what we now call Lucky Moon Cave (FEP 38-1). Cooke (1990) listed the species from Peabody Cave as *Megalotragus* sp., *Equus burchelli*, *Diceros* sp., *Antidorcas marsupialis*, *Connochaetes* cf. *taurinus*, *Damaliscus* sp., a hippotragine, *Giraffa* sp., *Phacochoerus* sp., and *Lycaon* sp.; these are housed at the University of California, Berkeley. It is worth noting that all of these taxa also appear in the Equus Cave assemblage, and thus the Peabody Cave fill may post-date the formation of the Norlim tufa.

LSN Cave

LSN Cave is a small lens of grey breccia containing a small amount of fossil microfauna. It outcrops on the quarry wall to the south of Lucky Moon Cave, 1.5 m up the wall from the top of a small talus slope of rubble. The deposit measures a maximum of 700 mm horizontally and 200 mm vertically, and is enclosed on the top and bottom by laminated tufa. No fossils have been recovered.

Innominate Cave

This is a small outcrop of greyish-brown breccia with limited microfauna and pebbles, found on the quarry wall at the apex of another talus slope north of Lucky Moon Cave. The pocket extends 1.2 m horizontally and 0.5 m vertically. It has an ill-defined shape with an apparent filled solution cavity coming down into it from the left. No excavation has been attempted.

Cut-through Alley

Cut-through Alley contains a series of fossiliferous, sediment-filled solution cavities. Although this particular exposure had not been cut before Peabody completed his study, Figure 6 in his publication

(Peabody 1954), taken from an adjacent section (FEP 38-11) accurately depicts the nature of this geological section. On the west wall of the alley, 12 m from the south edge and 43 m from the north edge, is a solution cavity with bone-bearing breccia. From the level of the quarry floor it slopes up to the north for a few metres. On the east wall, about 2 m to the north, is a similar solution cavity; it may be part of the same cavity or at least the same system dissected by the limeworker's access drive. At the top of the east wall, above the solution cavity, one can find loose red breccia with many small bone flakes. *Ex situ* brown breccia with large mammal bones can also be found on this top terrace. There are further small pockets of bone concentrations within the breccias of the east wall. It is likely that this system was deposited during the formation of the Oxland tufa, when the natural ravine (Figure 2) was cut through the Norlim tufa.

Quinney Cave

There are two fossiliferous deposits in Quinney Cave, a loose soil fill rich in microfauna, bovid bone and coprolites, and an underlying solid brown breccia with microfauna. This large cave extends for a maximum of 12.5 m horizontally at its base, and has a maximum height of approximately 3.9 m. The north edge of the deposit shows that the loose dirt fill came in as a solution cavity fill, as the bedding planes of the tufa are clearly intersected. The solid brown breccia may be older or just a calcified part of the same cave infill, but little can be said about it until it is adequately sampled. An excavation of the earth fill began in 1992, and an analysis is presently under way.

Black Earth Cave

Peabody and Camp conducted extensive excavations in Black Earth Cave, a system comprising three galleries (FEP 38-14, FEP38-18A, and FEP 38-18B). These are dealt with extensively by Peabody (1954), and reviewed by Humphreys (1978). The uncon–solidated earthen deposits contain stone artefacts (mostly MSA) as well as a wealth of fossil fauna. The faunal list of species identified in the University of California Berkeley collection can be found in Table 1. Peabody (1954 p686) mentioned the inclusion of "two types of *Homo*", but this author found the two teeth to be indistinguishable in size and morphology from modern *Homo sapiens*.

OXLAND TUFA

Equus Cave

Equus Cave was named by C.K. Brain and K. Butzer on the basis of its presumed association with Peabody's locality FEP 38-7, where he found an equid tooth. However, as described below, this locality is different from that found by Peabody. Equus Cave has been the subject of extensive excavations by P.B. Beaumont, and the details have been reported by Grine & Klein (1985), Klein *et al.* (1991), Scott (1987), and Lee-Thorp & Beaumont (1990). The faunal list for the site can be found in Table 1.

Peabody's Equus Site

The position where the *Equus* tooth was found by Peabody (1954 p689, Figure 7) is approximately 20 m to the south-east of the *Equus* Cave excavation. There one can find semi-consolidated reddish brown earth with chert artifacts and bone and tooth fragments. These are in an ill-defined deposit overlain by cemented cobbles, as shown in Peabody's diagram, extending to a height of 6.6 m. From there the section continues to an access road cutting, along which another section is exposed at a perpendicular toward the south-west for 20 m. Here the deposit thins out from 4.9 m at the corner to 1.5 m where it ends abruptly at its south-westerly extent. At the base of this section is up to 1 m of brown breccia containing bone fragments which is overlain by cobbles. These deposits do not appear to be cave deposits, but extensive, horizontally-bedded waterlain deposits leading toward the channel alluvium; indeed there are bones and artefacts in the channel alluvium as well.

Blom Cave

To the west of Equus Cave (across the current road), near the terminal edge of the Oxland tufa, is a site of a similar nature known as Blom Cave. The fossiliferous deposit is 2.3 m above ground level, has a maximum height of 1.1 m and maximum north-south extent of 2.3 m. The fossiliferous component is found in a semi-consolidated reddish-brown breccia which is overlain immediately by a horizon of fragmented rocks, upon which consolidated sterile breccia is exposed up to the quarried top surface. The southern end of the deposit shows some intersection of the tufa bedding planes by the deposit, suggesting that it may have been a solution cavity. Alternatively, it may be part of the Equus Cave system with the interconnecting portions having been quarried away. The deposit has not been excavated for fossils.

Acacia Cave

This is a small outcrop of reddish breccia containing only small bone fragments. It is found at the top of the northeastern quarry wall, reaching to a maximum depth of 2.5 m and extending 7 m laterally. It appears to have been a solution cavity as the breccia fill cuts across the bedding planes of the tufa.

Satan Cave

Satan Cave is immediately to the east of a quarrier's tunnel, and comprises large bones, stone artefacts, and ostrich egg shells in a semi-consolidated red breccia. It extends for 6.9 m along an oblique slope, with a maximum width of 3.7 m. The breccia overlies shales that would have served as the cave floor. The eastern and northern portions of the cave have been quarried away, making interpretation of its formation difficult. It is possible that this site is Peabody's locality FEP 38-29, but not enough details are given in his notes. No scientific excavations of the site have been conducted.

Table 1. Identified mammalian fauna from the excavated late Pleistocene sites of Equus Cave (EC), Black Earth Cave (BEC), and Tobias Cave (TC). (Known fauna from other sites are listed in the text or in cited references).

	EC	BEC	TC
Bovidae			
Aepycerus melampus		*	
Alcelaphus buselaphus	*		*
Antidorcas bondi	*	*	
Antidorcas marsupialis	*	*	*
Connochaetes gnou	*	*	*
Connochaetes taurinus	*		
Damaliscus dorcas	*	*	*
Kobus leche	*	*	
Megalotragus priscus	*		
Oreotragus oreotragus			*
Pelea capreolus	*		*
Raphicerus campestris	*		*
Raphicerus capra		*	
Redunca arundinum		*	
Redunca fulvorufula	*	*	*
Sylvicapra grimmia	*		*
Syncerus caffer	*	*	*
Taurotragus oryx	*		*
Tragelaphus strepsiceros	*		*
Canidae			
Canis adjustus		*	
Canis *mesomelas*	*	*	*
Lycaon sp.		*	
Lycaon pictus	*		
Otocyon megalotis	*		*
Vulpes sp.		*	
Vulpes chama	*		*
Cercopithecidae			
Papio cynocephalus	*		*
Equidae			
Equus burchelli	*	*	*
Equus capensis	*	*	*
Felidae			
Acinonyx jubatus	*		
Felis caracal	*		*
Felis libyca	*		
Felis nigripes	*		
Panthera leo	*	cf	*
Panthera pardus	*		*
Giraffidae			
Giraffa camelopardalis	*		
Hippopotamidae			
Hippopotamus amphibius	*		
Hominidae			
Homo sapiens	*	*	*
Hyaenidae			
Crocuta crocuta	*		*
Hyaena brunnea	*	*	*
Mustelidae			
Aonyx capensis	*		
Mellivora capensis	*		
Orycteropodidae			
Orycteropus afer	*		
Procaviidae			
Procavia capensis	*	*	*
Rhinocerotidae			
Diceros bicornis	*		*
Suidae			
Phacochoerus aethiopicus	*	*	*
Viverridae			
Atilax paludinosus	*		
Cynictis penicillata	*		
Herpestes ichneumon	*		
Suricata suricatta	*		
Soricidae			
Crocidura sp.		*	
Bathyergidae			
Cryptomys sp.		*	
Erinaceidae			
Erinaceus frontalis	*		
Hystricidae			
Hystrix sp.		*	
Histrix africaeaustralis	*		*
Pedetidae			
Pedetes capensis	*		

Oxland Large Mammal Site

This is a substantial deposit of red and reddish-brown breccia containing fossil bones of large mammals. It is approximately 50 m east of the terminal end of the upper portion of the quarry along the south quarry wall. The full extent of the cave is not yet known, as most of the material is *ex situ* along a large talus slope left by quarry activities. Some fossil bone remains *in situ*, approximately 4 m below the top surface of the tufa.

The Oxland Large Mammal Site may have been a large cave with two deposits or two closely associated caves. Most of the Middle Stone Age artefacts found in the breccia are found in blocks with fragmented bone, whereas the blocks rich in large white bone have few or no artefacts. No scientific excavations of the material have been conducted.

Tobias Cave

In 1952 a salvage excavation operation ahead of quarry activities in the Oxland Tufa was conducted by P.V. Tobias, J.W. Kitching, and A.R. Hughes. Although the exact location of the site is not known due to the continued quarrying, an approximate location near the Oxland Large Mammal Site can be reconstructed on the basis of Tobias's initial report, quoted by Humphreys (1978), and a visit to the site with P.V. Tobias in 1991. [Note: Tobias's field notes state that the deposit corresponds in position to that of Black Earth Cave, but such a placement is incompatible with the recollections of Tobias and Kitching as well as with the location gleaned from Peabody (1954).] The site has been called 'Tobias Cave' by Humphreys (1978) and Morris (1990).

The 1952 excavation of Tobias Cave in the Oxland tufa yielded an array of faunal material (Table 1), including cranial material of *Homo sapiens sapiens* (Quinney & McKee 1992). The upper level of the cave contained LSA artefacts, whereas artefacts of the lower levels consisted solely of MSA lithics. The fossils and artefacts are held at the University of the Witwatersrand.

Blue Pool Cave

On the north face of the Oxland Tufa, overlooking Blue Pool, was a cave shelter (FEP 38-12) described by Peabody (1954) which has since been destroyed by quarrying. If Satan Cave is Peabody's locality FEP 38-29, then Blue Pool Cave site would have been approximately 8 metres upstream and 15 m higher than Satan Cave. Along with LSA artefacts and ungulate long bones was a superficial layer of owl pellets that was accumulating during the time of Peabody's work at the site (October 1947). Peabody identified the contents of the pellets in his field notes as weaver birds, swifts, bats, shrews and rodents.

Spiers' Cave

Broom (1946) noted a cave in the Buxton Limeworks which he called "Spiers' Cave", and associated the cave and its contents, including the type specimen of *Mylomygale spiersi*, with the *Australopithecus* cave. He also noted that the deposit was about a half-mile north of the *Australopithecus* site, which would most probably mean that it was in the Oxland tufa, or perhaps the Blue Pool tufa. The University of California expedition attempted to relocate the site with no success (Peabody 1954).

BLUE POOL TUFA

Alcove Cave

On the north side of the Blue Pool tufa, where an intermittent waterfall has been dissecting the tufa, there is an exposure of breccia in an alcove. Much of the cave deposit has fallen away from the wall in large boulders containing bone fragments. The remaining *in situ* exposure of the cave infill extends approximately 2 m horizontally and 1.1 m vertically. The cream-coloured breccia abuts a concavity in the Schmidtsdrif shales to the East, with tufa overlying both, so it was probably deposited at an early stage of Blue Pool tufa formation.

CONCLUSION

Although much of the Buxton Limeworks has been destroyed, the quarry remnants hold a vast store of fossil deposits representing the Pliocene and Pleistocene. At least 17 sites remain, and more may exist unexposed within the depths of the tufa. The Buxton fossils and their context may provide a unique opportunity to investigate continuous environmental and evolutionary changes at a single location. It is hoped that future scholars will continue to investigate the clues to the evolution of man and other animals that are revealed in the fossil richness of the Taung area.

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FOSSIL WOOD OF CRETACEOUS AGE FROM THE NAMAQUALAND CONTINENTAL SHELF, SOUTH AFRICA

by

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ABSTRACT

Fossil wood was collected from sediments on the Namaqualand shelf, West Coast, South Africa, between the Orange River mouth and just to the south of Kleinzee. Forty three of these samples are here described. All the woods are gymnospermous and have abietinian tracheid pitting. Nineteen of them are well enough preserved to be identified to species level: *Podocarpoxylon* cf. *umzambense*, *Mesembrioxylon* cf. *stokesii*, *M.* cf. *sahnii*, *M.* cf. *woburnense* and *Protocupressinoxylon* cf. *purbeckensis*. The remainder of the woods have been placed in the artificial genus *Mesembrioxylon* without species names. The woods are probably primitive members of the Podocarpaceae growing during the Lower Cretaceous. They indicate a seasonal climate and inhabited the extensive low-lying coastal regions.

KEY WORDS: Lower Cretaceous, South Africa, Podocarpaceae, Cheirolepidiaceae.

INTRODUCTION

There are only a few indigenous conifers in southern Africa today, mainly restricted to the relict forests in the southern Cape, Knysna and isolated montane regions. These conifers are represented by a few members of *Podocarpus*, *Juniperus* and *Widdringtonia*. *Phyllocladus*, a genus with which some of the fossil woods show some similarity, is now restricted to New Zealand and Australia. The fossil record, therefore, indicates a greater diversity of conifers in south-western Africa in its geological past.

In the past there were large coniferous forests of unknown extent and duration along the west coast of Southern Africa. Evidence for this is from the huge collection of fossil logs which has been deposited (either *in situ* or transported) on what is today the Namaqualand continental shelf, West Coast of South Africa. Some of these logs have diameters of more than 1m. The land along the coast is now desert or semi-desert and has experienced several cycles of wet and dry climates during the Tertiary. The age of the present desert has been debated for many years but it is most likely that aridification began in Late Mesozoic times (Ward and Corbett 1990).

Nearly all of the 43 samples of fossil wood examined are podocarpaceous with abietinian tracheid pitting, thin and smooth walled ray parenchyma cells, and where preserved, podocarpoid or phyllocladoid cross-field pits. Gothan (1905) erected two genera for such wood, *Podocarpoxylon* and *Phyllocladoxylon*, the difference between them being the size of the cross-field pits. Seward (1919) claimed that it was impossible to distinguish between the genera and instead formed the artificial genus *Mesembrioxylon* which denies any generic affinity. Krausel (1949) favoured Gothan's genera and further clarified the differences. We have not assigned species names to the samples where the cross-field pits have not been preserved and these woods have been placed in the genus *Mesembrioxylon* because the other characters have been preserved.

There is an interesting first occurrence of wood of the Cheirolepidaceae, *Protocupressinoxylon* Eckold. Pollen of this family, *Classopollis*, has been recorded from several deposits elsewhere in southern Africa (McLachlan and McMillan 1976, Scott 1976) of Lower Cretaceous age. The foliage of this family, *Brachyphyllum* and *Pagiophyllum*, has been found in one of the deposits (Kirkwood formation, Algoa Basin; Seward 1903, Bamford 1986). Not all examples of *Brachyphyllum* and *Pagiophyllum*, however, belong to the family Cheirolepidiaceae.

LOCALITY AND GEOLOGY

The specimens of fossil wood described in this paper have been recovered from the continental shelf between the mouth of the Orange River and Kleinzee. The wood was collected in water depths of between 100mbsl. to 150mbsl. during exploration of the shelf by De Beers Marine (Pty) Ltd (Figure 1). The majority of the fossil wood specimens are angular blocks which show minimal evidence of transport. Large logs (diameters of 600 mm), with thin phosphatic rinds coating their surfaces, have occasionally been brought to surface when caught on the anchors of exploration vessels. It is probable that the fossil wood specimens are fragments broken off large trunks by the equipment used to sample the sands and gravels on the shelf for diamonds, and it is likely that even larger fossil tree trunks are present on the shelf.

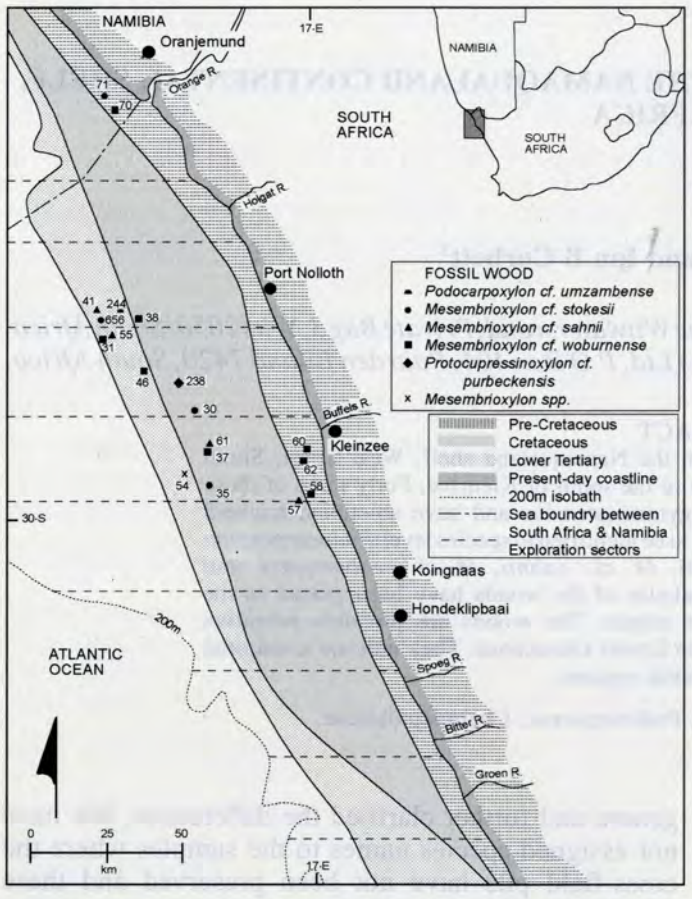


Figure 1. Locality map showing offshore deposits of fossil wood.

Vibracores which provide sections through the shelf sequence show that sub-rounded fossil wood fragments have been incorporated into shelly sand and gravel lags which were deposited during transgression of the Namaqualand shelf by a palaeoshoreline which developed during the Last Glacial between 24kyr. BP. to 12 kyr. BP. (oxygen isotope stage 2).

MATERIALS AND METHODS

Polished thin sections were made in the usual fashion but the thickness of each sample varied (between 25-120µm) depending on the preservation of the wood, and this had to be judged frequently under the microscope during grinding. Sections were made in three planes, transverse, tangential longitudinal and radial longitudinal. The slides were studied and photographed under a petrographic microscope.

DESCRIPTION OF MATERIAL

Podocarpoxylon cf. *umzambense* Schultze-Motel 1966.

BPI Number: BP/16/244
Locality: Namaqualand shelf.
Figures: 2-5.

Description

Growth rings are indistinct and appear as areas of cellular breakdown, 5-7mm apart.

The tracheids are regularly arranged, squarish in outline, and rays are prominent (Figure 2). The early wood tracheids have a mean tangential diameter of 48µm (range 40-59µm) and mean radial diameter of 47µm (range 40-59µm). The late wood tracheids have been crushed. The bordered tracheid pits are uniseriate, mostly separate but occasionally contiguous, and have a diameter of 19µm (Figure 3). They occur on the radial walls only.

Axial parenchyma was not seen but the preservation is poor. Rays are uniseriate with low biseriate portions of 1-4 cells, with an average ray height of 11 cells and range of 3-20 cells (Figure 4). The ray cell walls are thin and smooth. The cross-field pits are single, round, simple and 12-13µm in size (Figure 5). Very little resin is present and there are no ray tracheids or resin canals present.

Identification

This wood belongs to the genus *Podocarpoxylon* because it has small podocarpoid cross-field pits, thin and smooth ray cell walls and abietinian tracheid pitting.

Comparison

This wood is very similar to *Mesembrioxylon gothani* (Stopes 1915: *Phyllocladoxylon gothani*; Seward 1919: *M. gothani*; Thayn and Tidwell 1984: *M. gothani*). The original wood described by Stopes (1915) came from the Aptian deposits on the Isle of Wight. It has low rays (1-8 cells high, average 3), tracheid pits 15-17µm in diameter on the radial walls and elliptical cross-field pits of 7µm diameter.

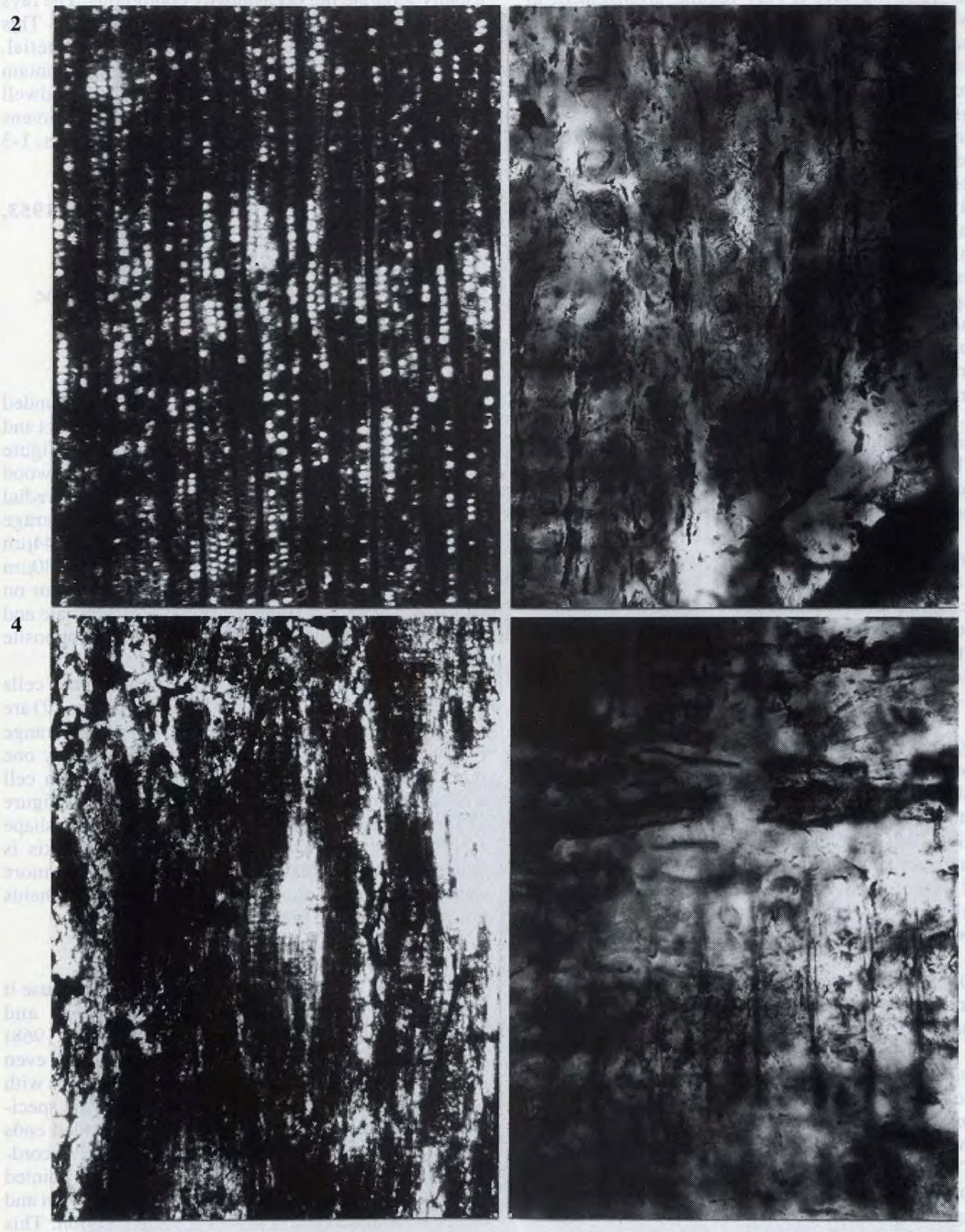
The wood with which this sample compares most closely is *Podocarpoxylon umzambense* (Schultze-Motel 1966) from the Upper Cretaceous of Pondoland, South Africa. This wood has an average tracheid diameter of 13-32µm, uniseriate bordered pits with a diameter of 11-16µm, uniseriate (occasionally biseriate) rays of 1-25 cells high and 1-2 pits per cross-field, 8x5-11x7µm. The Namaqualand shelf material has larger tracheids with larger pits but it is well known that cell sizes vary along the length of the living tree.

Mesembrioxylon cf. *stokesii* Thayn and Tidwell 1984.

Sample: BP/16/35
Locality: Namaqualand Shelf, reworked marine material.
Figures: 6-9
Others: BP/16/30, 65b, 71.

Description

The log is green-grey in colour, 6.5x3x3mm in size (length x radial diameter x tangential diameter) and has narrow growth rings of 1-1.5mm which are fairly regular. Under the microscope the late wood is only a few cells wide. Gum or resin deposits are numerous and randomly distributed.



Figures 2-5. *Podocarpoxylon* cf. *umzambense*, BP/16/244. **2**. TS. Very regular tracheids and prominent rays. Magn 30x. **3**. RLS. Tracheid pits rare but uniseriate and separate. Magn 270x. **4**. TLS. Poorly preserved rays of medium height. Magn 270x. **5**. RLS. Cross-field pits simple, ray walls thin and smooth. Magn 360x.

The tracheids have a very regular arrangement in transverse section, square to polygonal in outline, and the rays are not prominent (Figure 6). The average tangential diameter of the early wood tracheids is 49µm (range 34-60µm), average radial diameter of 48µm (range 40-59µm), and the late wood tangential diameter is 56µm (range 46-64µm), and radial diameter 23µm (range 17-32µm), (Figure 7). The bordered pitting on the radial walls of the tracheids is mostly uniseriate and occasionally biseriate and opposite (Figure 9), and the diameter of the pits is 16-19µm. The bordered pits are preserved as dark, solid circles and no apertures are visible. No bars of Sanio nor spiral thickenings were observed but there are occasional septa in the tracheids. In longitudinal section many of the tracheid and parenchyma cells have dark resinous contents.

Parenchyma is sparse and scattered, with smooth walls. The rays are uniseriate, high and often have two biseriate portions of around 10 cells at the ends of the rays (Figure 8). The average number of cells in a ray is 30 but they range from 2-47 cells high. The ray parenchyma cell walls are thin and smooth and end walls vertical to slightly oblique. The cross-field pits are small, simple with an average diameter of 8µm and there are 1-3 pits per field (Figure 5). There are no ray tracheids nor resin canals.

The three other woods placed in this species have the same tracheid and cross-field pitting and very high rays (BP/16/30, 11-45 cells; BP/16/65b, 7-55 cells; BP/16/71, 7-53 cells).

Identification

The abietinian tracheid pitting and simple cross-field pits place this specimen within the Podocarpaceae. In extant woods only a few species have very high rays (Phillips 1941) and they are rare in the fossil record. Ramanujam and Stewart (1969) and Ramanujam (1972) mentioned several fossil species but these ususally have biseriate to multiseriate rays. The multiseriate condition could be caused by damage or other traumatic conditions (Phillips 1941, Peirce 1936). The Namaqualand woods have very high uniseriate rays and these were unlikely to have been of traumatic origin.

Comparison

The wood shows some similarities with *Mesembrioxylon tiruvakkeraianum* (Ramanujam 1953, Agashe 1968) and *Mesembrioxylon stokesii* (Thayn and Tidwell 1984). *M. tiruvakkeraianum* has sparse, resinous parenchyma, uniseriate, high rays (3-50 cells, average 18) and the cross-field pits are larger, 15-20µm. The tracheid bordered pits are 10µm in diameter, which are smaller than the Namaqualand specimen, and also occur on the tangential walls.

Mesembrioxylon stokesii has septate tracheids and these are also present in BP/16/35 and BP/16/71 but not as numerous. *M. stokesii* also has uniseriate, bordered pitting on the radial walls of the tracheids and they are usually separate but occasionally contiguous. The rays are on average 8-16 cells high (range 1-50). This species is very similar to the Namaqualand material, and is from the Lower Cretaceous Cedar Mountain formation of Utah and Colorado (Thayn and Tidwell 1984). *M. stokesii* and the Namaqualand specimens differ in that *M. stokesii* has small cross-field pits, 1-3 per field, as well as the larger single pits.

Mesembrioxylon cf. _sahnii_ Ramanujam 1953, Agashe 1968.

Sample: BP/16/57
Locality: Namaqualand Shelf, reworked marine
Figures: 10-13
Others: BP/16/41, 45, 61, 66.

Description

The log is 8x4x4cm, black and green and well rounded from transportation. The growth rings are indistinct and there are only a few rows of late wood tracheids (Figure 10). The average tangential diameter of the early wood tracheids is 50µm (range 35-62µm), average radial diameter is 58µm (range 40-71µm). The average tangential diameter of the late wood tracheids is 44µm (range 24-59µm) and average radial diameter is 30µm (range 24-40µm). Bordered pits (24x20µm) occur on the radial walls only (Figure 11) and are uniseriate and contiguous, very occasionally biseriate and opposite and with bars of Sanio.

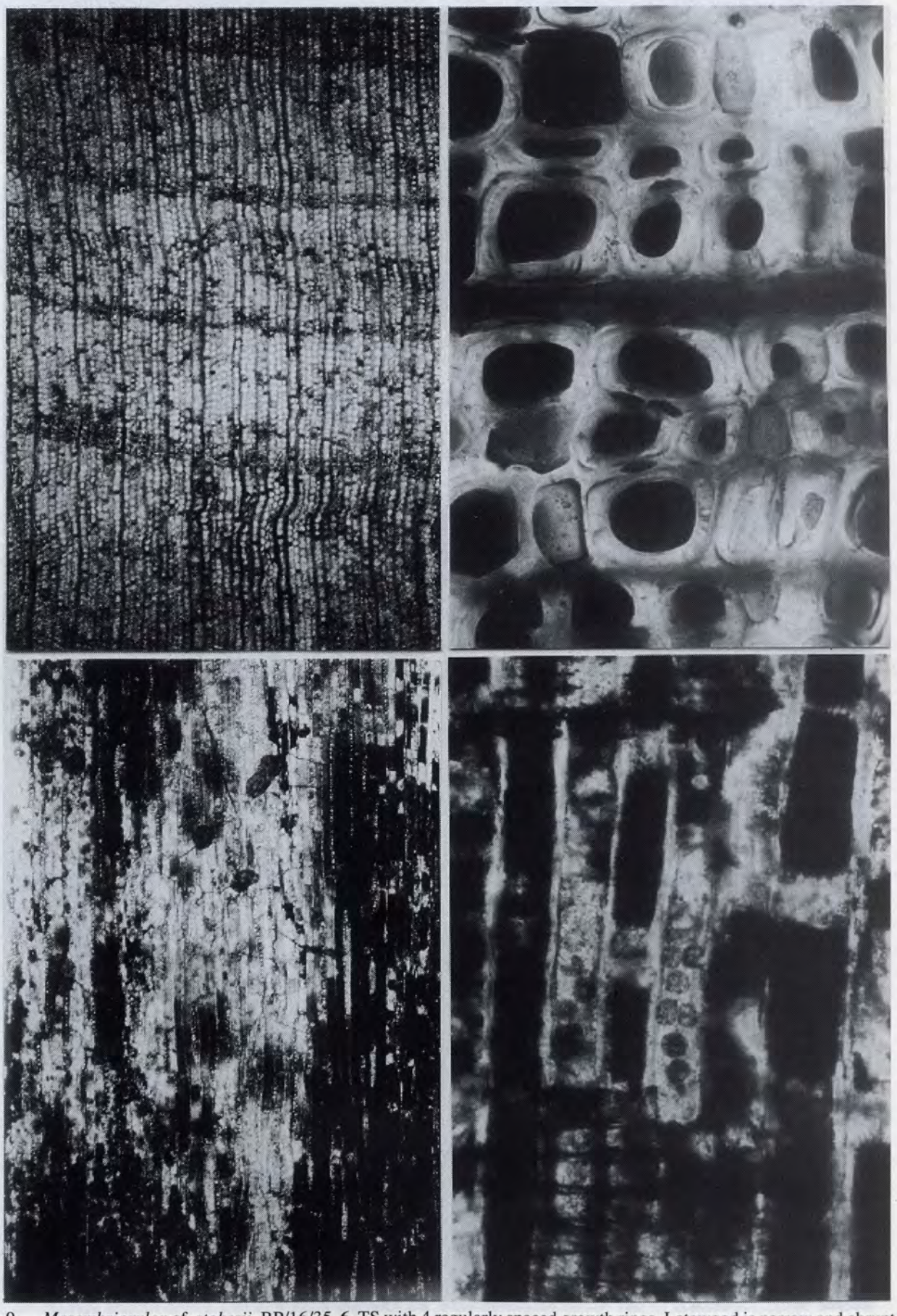
There are numerous resin-filled parenchyma cells scattered throughout the wood. The rays (Figure 12) are uni- to biseriate and on average 15 cells high (range 3-30). The biseriate portions of the rays are only one third of the height of the ray. Ray parenchyma cell walls are thin and smooth. The cross-field pits (Figure 13) are single, large and simple but are elliptic in shape with pointed ends (i.e. fusiform). The long axis is 18µm and the short axis 11µm. Some pits appear more rounded and have a diameter of 16µm. No ray tracheids nor resin canals are present.

Identification

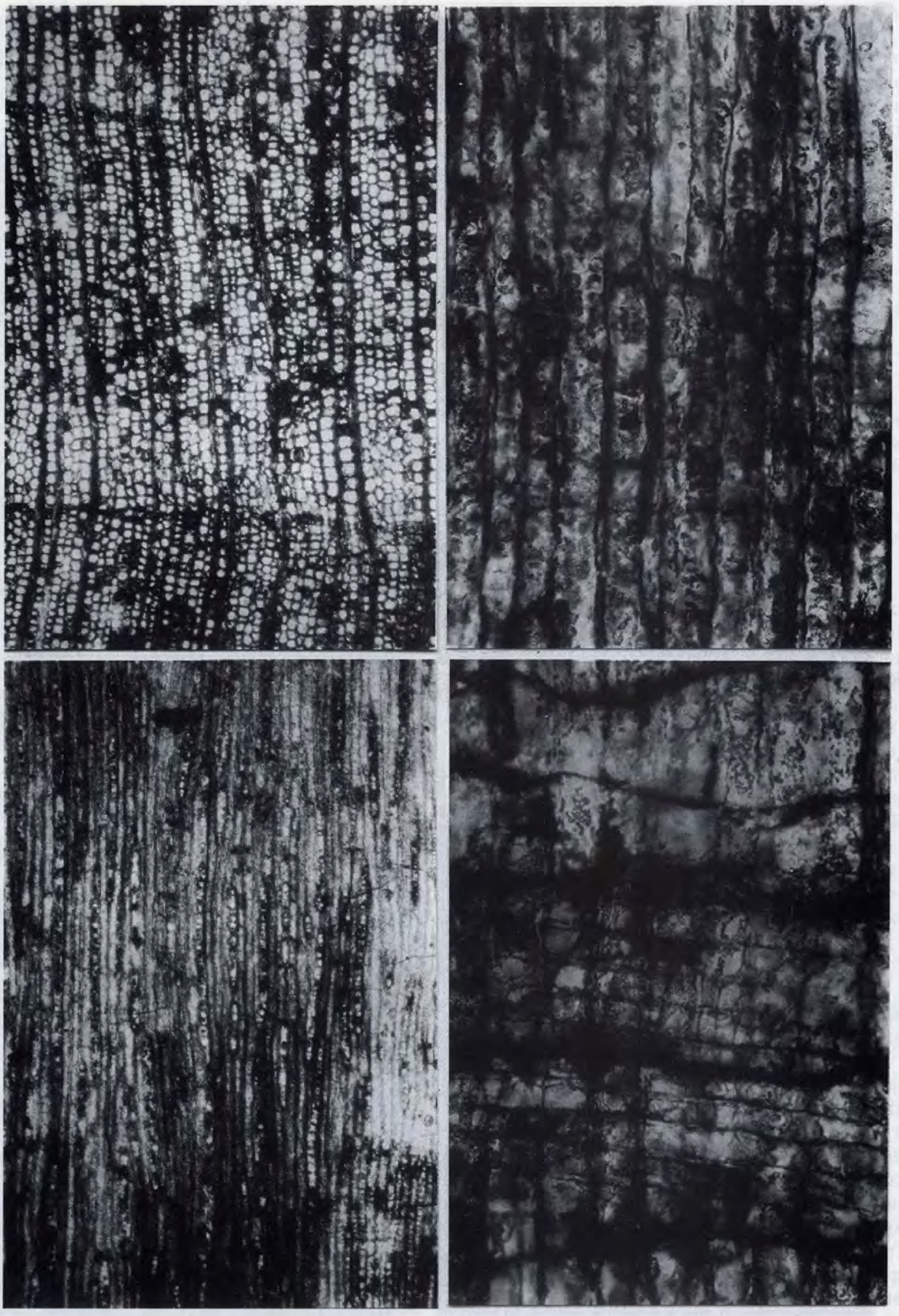
This wood belongs to the Podocarpaceae because it has the large phyllocladoid cross-field pits and abietinian tracheid pitting. Vogellehner (1967, 1968) distinguished between the cross-field pits to an even greater extent than Gothan (1905): large, oval pits with pointed ends as opposed to rounded ends. This specimen has mostly pointed ends with rare rounded ends and that seems to be an artifact of preservation. According to Vogellehner (1968, p. 140) the fusiform (pointed ends) pits would be placed on in *Phyllocladoxylon* and the oval (rounded ends) pits in *Circoporoxylon*. This wood certainly does not have the very rounded pits of the *Circoporoxylon* species described by Krausel and Jain (1963).

Comparison

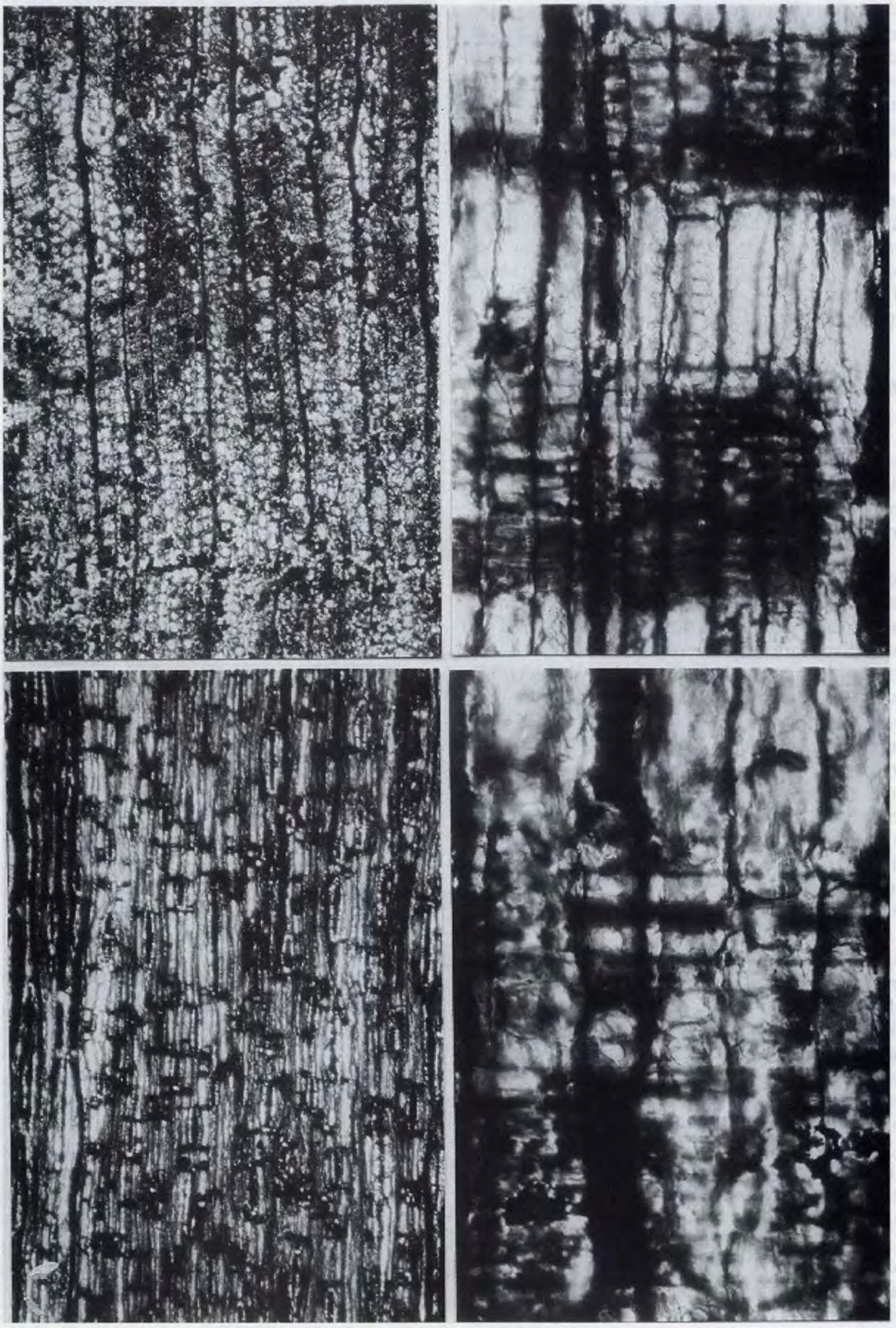
The Namaqualand Shelf wood is very similar to *Mesembrioxylon sahnii* (Ramanujam 1953, Agashe



Figures 6-9. *Mesembrioxylon* cf. *stokesii*, BP/16/35. **6.** TS with 4 regularly spaced growth rings. Latewood is narrow and abrupt. Magn 33x. **7.** TS at a higher magnification to show the tracheid walls, resin contents and the bordered pits between adjacent cells. The left side shows earlywood and the right shows latewood radially compressed cells. Magn 420x. **8.** TLS showing high rays (i.e. more than 30 cells), mostly uniseriate but occasionally biseriate. Some tracheids and parenchyma cells have resinous contents. Magn 42x. **9.** Tracheid bordered pits are single or paired and opposite (abietinian). The cross-field pits are small, simple and 1-3 per field. Magn 270x.



Figures 10-13. *Mesembrioxylon* cf. *sahnii*, BP/16/57. **10.** TS showing the regular and square tracheids and two growth rings with only 2-3 rows of latewood. Magn 42x. **11.** RLS. Tracheid pitting is uniseriate, and where biseriate the pits are opposite or subopposite and round, i.e. not flattened and alternate as in araucarioid pitting. Magn 270x. **12.** TLS. Rays are mostly uniseriate but some have biseriate portions. The axial parenchyma is resinous. Magn 170x. **13.** RLS. Cross-field pits are simple, oval (fusiform) with the long axis oblique. Magn 420x.



Figures 14-17. *Mesembrioxylon* cf. *woburnense*, BP/16/46. **14.** TS showing prominant rays and faint growth rings at the top and bottom of the photograph. Magn 42x. **15.** RLS showing faint bordered pitting on the tracheids, uniseriate, contiguous and very slightly flattened. Magn 170x. **16.** TLS with uniseriate rays and resin plugs which are the dark, horizontal bands opposite the tops and bottoms of rays. Magn 42x. **17.** RLS. The cross-field pits are large, simple and oblique. Magn 420x.

1968) which has uniseriate, occasionally biseriate and opposite tracheid pits which are contiguous but not flattened. Both woods have the elliptic and oblique cross-field pits with pointed ends. In the Indian wood these pits are much the same size, 15-20mm, and in this wood they are 18x11mm long. The rays of the Indian wood are a bit shorter, 1-20 cells high, mostly 8 cells. The postulated age of the Indian wood is Upper Miocene to Pliocene.

Another wood which has very similar cross-field pits is *Mesembrioxylon fusiforme* Sahni (1920) from the Jurassic or Tertiary of Queensland, Australia. *M. fusiforme* has 1-4 pits per field (no size or magnification is given), and it has low rays (3-5-10 cells).

Mesembrioxylon cf. _woburnense_ (Stopes) Seward 1919.

Sample: BP/16/46
Locality: Namaqualand Shelf, reworked marine.
Figures: 14-17.
Others: BP/16/31, 37, 38, 58, 62, 70.

Description

The log is beige and green in colour and 7x2x3cm in size. Growth rings occur as shear or crush zones and so the latewood appears very narrow.

The tracheids are rounded or occasionally squarish and thin walled in transverse section (Figure 14). The average tangential diameter of the early wood tracheids is 59µm (range 48-72µm) and average radial diameter is 63µm (range 51-80µm). The latewood has up to 6 rows of cells and the average tangential diameter is 52µm (range 46-64µm). The average radial diameter of the late wood is 20µm (range 17-27µm). Bordered tracheid pits occur on the radial walls only (Figure 15) and are uniseriate and contiguous and slightly flattened with the line of contact appearing darker. Occasionally the pits are biseriate and opposite. The diameter of the pits is 1µm.

Parenchyma is scattered and resinous. In longitudinal section numerous resin plugs are visible in the tracheids and parenchyma, frequently in line with the top and bottom of each of the rays (Figure 16). The rays are uniseriate and very rarely have low biseriate portions. Whole rays are 9-35 cells high, mostly 15 cells. Ray parenchyma cell walls are thin and smooth. The cross-field pits (Figure 17) are simple, single or paired, round to oval and 18-24µm in diameter. Neither ray tracheids nor resin canals are present.

Identification

The abietinian tracheid pitting and 1-2, large, simple cross-field pits place this wood in the Podocarpaceae. It differs from *Mesembrioxylon* cf. *stokesii* described here, in having much lower rays with less frequent biseriate portions and larger cross-field pits.

Comparison

This wood is most similar to *Mesembrioxylon woburnense* (Stopes 1915: *Podocarpoxylon woburnense*, Seward 1919: *Mesembrioxylon woburnense*) from the Aptian of Bedfordshire, England. The English wood has similar shaped cross-field pits which are 9-15mm in size; the rays are 1-40 cells high, uni- to occasionally biseriate and the tracheid pits are mostly uniseriate, sometimes paired and opposite. Crassulae are reported in the English wood but do not occur in the Namaqualand wood.

***Mesembrioxylon* sp.**

Sample: BP/16/54
Locality: Namaqualand Shelf, reworked marine.
Figures: 18-21
Others: 24 specimens.

Description

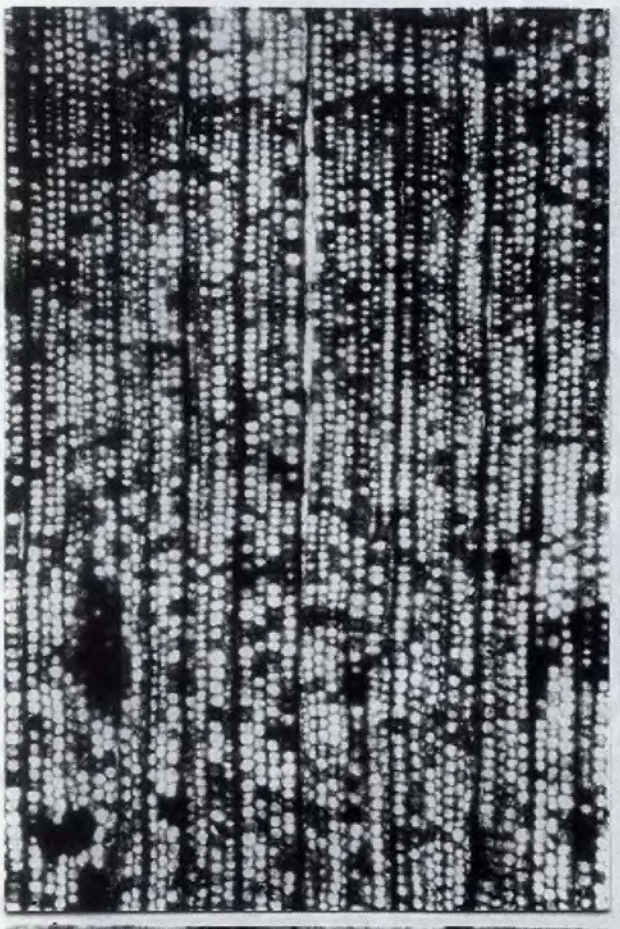
The log is grey and white and is 7x1.5x1.5cm. The growth rings are indistinct and variable, and the tracheids have a very regular distribution in transverse section (Figure 18). They are square to polygonal in outline. The average tangential diameter of the early wood is 53mm (range 40-64mm) and the average radial diameter is 51mm (range 40-62mm). The late wood forms only 2-3 rows and the average tangential diameter of the tracheids is 50mm (range 43-59mm); the average radial diameter is 31mm (range 25-39mm). The radial pits are uniseriate, contiguous and 17-18mm (Figure 19). Resin occurs in the tracheids and the parenchyma.

Parenchyma is sparse but occasionally columns of the horizontal walls are seen in TLS (Figure 20). The rays are uniseriate, with rare biseriate portions of 4-5 cells. Ray height is 5-34 cells with an average of 10 cells. The ray cell walls are thin and unpitted and the endwalls vertical or slightly oblique. Cross-field pits are not preserved (Figure 21). Neither spiral thickening nor resin canals are present.

Identification

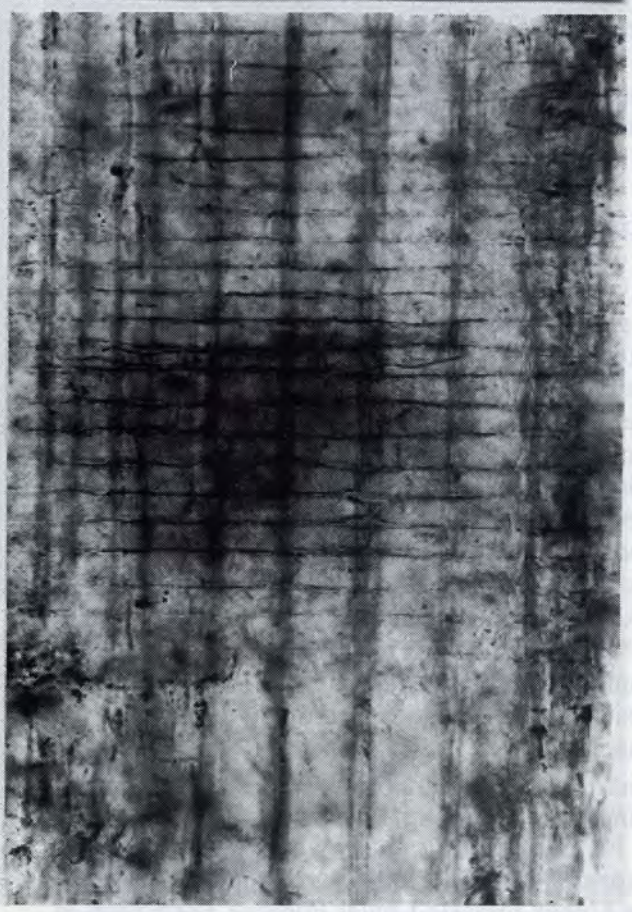
All the specimens of wood in this section have the abietinian tracheid pitting and rays of medium height with thin, unpitted walls which belong to the Podocarpaceae, but without preserved cross-field pits they cannot be placed in any species. We have, therefore, placed them in the artificial genus Mesembrioxylon (Seward 1919) which has a variety of cross-field pits depending on the interpretation of author. These specimens may well fit into the species described above, and others too, but the preserved features give no indication of which genus or species. The exception is BP/16/30 which has the very high rays characteristic of *Mesembrioxylon* cf. *stokesii*.

These woods have been added to the recently established database at the Bernard Price Institute for Palaeontological Research, Johannesburg, as even if incompletely identified, their occurrence, is important for the distribution of these wood types.









Figures 18-21. *Mesembrioxylon sp.* BP/16/54. **18.** TS. A growth ring is visible at the top, with narrow latewood. Magn 42x. **19.** RLS. The bordered pits on the tracheids are uniseriate, contiguous and slightly squashed, with small apertures. Magn 270x. **20.** Uniseriate rays with occasional biseriate portions. Magn 170x. **21.** RLS. The ray parenchyma walls are thin and smooth, as in all the other specimens. The end walls are vertical to oblique and also smooth. The cross-field pits are not preserved. Magn 270x.

Cheirolepidiaceae

Protocupressinoxylon cf. *purbeckensis* Francis 1983.

Sample: BP/16/238
Locality: Namaqualand shelf.
Figures: 22-25

Description

The specimen is a small pebble with a 20mm diameter, and was probably a branch. Seven growth rings were preserved of uneven diameter but with an average of 1.3mm.

The tracheids are thin walled and were probably regularly arranged before the slight distortion during preservation (Figure 22). The early wood tracheid tangential diameter has an average of 18µm (range 10-25µm), and average radial diameter of 17µm (range 13-24µm). The latewood is very narrow and squashed with 3-8 rows of cells. The average tangential diameter is 18µm (range 14-24µm) and average radial diameter is 10µm (range 6-16µm) for the late wood tracheids. Wall thickness (two adjacent cells) is 7µm. The tracheid bordered pitting (Figure 23) is on the radial walls only, and is uniseriate, separate or contiguous, never compressed as in araucarian pitting. The diameter of the pits is 13-16µm.

Axial parenchyma is absent. The rays are uniseriate and very low (Figure 24), average number of cells is 2-5, (range 1-6). The ray cell walls are much thinner than the tracheid walls and smooth. The cross-field pits are cupressoid, 2-7 per field and arranged in two horizontal rows. The pit diameter is 6-8µm and the pore oblique and 3µm in diameter (Figure 25).

Identification

The cross-field pits are cupressoid, vertical parenchyma is absent but resiniferous tracheids are present and resin also occurs in the ray cells which are all features of the Cheirolepidiaceae. The only discrepancy is in the tracheid pitting. The members of Cheirolepidiaceae have uni- and biseriate pitting but this specimen is a small branch with relatively narrow tracheids and no biseriate pitting is found. It is most like *Protocupressinoxylon*. This genus has biseriate and opposite tracheid pitting. The Namaqualand wood is also similar to several species of *Cupressinoxylon* except for the absence of parenchyma. Parenchyma and various wall ornamentations, such as pits or nodules, are common features of extant members (Peirce 1937) and fossil members (Vaudois and Prive 1971) of the Cupressaclal.

Comparison

The Namaqualand shelf wood is similar to *Protocupressinoxylon purbeckensis* (Francis 1983) from the Upper Jurassic Lower Purbeck Formation of Dorset, England. *P. purbeckensis* has an average tracheid diameter of 47µm, uniseriate (rarely opposite) bordered pits, diameter 17µm. The rays are uniseriate with an average height of 3 cells (range 2-9), with thin, smooth walls. There are 2-7 small cupressoid pits per cross-field with a diameter of 7-µm and the apertures inclined at 45°. The wood described here has no biseriate pitting and so is called *Protocupressinoxylon* cf. *purbeckensis*.

DISCUSSION

Deposition

The fossil wood specimens show no evidence of degeneration from biotic factors such as bacteria, fungi or boring insects. This suggests that burial of the wood occurred shortly after deposition on the continental margin. In view of the good preservation and age of the fossil wood, initial burial must have occurred during the late Early Cretaceous, when sedimentation rates along the west coast of southern Africa were particularly high (Dingle *et al.* 1983), which resulted in the depositon of a large Cretaceous wedge of sediment as the continental shelf prograded to the west. The silicification of the wood probably also occurred post-depositionally during the Cretaceous. It is not known whether the wood was deposited in close proximity to a Cretaceous palaeoshoreline or not. The examination of the Cretaceous deposits exposed on the continental shelf suggests that the wood is more likely to have been deposited in continental clastic sequences which were probably sand and gravel dominated.

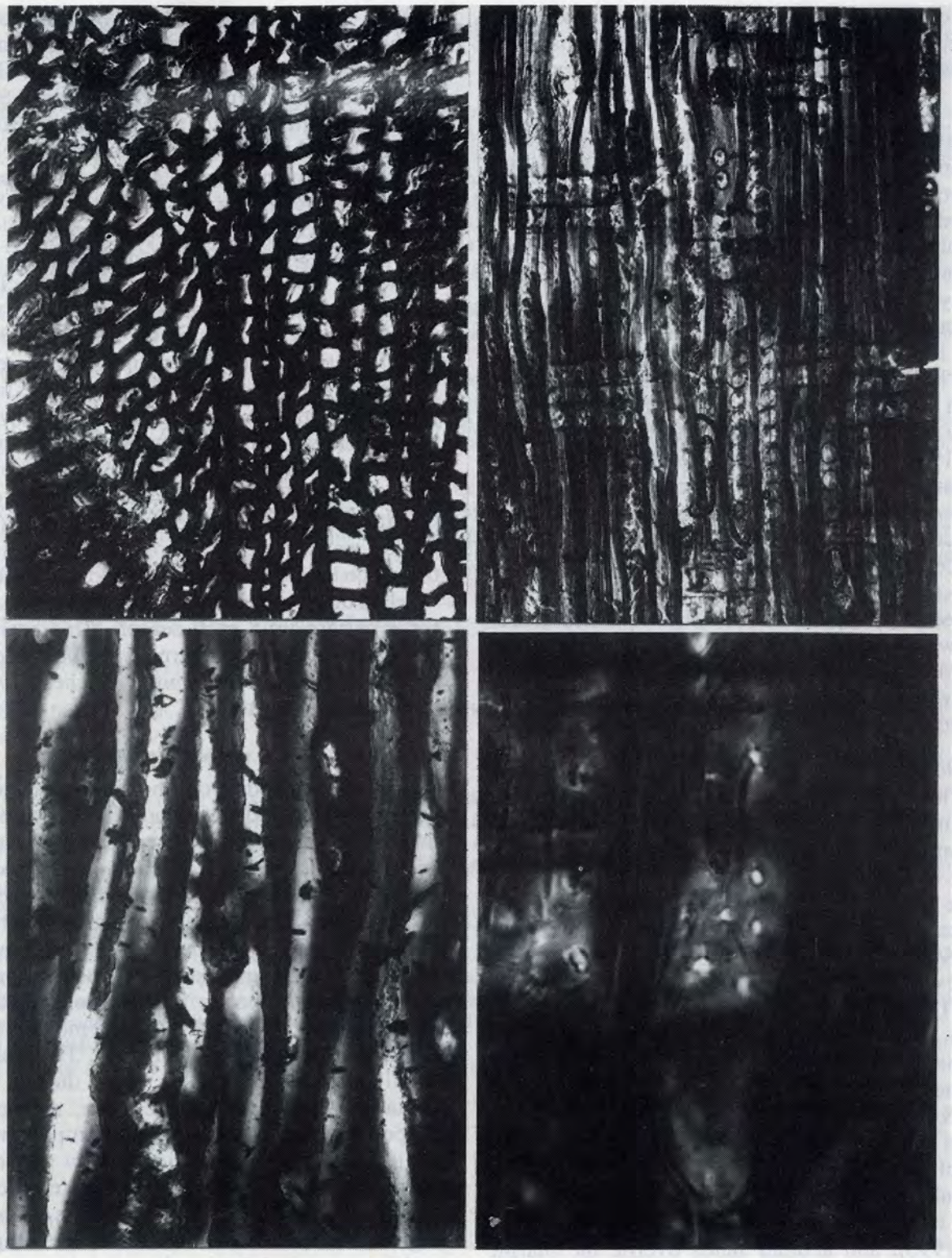
Rapid burial and silicification of the wood probably reduced compression during burial, which was possibly further reduced by burial of the wood in sand-dominated rather than mud-dominated clastic sequences (Ward pers. comm.).

Many of the specimens of fossil wood described in this report have been recovered from the portion of the Namaqualand continental shelf that is floored by Cretaceous sediments (Figure 1) which were overlain by a thin marine Late Pleistocene to Late Holocene sequence. The fossil wood has probably been derived by the erosion of late Early Cretaceous and Late Cretaceous continental clastic sequences on the shelf during later marine transgressions and regressions which have removed and reworked the entire Palaeogene and Neogene section across much of the inner and middle shelf. The last trangressive event resulted in the incorpation of the wood in to the marine Late Pleistocene sequence during the Last Glacial.

Diversity

It is interesting that relatively few wood types represented here occur over such a large area. Forests with a low diversity are fairly common in the fossil record, for example *Protocupressinoxylon purbeckensis* is the dominant conifer in the Jurassic Purbeck formation, England (Francis 1983) and *Araucarioxylon arizonicum* is dominant in the Chinle formation (Upper Triassic) in Arizona (Ash & Creber 1992).

The fossil wood distribution across the continental shelf does not appear to be uniform (Figure 1), however, this is partly due to the method of sampling, together with subsequent changes in the lateral extent



Figures 22-25. *Protocupressinoxylon* cf. *purbeckensis*, BP/16/238. **22.** TS. Rectangular tracheids distorted after preservation. Magn 360x. **23.** RLS. Uniseriate tracheid pitting, not squashed. Magn 270x. **24.** TLS. Low rays. Magn 360x. **25.** RLS. Cupressoid cross-field pits. Magn 1000x.

of the Cretaceous sequences which contain wood, and the extent of erosion which has occurred across the continental shelf. The distribution (Figure 1) is therefore unlikely to reflect the actual distribution of the living wood.

The woods are very similar to each other in structure but the preservation varies considerably, in both the quality and the mineral content, which means that different areas of deposition had different minerals in solution. (Here an "area" could be only metres or kilometres apart).

The homogeniety of the wood, nonetheless, implies that the flora, as far as the trees were concerned, had a low diversity, and probably the coniferous forests covered fairly large areas. The understorey vegetation is unknown and would depend to a large extent on the

amount of light reaching the forest floor and water availability. As some of the wood has been transported there is no knowing how dense this conifer "forest" was.

Age

The taxonomic status of the early coniferous woods is problematic and changes frequently. Nonetheless the wood's characters do not. These woods have been compared with both northern and southern hemisphere woods and have been found closest to the Lower Cretaceous woods. *Mesembrioxylon* cf. *stokesii* is obviously comparable with *M. stokesii* of the Lower Cretaceous Cedar Mountain formation (Thayn and Tidwell 1984). *M. woburnense* is from the Aptian deposits in Bedfordshire (Seward 1919). *M.* cf. *sahnii* has been compared with *M. sahnii* from the Upper Miocene to Pliocene of India (Ramanujam 1953, Agashe 1968) and with *M. fusiforme* from the Jurassic or Tertiary of Queensland, Australia (Sahni 1920). *Protocupressinoxylon* cf. *purbeckensis* is very similar to the Lower Jurassic *P. purbeckensis*, the only difference being the tracheid size and the absence of biseriate tracheid pitting in the very small piece of wood from Namaqualand. The Namaqualand woods also show some similarities with Tertiary Indian woods but it is most unlikely that the climate, anywhere along the west coast or inland during the Tertiary, could have supported the growth of these large diameter trees.

Palaeoclimate

Aridification of the west coastal belt most probably began during the Late Mesozoic when the opening of the Atlantic started from the south and the South Atlantic anticyclonic circulation system developed (Ward & Corbett 1990). Also the Namib would then have been on the rainshadow side of the subcontinent (Ward & Corbett 1990). Offshore sedimentation followed during the middle and Late Cretaceous in the Orange, Luderitz and Walvis basins, and this is when the logs may have been washed out to sea. The sediments laid down during the Tertiary, the Tsondab sandstones, were formed under desert conditions (Ward & Corbett 1990). The Tsondab sandstone outcrops are in the central Namib. The Lower Rooilepel sandstone to the east of Oranjemund, on the north bank of the Orange River, is Lower Miocene or possibly older according to Pickford and Senut (pers. comm. 1993), and aeolian sands overlie the marine sequence preserved at Buntfeldschuh in southern Namibia. These are tentatively dated as Late Palaeocene to Early Eocene.

Extant members of the Podocarpaceae occupy mainly tropical montane regions yet the ancestral members occurred in low-lying plains (Duperon-Laudoueneix & Pons 1985). The West Coast "forests" probably also occupied the low-lying plains. The Cheirolepidiaceae from all over the world occupied a variety of climatic regimes but they show evidence of tolerating some drought (Vakhrameev 1970). Francis (1983, 1984) described *Protocupressinoxylon purbeckensis* as a large, shallow-rooted, monopodial tree forming a closed canopy forest alongside a hypersaline lagoon in England. It probably experienced a winter rainfall and arid summer climate. The Namaqualand *P.* cf. *purbeckensis* most probably grew in the low-lying coastal plains and experienced a strongly seasonal climate.

The growth rings which are present in all the specimens vary in width from 0.5mm to 11mm and show that the wood grew in a seasonal climate. The variability has no real meaning in such a widespread collection of wood because the trees could have grown in different areas, at different times and therefore do not indicate any particular local climate. The large size of the trees, over 1m in diameter, and the width of the growth rings, indicate a good growth regime. The growing season is represented by the large amount of earlywood and this may well have been quite rapid because there are frequent shear zones (large, thin walled cells which collapse under pressure). The transition to latewood is abrupt and very little latewood was laid down which means that growth was suspended for a certain time each season. This seems to be a common feature of southern hemisphere trees, whereas the northern hemisphere pines, larches, firs, etc. have large regions of latewood.

CONCLUSION

The fossil woods from the Namaqualand Shelf are predominantly podocarpaceous and have been placed in five taxa. The rest have been lumped into an artificial genus only because the crucial features have not been preserved. These specimens are still podocarpaceous. Modern Podocarpaceae have a distribution restricted to the southern hemisphere, but were much more widespread during Palaeozoic and Mesozoic times. One specimen belongs to the Cheirolepidiaceae, an extinct family of conifers, some members of which could tolerate periods of drought. The Namaqualand fossil trees most probably grew during the Lower Cretaceous, in a seasonal climate, and growth was suspended when water and/or temperature became limiting. Burial and silicification most probably occurred during the mid and Late Cretaceous erosion phase. Subsequent marine transgressions and regressions have resulted in the woods being reworked and incorporated into sediments deposited on Late Pleistocene palaeoshorelines.

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LIST OF ABBREVIATIONS

BP/16/ – Bernard Price Institute, Johannesburg fossil wood collection.

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PERMIAN PALYNOMORPHS FROM THE NUMBER 5 SEAM, ECCA GROUP, WITBANK/HIGHVELD COALFIELDS, SOUTH AFRICA.

by

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ABSTRACT

A palynological study of the number 5 seam in the Ecca group has yielded a wide variety of miospores, with a lateral and vertical consistency in their relative abundance, diversity and composition. Striate bisaccate pollen genera predominate, particularly *Protohaploxypinus* Samoilovich *emend.* Morbey 1975, *Striatopodocarpites* Zoricheva & Sedova *ex* Sedova *emend.* Hart 1964 and *Weylandites* Bharadwaj & Srivastava 1969. On a regional scale the number 5 seam palynomorphs correlate both quantitatively and qualitatively with Biozone F of MacRae (1988) from the Waterberg and Pafuri coal-bearing basins, and Hammanskraal plant locality. Broad palaeoenvironmental inferences drawn from both the palynology and sedimentology of this seam, support a flood plain setting, comprising shallow wide open pans and peat swamps interspersed with wide water-logged mud flats. The surrounding highlands would have been forested mostly by plants adapted to wind dispersal with colonisation of the levees and margins of small ponds by spore producers. The age of the number 5 seam is tentatively suggested as Guadalupian, which in turn is equated with the Tatarian (European Standard usage); Midian to Dzhulfian (Tethys usage).

KEY WORDS: Ecca, Karoo, Palynology, Permian, Biostratigraphy.

INTRODUCTION

The coalfields falling within the study area are part of the northern Karoo Basin and are situated approximately 100km to the east of Johannesburg (Figure 1). In this area a major depositional sequence of 120m is represented. This sedimentary package contains six bituminous coal seams and the sequence is underlain by diamictite of the Dwyka Group or pre-Karoo basement rocks. Coal seams are numbered 1-6 from the base. The No 6 seam is laterally impersistent and is rarely found in the Witbank and Highveld Coalfields.

PREVIOUS PALYNOLOGICAL INVESTIGATIONS

To date the only published palynological work on the number 5 seam in the Witbank and Highveld Coalfields has been that of Falcon *et al.* (1984), who documented the qualitative/quantitative characteristics of samples from five main seams (1-5) at Greenside Colliery. Palynological comparisons of these seams were made using a palynobiostratigraphic type sequence from Zimbabwe (Falcon 1975, 1978).

MATERIALS AND METHODS

The number 5 seam in the Witbank/Highveld Coalfields varies in thickness laterally, but generally averages about 2.5 metres. For the present study four mine sites were investigated, namely Matla, Khutala, Greenside and Rietspruit.

Twenty to thirty samples, each weighing ± 500 grams, were collected from a number of sites at each mine. Extraction of the palynomorphs from the samples was carried out using a routine process developed at the U.S Geological Survey (Dohler 1980). This process enabled the rapid maceration of a wide variety of lithotypes, and individual steps were carried out according to the characteristics of each of the samples.

Visual counts of a minimum of 250 and maximum of 500 miospore specimens were undertaken. The relative abundance of species involved absolute counts within the first 250-500 and the supra-generic analysis comprised of these initial 250-500 miospores.

GEOLOGY

The Karoo Basin of South Africa contains the subcontinent's most complete geological record of late Palaeozoic to early Mesozoic 'Gondwanan' sediments (Le Blanc Smith 1980). This asymmetrically filled basin represents a depository formed between the Cape Fold Belt to the south and the Kaapvaal Craton to the north.

In 1980 the South African Committee for Stratigraphy introduced a formal lithostratigraphic nomenclature for the Northern Karoo Sequence, which replaced the Lower, Middle and Upper subdivisions of the Ecca Group with the Pietermaritzburg Shale Formation, the Vryheid Formation, and the Volksrust Shale Formation, respectively (Figure 2).

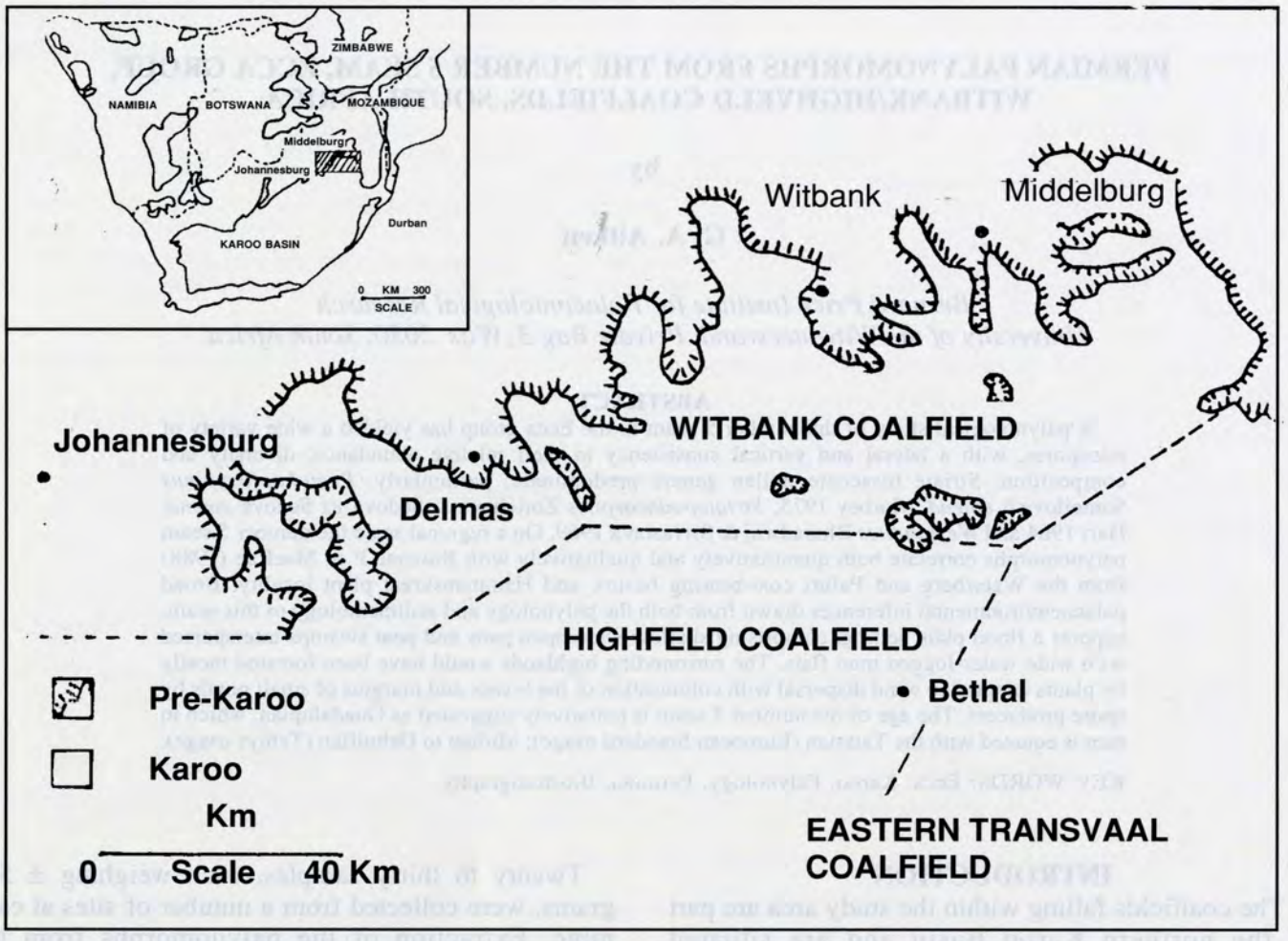


Figure 1. Geological map illustrating the location of the Witbank/Highveld Coalfields (adapted from Cairncross, 1986)

Coal seams in the Witbank and Highveld Coalfields are situated in the Vryheid Formation which conformably overlies the glaciogenic Dwyka Group or unconformably overlies pre-Karoo rocks. The rocks of the Karoo Sequence in the study area are represented only by the Dwyka Group and the Vryheid Formation. This is due to the northern pinch out of the Pietermaritzburg Shale Formation and the removal through erosion of the Volksrust Formation. The Dwyka Group comprises diamictites, mudrocks and sandstones, while the Vryheid Formation is dominated by grey mudrocks, sandstones and coal seams.

LITHOSTRATIGRAPHY	GENETIC STRATIGRAPHY
VOLKSRUST FORMATION	ABSENT THROUGH EROSION
VRYHEID FORMATION	6 SEAM GENETIC SEQUENCE
	5 SEAM GENETIC SEQUENCE
	4 SEAM GENETIC SEQUENCE
	2 SEAM GENETIC SEQUENCE
PIETERMARITZBURG SHALE FORMATION	ABSENT THROUGH EROSION
DWYKA GROUP	

Figure 2. Diagram illustrating the sub-division of the Vryheid Formation into informal genetic sequences (adapted from Winter, Cairncross & Cadle, 1987).

The regional stratigraphy in the northern Highveld Coalfield is essentially similar to that of the Vryheid Formation in the adjacent central Witbank Coalfield (Le Blanc Smith 1980). Cairncross and Cadle (1987) subdivided the Vryheid Formation into 6 informal Genetic Sequences which are each terminated by coal seams.

The 5 Seam Genetic Sequence comprises the interval of Karoo strata between the roof of the number 4 Upper Seam and the roof of the number 5 Seam. The number 5 Seam is laterally continuous over a large area and displays little variation in gross thickness and is characterised by negligible variations in litho-stratigraphic composition (Cairncross & Cadle 1987).

The 5 Seam Genetic Sequence is represented by a thin, laterally continuous, brown glauconitic interlaminated sandstone-siltstone, capped by a sporadically developed number 4 Local Seam and a white well-sorted, glauconitic sandstone. The number 4 Seam is overlain by an upward-coarsening succession comprising, from the base upwards, carbonaceous siltstone, lenticular-laminated siltstone, interlaminated sandstone-siltstone, flaser-laminated sandstone and cross laminated sandstone, capped by the laterally continuous, uniformly thick number 5 Seam (Winter, Cairncross & Cadle 1987).

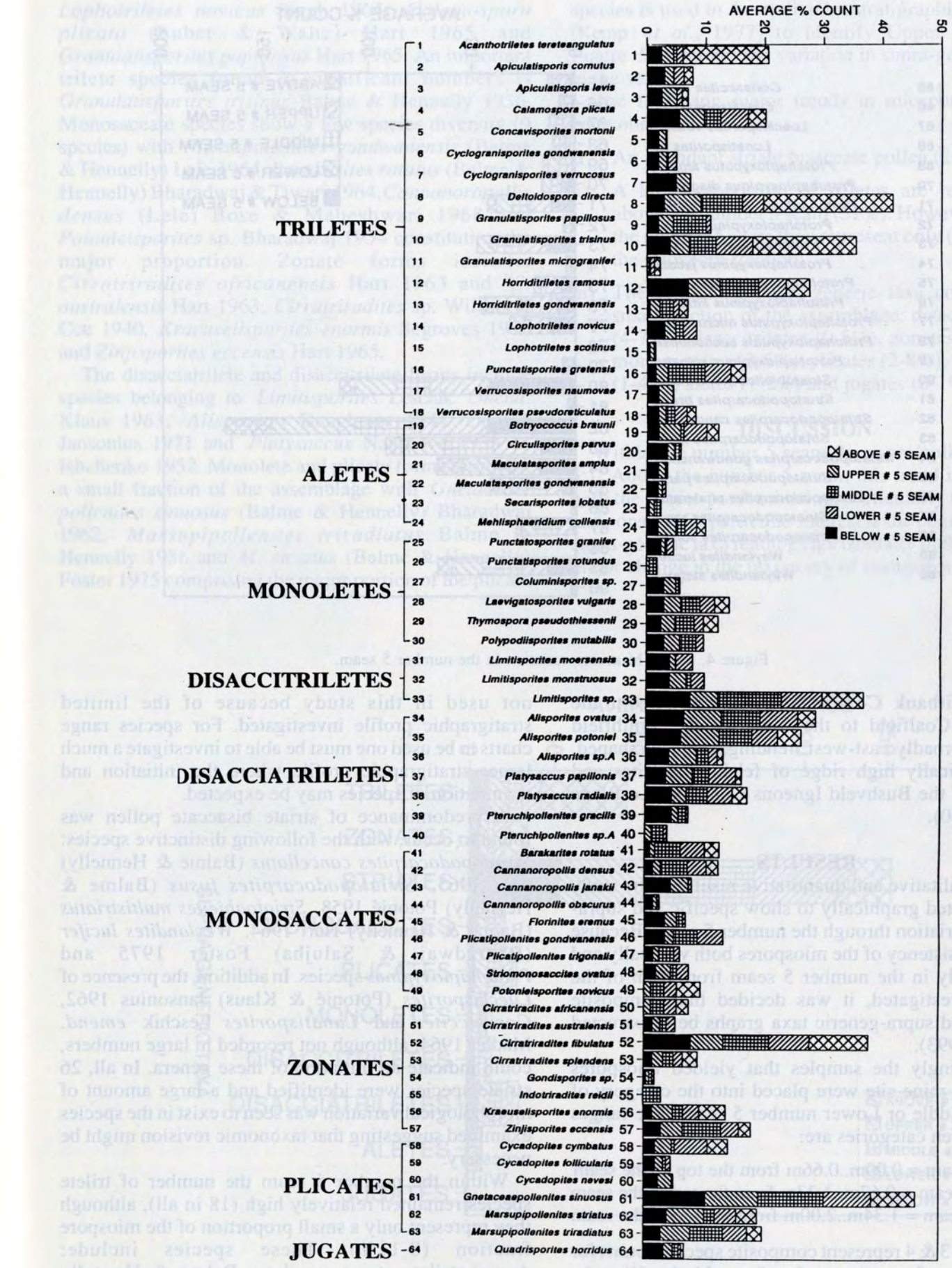


Figure 3. Species variation in the number 5 seam.

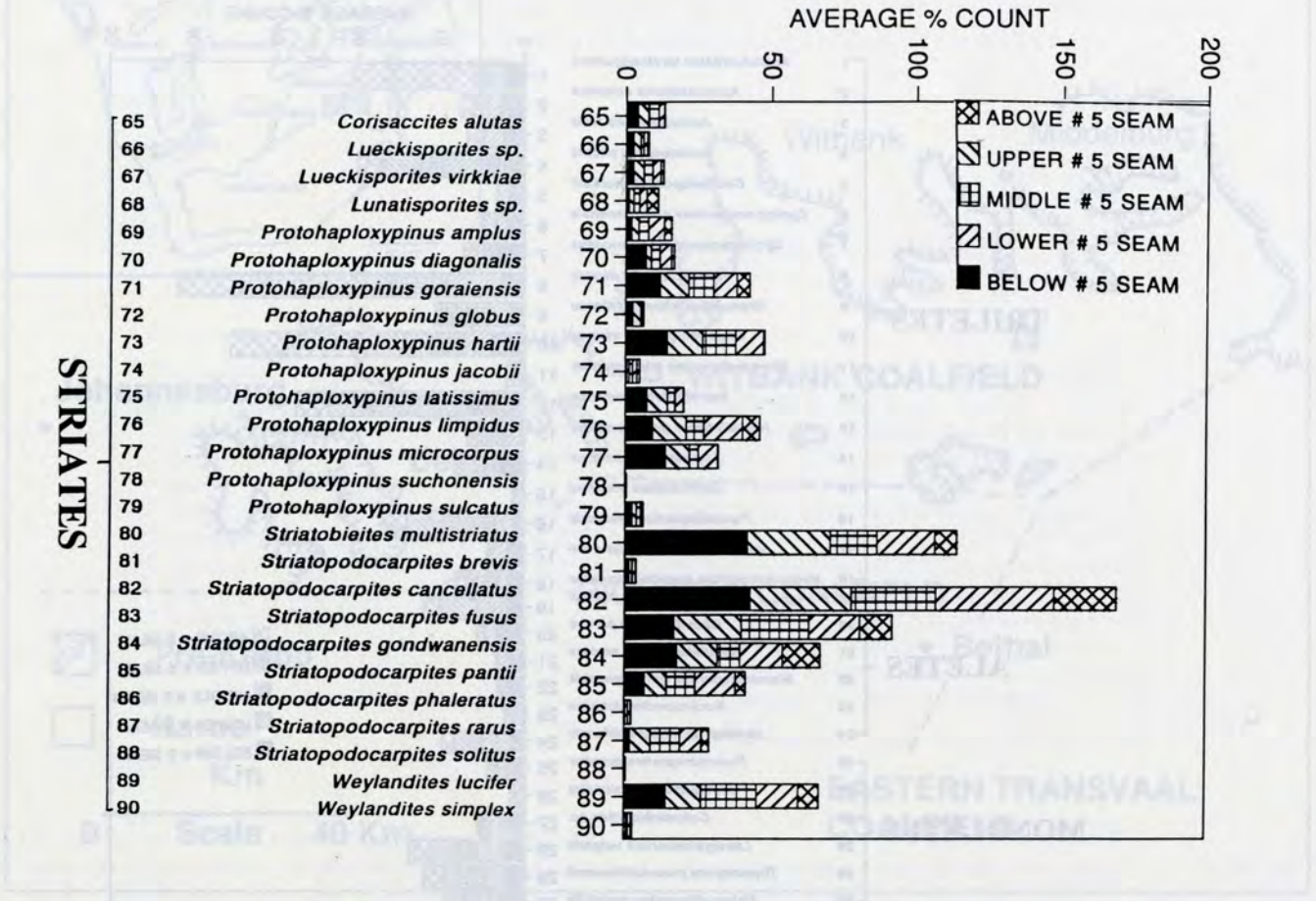


Figure 4. Striate bisaccate variation in the number 5 seam.

The Witbank Coalfield is separated from the Highveld Coalfield to the south by the Smithfield Ridge, a broadly east-west trending, crescent-shaped, topographically high ridge of felsites, granites and diabase of the Bushveld Igneous Complex (Le Blanc Smith 1980).

RESULTS

The qualitative and quantitative results of the study are presented graphically to show specific and supra-generic variation through the number 5 seam. Because of the consistency of the miospores both vertically and horizontally in the number 5 seam from each of the mines investigated, it was decided that composite species and supra-generic taxa graphs be constructed (Aitken 1993).

Accordingly the samples that yielded miospores from each mine site were placed into the category of Upper, Middle or Lower number 5 seam. The ranges for the given categories are:

Upper 5 seam = 0.00m..0.66m from the top of the seam
Middle 5 seam = 0.67m..1.33m from the top of the seam
Lower 5 seam = 1.34m..2.00m from the top of the seam

Figures 3 & 4 represent composite species counts for the number 5 seam samples from Matla, Khutala, Greenside and Rietspruit. Species range charts were not used in this study because of the limited stratigraphic profile investigated. For species range charts to be used one must be able to investigate a much larger stratigraphic profile where the initiation and termination of species may be expected.

A predominance of striate bisaccate pollen was found to occur, with the following distinctive species: *Striatopodocarpites cancellatus* (Balme & Hennelly) Hart 1965, *Striatopodocarpites fusus* (Balme & Hennelly) Potonié 1958, *Striatoabieites multistriatus* (Balme & Hennelly) Hart 1964, *Weylandites lucifer* (Bharadwaj & Salujha) Foster 1975 and *Protohaploxypinus* species. In addition, the presence of *Lueckisporites* (Potonié & Klaus) Jansonius 1962, *Corisaccites* and *Lunatisporites* Leschik *emend.* Madler 1964, although not recorded in large numbers, could indicate an initiation of these genera. In all, 26 striate species were identified and a large amount of morphological variation was seen to exist in the species examined suggesting that taxonomic revision might be necessary.

Within the number 5 seam the number of trilete species remained relatively high (18 in all), although they represent only a small proportion of the miospore fraction (8-11%). These species include: *Acanthotriletes tereteangulatus* Balme & Hennelly 1956, *Deltoidospora directa* (Balme & Hennelly) Norris 1965, *Apiculatisporis cornutus* (Balme &

Hennelly) Hoeg & Bose 1960, *Horriditriletes ramosus* (Balme & Hennelly) Bharadwaj & Salujha 1964, *Lophotriletes novicus* Singh 1964, *Calamospora plicata* (Luber & Waltz) Hart 1965 and *Granulatisporites papillosus* Hart 1965. An important trilete species found in significant numbers is *Granulatisporites trisinus* Balme & Hennelly 1956. Monosaccate species show a low species diversity (9 species) with *Plicatipollenites gondwanensis* (Balme & Hennelly) Lele 1964, *Barakarites rotatus* (Balme & Hennelly) Bharadwaj & Tiwari 1964, *Cannanoropollis densus* (Lele) Bose & Maheshwari 1968 and *Potonieisporites* sp. Bharadwaj 1954 constituting the major proportion. Zonate forms include: *Cirratriradites africanensis* Hart 1963 and *C. australensis* Hart 1963, *Cirratriradites* sp. Wilson & Coe 1940, *Kraeuselisporites enormis* Segroves 1970 and *Zinjisporites eccensis* Hart 1965.

The disacciatrilete and disaccitrilete forms include species belonging to *Limitisporites* Leschik *emend.* Klaus 1963, *Alisporites* Daugherty 1941 *emend.* Jansonius 1971 and *Platysaccus* Naumova 1939 ex Ishchenko 1952. Monolete and plicate forms represent a small fraction of the assemblage with *Gnetaceae-pollenites sinuosus* (Balme & Hennelly) Bharadwaj 1962, *Marsupipollenites triradiatus* Balme & Hennelly 1956 and *M. striatus* (Balme & Hennelly) Foster 1975 comprising the major portion of the plicate fraction. *Gnetaceaepollenites sinuosus* is found in relatively large numbers in the number 5 seam. This species is used in Australian biostratigraphic schemes (Kemp *et al.*, 1977) to identify Upper Stage 4a. Figure 5 illustrates the variation in supra-generic taxa in the seam.

The following major trends in miospore content were observed:

i) An abundant striate bisaccate pollen (26-61%);

ii) A large proportion of triletes are represented above the number 5 seam (51%). However, within the number 5 seam they represent only (8-12%) of the miospore fraction;

iii) The remaining supra-generic taxa constitute a small fraction of the assemblage, disacciatriletes (4-7%), disaccitriletes (0-5%), zonates (3-13%), monosaccates (2-6%), plicates (2-8%), monoletes (1-4%), aletes (1-2%) and jugates (0-1%).

DISCUSSION

Within the number 5 seam the spore/pollen ratio is 3:1. Above the number 5 seam, this trend is reversed with the spores predominating, particularly the triletes and zonates. Of particular interest is the consistency of supra-generic taxa readings horizontally in the seam. A major change in the taxonomy of miospores is evident

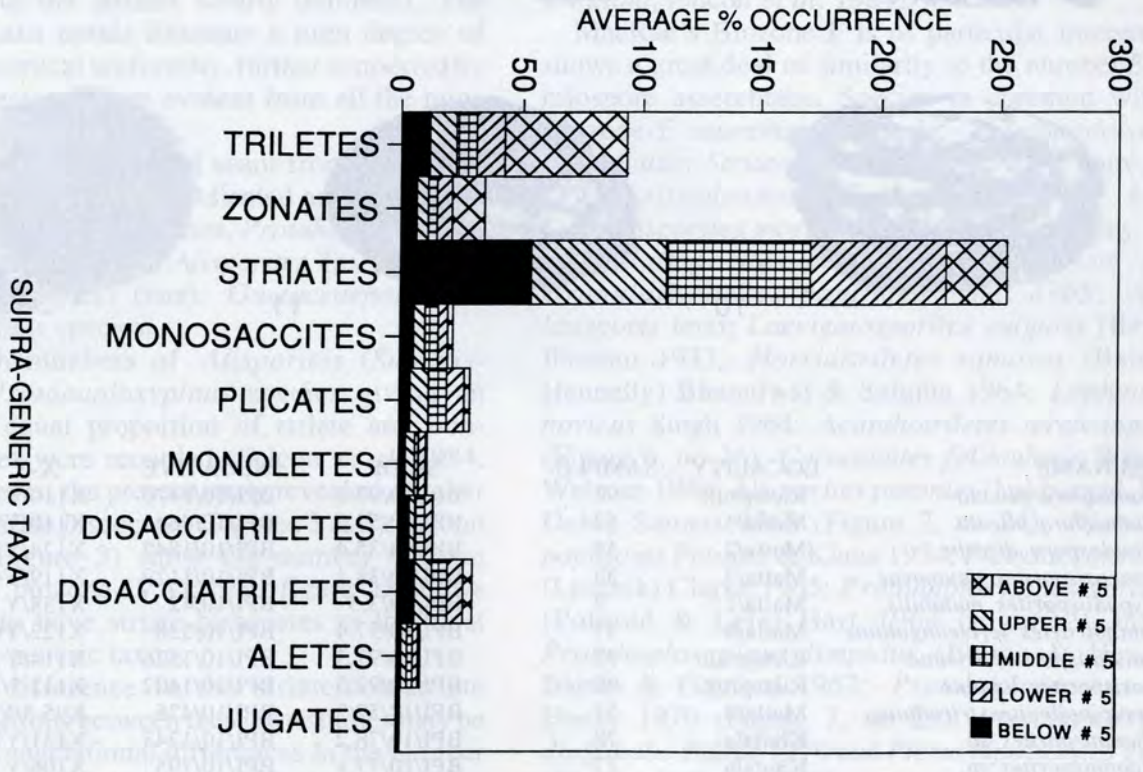
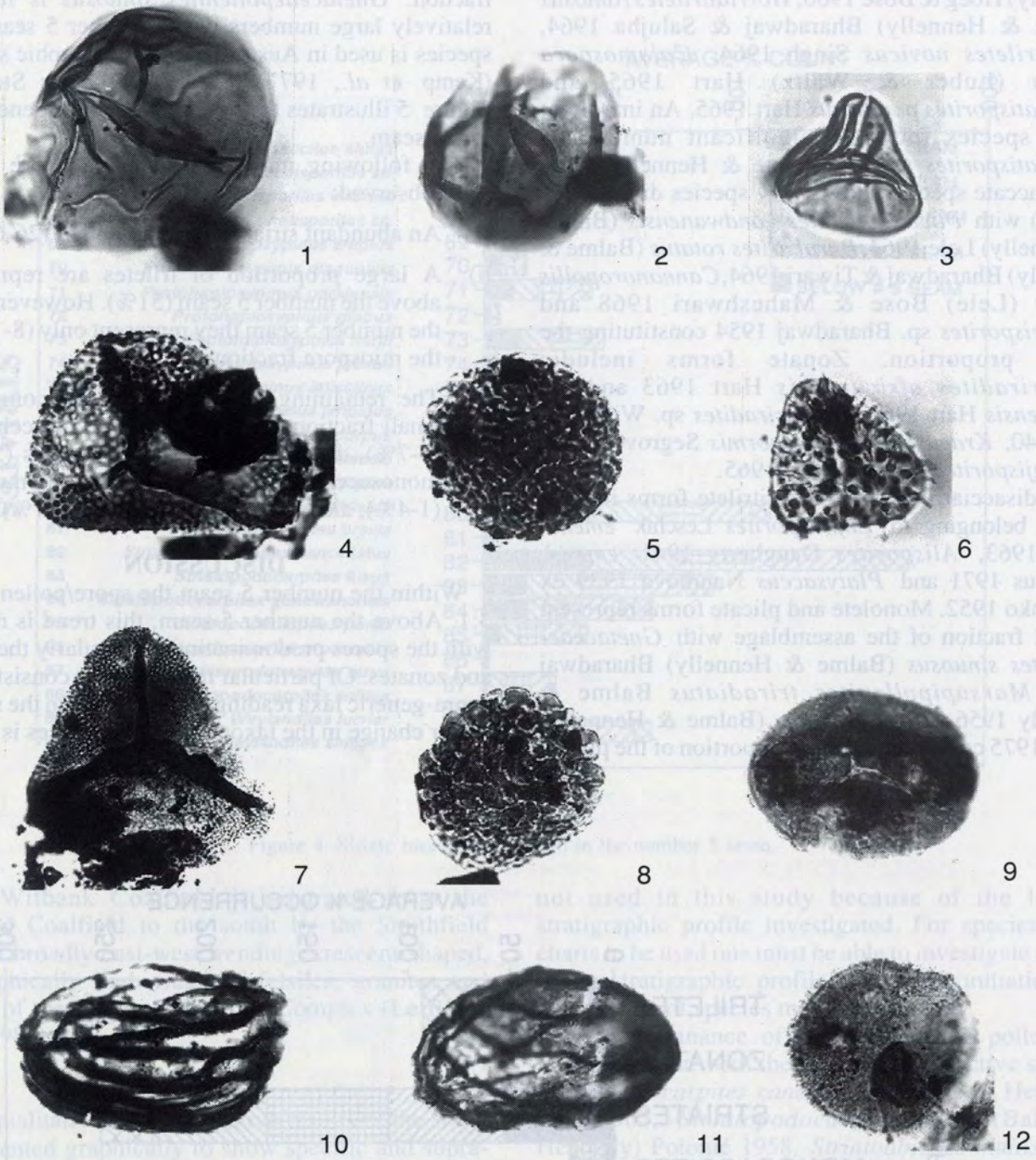


Figure 5. Quantitative variation of supra-generic taxa in the number 5 seam.



SPECIES NAME	LOCALITY	SAMPLE	SLIDE	NEGATIVE	X-Y	SIZE µm
1. *Calamospora plicata*	Rietspruit	97	BPI/10/97.1	BPI/10/1470	X110/Y19	48
2. *Calamospora plicata*	Matla/4	57	BPI/10/57.2	BPI/10/464	X110/Y9	35
3. *Deltoidospora directa*	Matla/2	35	BPI/10/35.4	BPI/10/1847	X124/Y22	33
4. *Verrucosisporites naumovae*	Matla/3	38	BPI/10/38.1	BPI/10/1129	X119/Y4	59
5. *Polypodiisporites mutabilis*	Matla/1	3	BPI/10/3.3	BPI/10/42	X138/Y14	29
6. *Acanthotriletes tereteangulatus*	Matla/4	57	BPI/10/57.4	BPI/10/538	X122/Y6	31
7. *Granulatisporites trisinus*	Rietspruit	97	BPI/10/97.3	BPI/10/1526	X114/Y19	64
8. *Secarisporites lobatus*	Rietspruit	97	BPI/10/97.3	BPI/10/1402	X112.5/Y3	43
9. *Marsupipollenites triradiatus*	Matla/4	57	BPI/10/57.2	BPI/10/476	X95.5/Y8	50
10. *Columinisporites sp.*	Khutala	78	BPI/10/78.2	BPI/10/1243	X131/Y21	48
11. *Columinisporites sp.*	Khutala	77	BPI/10/77.1	BPI/10/795	X106/Y18.5	45
12. *Mehlisphaeridium colliensis*	Matla/4	57	BPI/10/57.2	BPI/10/487	X105/Y10	41

Figure 6. Selected tribete, monolete and alete palynomorphs from number 5 seam.

above the number 5 seam. This can be attributed to a change in the palaeodepositional environment. The vertical consistency of supra-generic taxa in the number 5 seam shows that no major floral changes occurred in the accumulation of this peat swamp and the plant forms were well established in this environment. The horizontal consistency of supra-generic taxa at all of the mine sites also reflects a stable flora and confirms that the same seam was sampled.

The spore colour index technique has been used in the past to determine the degree of thermal maturation of carbonaceous sediments by differences observed in the colour of organic matter (Batten 1981; Burne & Kantsler 1977; Correia 1971; Dow 1977 & Staplin 1969, 1977). The technique involves an expression of the colour range of organic matter from transparent light yellow, with a value of 1 to opaque black with a value of 5. This particular method has also been more commonly termed thermal alteration index (T.A.I.).

The palynological material from the number 5 seam samples is a dark orange to brown colour. The organic material would therefore be assigned a T.A.I. of between 3,0 and 3,5 with the equivalent vitrinite reflectance (% RoV) of 0,7 to 1,25.

This compares favourably with a figure of 0,7% RoV quoted for the number 5 seam at Greenside mine (Boshoff *et al.*, 1993).

REGIONAL CORRELATION (SOUTH AFRICA)

The number 5 seam samples from the Witbank and Highveld Coalfields show a distinctive miospore assemblage with the striates clearly dominant. The supra-generic taxa trends illustrate a high degree of horizontal and vertical uniformity, further supported by a consistent species pattern evident from all the mine sites.

Previous studies of this coal seam from Greenside mine by Falcon *et al.* (1984) indicated an assemblage consisting of *Striatopodocarpites*, *Protohaploxypinus*, *Weylandites* (as *Vittatina*), *Alisporites* (as *Sulcatisporites*), *Lueckisporites* (rare), *Gnetaceaepollenites* and *Cirratriradites* species.

Equally high numbers of *Alisporites* (*Sulcatisporites*) and *Protohaploxypinus* species giving an approximately equal proportion of striate and non-striate bisaccates were recorded (Falcon *et al.* 1984, Figure 3). However, the present study revealed a higher proportion of striate bisaccates (Figures 3 & 5). Falcon *et al.*, (1984 Figure 3) show the number 5 seam correlated with biozone IV G; their figure 4a shows biozone IV G to have striate bisaccates as the most abundant supra-generic taxon.

A possible difference in the striate/non-striate bisaccate proportions between these two studies may be due to regional vegetational differences in the number 5 seam. This study does, nevertheless, show a consistent trend, with the striate bisaccate forms being far more abundant than the non-striate forms in the ratio of 3:1.

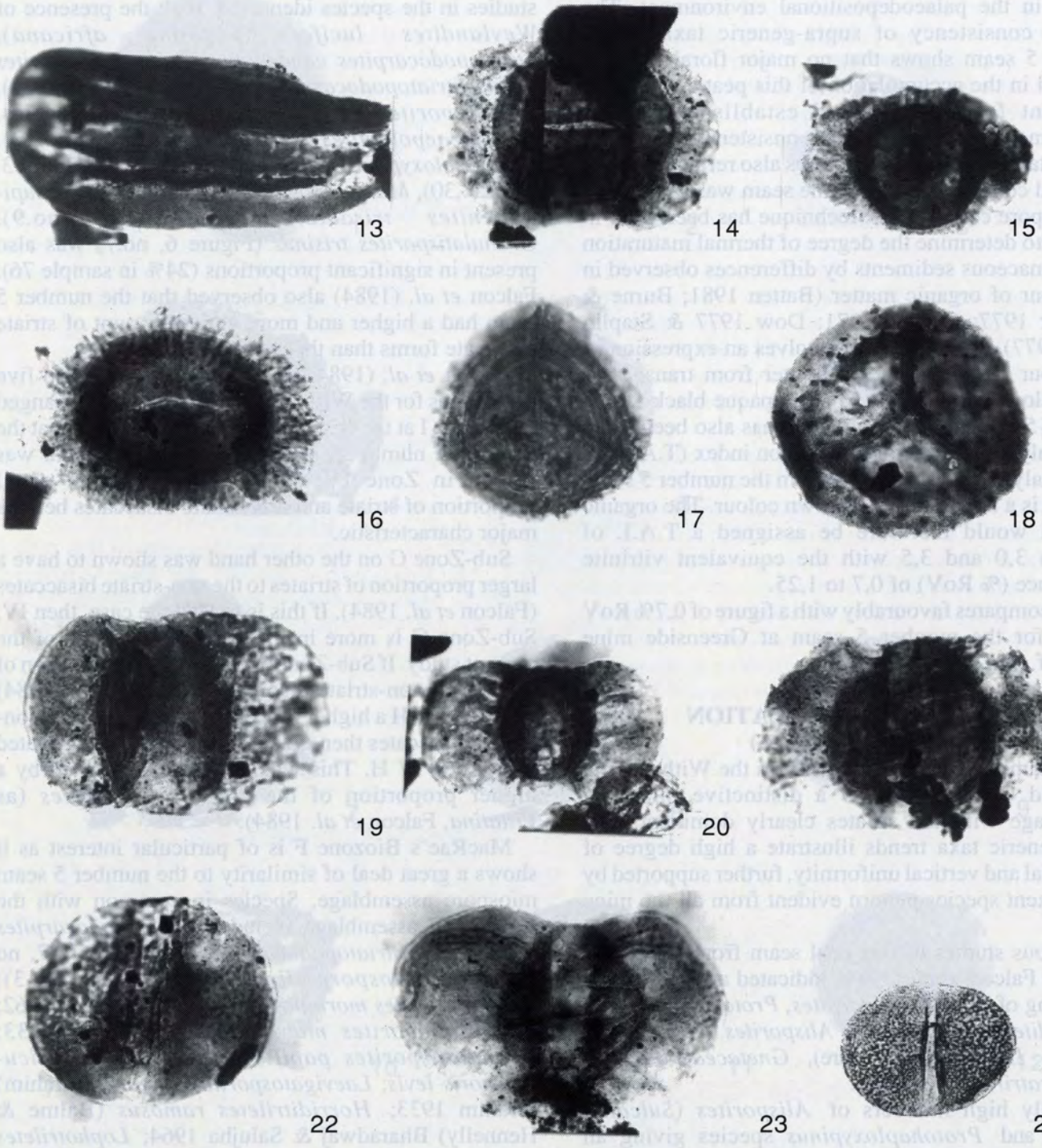
There is, however, a large similarity between the two studies in the species identified, with the presence of *Weylandites lucifer* (*Vittatina africana*), *Striatopodocarpites cancellatus*, *Striatopodocarpites fusus*, *Striatopodocarpites rarus* (Figure 7, no.21), *Lueckisporites virkkiae*, *Lueckisporites* species, *Gnetaceaepollenites sinuosus* (Figure 7, no.13), *Protohaploxypinus* species (Figure 7, no's 14,23; pl.3, no's 27,30), *Marsupipollenites striatus*, and *Marsupipollenites triradiatus* (Figure 6, no.9). *Granulatisporites trisinus* (Figure 6, no.7) was also present in significant proportions (24% in sample 76). Falcon *et al.* (1984) also observed that the number 5 seam had a higher and more varied amount of striate bisaccate forms than the number 4 seam.

Falcon *et al.* (1984) proposed four Zones and five Sub-Zones for the Witbank Basin. These Zones ranged from Zone I at the base of the coal sequence to IV at the top of the number 5 seam. The number 5 seam was placed in Zone IV, Sub-Zone G with an equal proportion of striate and non-striate bisaccates being a major characteristic.

Sub-Zone G on the other hand was shown to have a larger proportion of striates to the non-striate bisaccates (Falcon *et al.* 1984). If this is indeed the case, then IV, Sub-Zone G is more in line with the findings of the present study. If Sub-Zone G has an equal proportion of striate and non-striate disaccates (Falcon *et al.* 1984) and Zone IV H a higher proportion of striates than non-striate disaccates then the number 5 seam is correlated with Zone IV H. This would also be supported by a higher proportion of the genus *Weylandites* (as *Vittatina*, Falcon *et al.* 1984).

MacRae's Biozone F is of particular interest as it shows a great deal of similarity to the number 5 seam miospore assemblage. Species in common with the Biozone F assemblage include: *Striatopodocarpites cancellatus; Striatopodocarpites rarus* (Figure 7, no 21); *Deltoidospora directa* (Figure 6, no 3); *Concavisporites mortonii* (de Jersey) de Jersey 1962; *Granulatisporites microgranifer* Ibrahim 1933; *Granulatisporites papillosus* Hart 1965; *Apiculatisporis levis*; *Laevigatosporites vulgaris* (Ibrahim) Ibrahim 1933; *Horriditriletes ramosus* (Balme & Hennelly) Bharadwaj & Salujha 1964; *Lophotriletes novicus* Singh 1964; *Acanthotriletes tereteangulatus* (Figure 6, no 26); *Cycadopites follicularis* Wilson & Webster 1946; *Alisporites potoniei* (Lakhanpal, Sah & Dube) Somers 1968 (Figure 7, no 24); *Platysaccus papilionis* Potonié & Klaus 1954; *Platysaccus radialis* (Leschik) Clarke 1965; *Protohaploxypinus goraiensis* (Potonié & Lele) Hart 1964 (Figure 9, no 30); *Protohaploxypinus limpidus* (Balme & Hennelly) Balme & Playford 1967; *Protohaploxypinus hartii* Foster 1979 (Figure 7, no 23); *Protohaploxypinus diagonalis* Balme 1970 and *Pteruchipollenites gracilis* (Segroves) Foster 1979.

MacRae selected *Gnetaceaepollenites sinuosus* (Figure 7, no 13); *Striatopodocarpites fusus* and *Weylandites lucifer* as being distinctive species of



SPECIES NAME	LOCALITY	SAMPLE	SLIDE	NEGATIVE	X-Y	SIZE µm
13. *Gnetaceaepollenites sinuosus*	Khutala	77	BPI/10/77.1	BPI/10/772	X133/Y15	90
14. *Protohaploxypinus globus*	Rietspruit	97	BPI/10/97.2	BPI/10/1493	X133/Y18	63
15. *Limitisporites monstruosus*	Khutala	72	BPI/10/72.2	BPI/10/753	X115/Y14	98
16. *Limitisporites sp.*	Rietspruit	97	BPI/10/97.2	BPI/10/1543	X109/Y21	92
17. *Gondisporites sp.*	Matla/4	57	BPI/10/57.2	BPI/10/496	X102.5/Y14	55
18. *Indotriradites reidii*	Khutala	82	BPI/10/82.1	BPI/10/1014	X136/Y9	60
19. *Platysaccus radialis*	Rietspruit	97	BPI/10/97.2	BPI/10/1528	X132/Y19	85
20. *Striatopodocarpites solitus*	Rietspruit	97	BPI/10/97.1	BPI/10/1419	X107.5/Y16	67
21. *Striatopodocarpites rarus*	Rietspruit	97	BPI/10/97.3	BPI/10/1382	X121/Y7	79
22. *Alisporites potoniei*	Rietspruit	97	BPI/10/97.2	BPI/10/1521	X122/Y5	73
23. *Protohaploxypinus hartii*	Rietspruit	97	BPI/10/97.3	BPI/10/1440	X123.5/Y16	68
24. *Alisporites potoniei*	Matla/1	3	BPI/10/3.1	BPI/10/1714	X122.5/Y19	62

Figure 7. Selected plicate, zonate and bisaccate palynomorphs from the number 5 seam.

Biozone F. All of these are found to be present in significant numbers in the number 5 seam. *Thymospora pseudothiessenii* (Kosanke) Wilson & Venkatchala 1963 which terminates just below Biozone F (MacRae 1988) is present in the number 5 seam and there are a number of species in the number 5 seam which are not listed as being present in Biozone F. These are *Corisaccites alutas* (rare), *~~Lu~~eckisporites virkkiae* (Figure 9, no 28) (rare), *Lueckisporites* species (Figure 9, no 29) (rare), *Granulatisporites trisinus* (Figure 6, no 7) (abundant), *Lunatisporites* species (Figure 9, no 32) (very rare), *Limitisporites* species (Figure 7, no's 15, 16) and *Columinisporites* sp. (Figure 6, no's 10,11).

Comparison of the relative proportions of supra-generic taxa and the species profile would indicate a very close similarity between Biozone F and the number 5 seam. MacRae (1988) reports an increasing trend of striates and a decreasing trend of non striate forms towards the top of his Biozone F (striates 60-80%, disacciatriletes/disaccitriletes 10-20%).

It is suggested that the number 5 seam may be correlated with Biozone F (Figure 8). Alternatively, a new Biozone is indicated, based on the presence of *Corisaccites alutas*, *Lueckisporites virkkiae*, *Lueckisporites* species, *Granulatisporites trisinus* and *Lunatisporites* species.

The number 5 seam miospore assemblage is equated with the more broadly defined *Striatiti* florizone from South Africa of Hart (1967). Species in common include: *Weylandites lucifer* (as *Vittatina africana*), *Striatopodocarpites cancellatus, Striatopodocarpites fusus* (as *S. paralicus*) and *Gnetaceaepollenites sinuosus* (as *Schopfipollenites sinuosus).*

A broad similarity exists between the miospore content of the number 5 seam and Zone 5 described from the northern Karoo Basin, South Africa (Anderson 1977). A high proportion of striates are present in Zone 5 and many species are common. These include *Protohaploxypinus goraiensis* (as *Pitysporites goraiensis*), *Striatopodocarpites cancellatus* (as *Protohaploxypinus cancellatus*), *Protohaploxypinus amplus* (as *Pityosporites amplus*), *Protohaploxypinus micros* (as *Pityosporites micros*) and various *Lueckisporites* species.

CHRONOSTRATIGRAPHIC UNITS *VIDE* HARLAND *ET AL.* 1982			WATERBERG & PAFURI BASINS SOUTH AFRICA	ZIMBABWE	WITBANK HIGHVELD COALFIELDS SOUTH AFRICA
PERIOD	EPOCH	AGE	MACRAE 1988	FALCON 1978	PRESENT STUDY
PERMIAN	UPPER PERMIAN	TATARIAN	F	H'	**No. 5 SEAM**
		KAZANIAN		**H**	
		UFIMIAN	**E**	**G**	

Figure 8. Correlation chart of Biozones in the present study with international chronostratigraphic units (adapted from MacRae, 1988)

PALAEOENVIRONMENTAL SETTING

A great deal of literature exists on the interpretation of the palaeodepositional and palaeoenvironmental setting of the coal seams in the Witbank and Highveld Coalfields (Cadle *et al.* 1993; Cairncross 1980, 1986, 1989, Cairncross & Cadle 1988a, 1988b; Falcon 1980, 1986, 1989; Falcon *et al.* 1984; Le Blanc Smith & Erikkson 1979; Le Blanc Smith & Falcon 1982; Plumstead 1957, 1966).

Climatic amelioration during the Late Carboniferous and Early Permian was accompanied by glacial thawing and retreat to the north and northeast of the present day Karoo Basin (Crowell & Frakes 1975; Stratten 1968). The retreat of these glaciers has been proposed as being pulsatory rather than continuous (Falcon 1986). In the early stages of the Vryheid Formation glaciogenic conditions still prevailed causing infilling of palaeo-valleys by glaciofluvial braided alluvium (Cairncross 1989). Epicontinental coal-forming environments follow conformably above these paraglacial sediments and are related to major sedimentation across the entire northeastern stable shelf area of the Karoo basin.

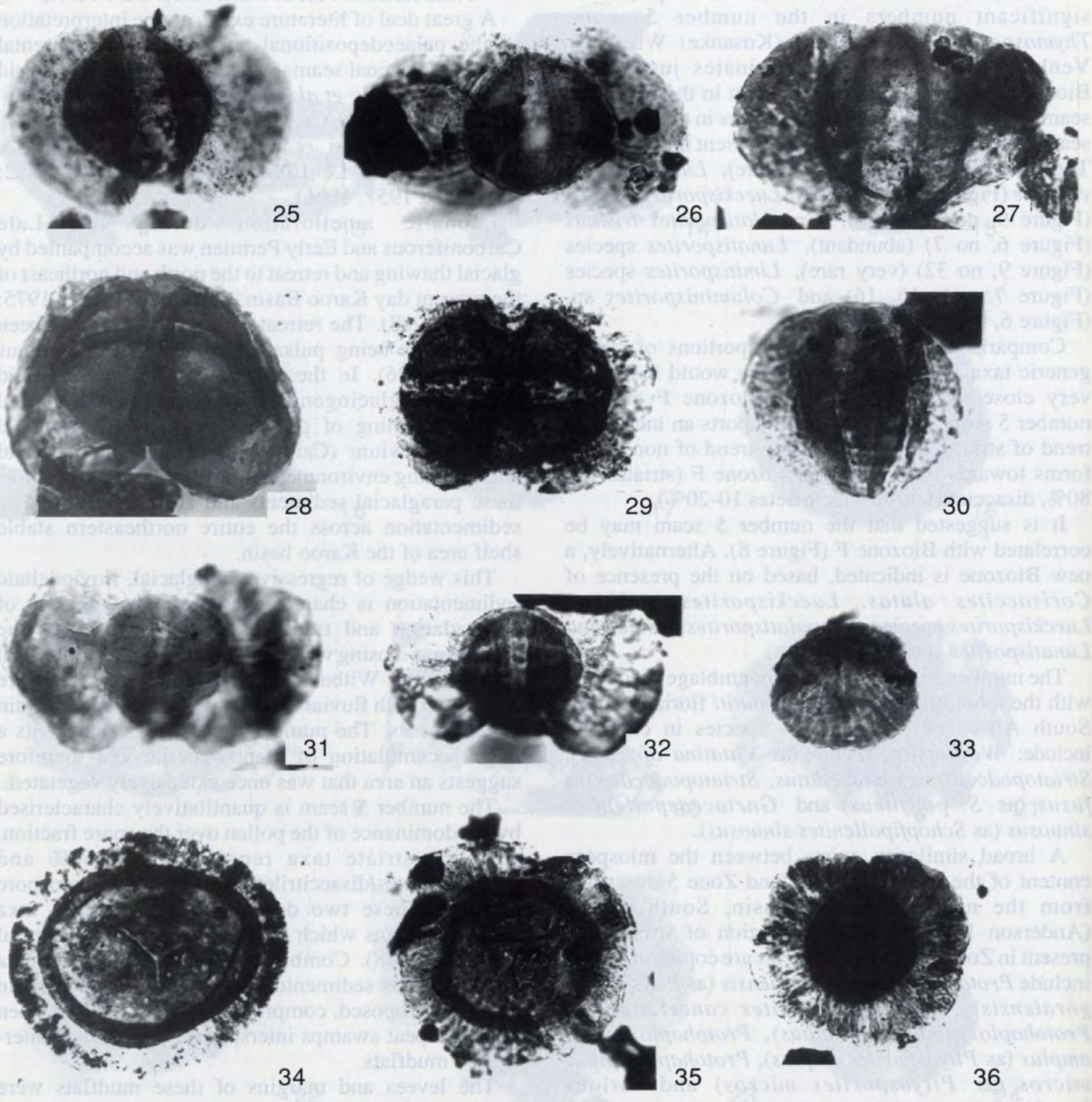
This wedge of regressive, nonglacial, fluviodeltaic sedimentation is characterised by eight episodes of progradation and transgression with many of the regressions closing with a peat bed (Falcon 1989). Coal seams in the Witbank and Highveld Coalfields are associated with fluvial and delta dominated flood plain environments. The number 5 coal seam represents a large accumulation of plant material and therefore suggests an area that was once extensively vegetated.

The number 5 seam is quantitatively characterised by the dominance of the pollen over the spore fraction, with the striate taxa representing ± 60% and disacciatriletes/disaccitriletes ± 15% of the miospore fraction. These two dominant supra-generic taxa represent grains which are adapted to wind dispersal (MacRae 1988). Combining this evidence with data from previous sedimentological studies a flood plain setting is proposed, comprising of shallow, wide open pans and peat swamps interspersed with wide, water-logged mudflats.

The levees and margins of these mudflats were possibly colonised by the lower order spore producers. Cryptogam spore producers are also most likely to have occurred as part of the understorey on the lake/pond margins and as the primary colonisers of the emerged portions of the shallow depository.

The abundance of striates in the samples might indicate that well away from the margin of these mudflats a fairly stable forest vegetation of high order pollen producing plants was situated. Long distance wind blown transport of this higher order pollen could account for dominance of the striates in the number 5 seam.

The dramatic increase in the striates and the decrease in all other taxa could conceivably indicate a vegetational response to a change in climate. This possibly occurred because of the drifting of the sub-



SPECIES NAME	LOCALITY	SAMPLE	SLIDE	NEGATIVE	X-Y	SIZE µm
25. *Striatopodocarpites pantii*	Khutala	72	BPI/10/72.1	BPI/10/702	X123/18	70
26. *Striatopodocarpites pantii*	Khutala	72	BPI/10/92.2	BPI/10/754	X115.5/Y15.5	60
27. *Protohaploxypinus amplus*	Rietspruit	97	BPI/10/97.2	BPI/10/1387	X102.5/Y12.5	91
28. *Lueckisporites virkkiae*	Rietspruit	97	BPI/10/97.3	BPI/10/1533	X103/Y8.5	73
29. *Lueckisporites sp.*	Rietspruit	97	BPI/10/97.2	BPI/10/1358	X94.5/Y15	81
30. *Protohaploxypinus goraiensis*	Rietspruit	97	BPI/10/97.2	BPI/10/1557	X114.5/Y2.5	87
31. *Striatopodocarpites pantii*	Rietspruit	97	BPI/10/97.2	BPI/10/1463	X112/Y17	103
32. *Lunatisporites sp.*	Rietspruit	97	BPI/10/97.2	BPI/10/1432	X116/Y4	71
33. *Weylandites simplex*	Rietspruit	97	BPI/10/97.1	BPI/10/1412	X117/Y12	33
34. *Cannanoropollis densus*	Rietspruit	97	BPI/10/97.1	BPI/10/1167	X125/Y7	115
35. *Cannanoropollis* sp.	Khutala	78	BPI/10/78.3	BPI/10/1242	X124.5/Y5.5	85
36. *Cannanoropollis densus*	Matla/1	5	BPI/10/5.2	BPI/10/1168	X102.5/Y13.5	98

Figure 9. Selected striate bisaccate and monosaccate polynomorphs from the number 5 seam.

continent into lower latitudes, and signals the first stages of the warmer temperate climates of Beaufort Permo-Triassic times.

AGE

Palaeobotanical age determination for Permian sediments remains a controversial subject. Two approaches have been described. The first, direct correlation, is based on a bio- and chrono-stratigraphic correlation comparing fossil plant assemblages found in spatially separated areas and the second, indirect correlation where the age of the flora is determined by comparison with marine faunas (Kovács Endrödy, 1991).

These different approaches result in age determinations that frequently differ. Kovács Endrödy (1991) discusses the validity of these two approaches. It is considered beyond the scope of this paper to critically analyze these two approaches; ages referred to in the preceding section are subject to revision when more palynological information becomes available.

The number 5 seam was correlated with the upper portion of Biozone F of MacRae (1988). MacRae (1988) dated his Biozone E as extending from the Ufimian to the lower part of the Kazanian Age and Biozone F was tentatively suggested as having extended over the remainder of the Kazanian, including part of the Tatarian. The number 5 seam was also correlated with the *Striatiti* Florizone for which Hart (1967) showed a Tatarian Age.

CONCLUDING REMARKS

An important palynological trend in Upper Permian sediments both in South Africa and its Gondwana counterparts is the emergence of abundant striate bisaccate forms, in particular genera such as *Striatopodocarpites, Protohaploxypinus, Weylandites, Lueckisporites, Lunatisporites, Corisaccites* and *Guttulapollenites* Goubin 1965. In the stratigraphy, the number 5 seam is situated towards the top of the Vryheid Formation. This has led to this seam being placed in the Upper/Lower to Lower/Middle Permian Epoch and hence of Aktastinian to Baigendzinian age. However, this study and previous work by Falcon (1984) and MacRae (*pers comm.*) place this seam in the Lower Upper Permian Epoch, which in turn supports a Kazanian to Tatarian age. An investigation of material stratigraphically higher and lower in the South African succession than the number 5 seam is needed to help resolve the age discrepancies.

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