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A REVISED CLASSIFICATION OF CYNODONTS (REPTILIA; THERAPSIDA)

by

* James A. Hopson and †James W. Kitching

INTRODUCTION

Cynodonts are very advanced mammal-like reptiles of the Permo-Triassic which are of special interest to evolutionists because they gave rise to the Class Mammalia during Middle or Late Triassic time. Cynodonts have been known from strata of Early Triassic age in South Africa for over one hundred years, and numerous specimens have been collected and described. In recent years the record of cynodonts has been extended into earlier and later time zones, not only in southern Africa, but in East Africa, South America, Russia, China, and, most recently, in North America. Much of the material from outside of Africa has not yet been fully described.

Approximately 125 species of cynodonts (including ictidosaurs and tritylodonts, herein considered to be cynodonts) have been named. Of these, however, only a very small handful has been adequately characterized so that any one species can be reliably distinguished from all others. As a result of the taxonomic confusion which prevails in the Cynodontia, our knowledge of the patterns of evolution within the group is based on detailed knowledge of a few species.

The stimulus for the present revised classification of cynodonts was an extended research visit to the Bernard Price Institute for Palaeontological Research by the senior author in late 1971. The purpose of the visit was to study primitive cynodonts, but all available cynodont material in this and many other South African museums was examined.†† The junior author has also studied most of the cynodont material in South Africa as part of a revision of the stratigraphy and vertebrate fauna of the Beaufort Series. Many of the taxonomic conclusions independently reached by the two authors have proven to be identical, though based in great part on different evidence. Because of the large amount of overlap in our work, we have decided to publish our taxonomic conclusions as a joint report, reserving for separate future papers the presentation of the detailed evidence upon which these conclusions are based. For the sake of completeness, the senior author has reviewed the non-South African cynodonts, though many of the taxonomic judgments on these forms are less securely based than are the judgments on the South African cynodonts. The revision of the family Tritylodontidae is based on the senior author's unpublished studies.

We wish to thank the following colleagues for access to unpublished information which has been incorporated into this paper: Dr. J. F. Bonaparte, Fundacion Miguel Lillo, Tucumán, Argentina; Dr. A. W. Crompton, Museum of Comparative Zoology, Harvard University; and Mr. J. W. A. van Heerden, National Museum, Bloemfontein.

Several aspects of this classification require comment. In deciding whether to consider a generic or specific name to be valid, we have taken the position that the burden of proof is on the describer to convince us that the named taxon is distinct from earlier-named taxa. Where there is a reasonably high probability that two named taxa are synonymous, we have usually synonymized them, even though the evidence for their identity is not conclusive. We have done this because: (1) the cynodonts have been excessively split (as, in fact, have most therapsid groups), so that our first priority seemed to be the reduction of the confusing welter of inadequately-characterized genera and species to fewer, more adequately defined taxa; (2) many of the type specimens are fragmentary and poorly-preserved so that diagnostic characters are lacking; (3) where locality and stratigraphic data are available, it is evident that an excessive number of closely-related species have been named from very limited geographic areas and from within very narrow stratigraphic intervals. In those cases where taxa based on inadequate types could be reasonably synonymized with adequately-characterized species, we did so, but where inadequate types could not be so allocated we have chosen to declare the names on which they are based to be *nomina vana*.

The higher-level classification adopted here differs substantially from that used in most earlier classifications (e.g., Watson and Romer, 1956; Romer, 1966; Lehman, 1961; but see Haughton and Brink, 1954). We have abandoned separate infraordinal rank for the "Ictidosauria" (i.e., Tritheledontidae) and Tritylodontidae; instead they are listed as families within the Infraorder Cynodontia. These groups are clearly cynodont derivatives and we believe that their positions as

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advanced end-members of two major adaptive lines within the cynodont radiation are best indicated by incorporating them within the Cynodontia. Their respective positions as the culmination of the carnivorous and herbivorous rami of the cynodonts has been expressed in the classification by dividing the infraorder into two main groups at the level of superfamily. For the carnivorous group, we have adopted Brink's (1963) term *Cynognathoidea*; for the herbivorous group, we have chosen to use Simpson's (1928) term *Tritylodontoidea*. These choices were determined by: (1) familiarity of the root genera, *Cynognathus* and *Tritylodon* and (2) the fact that these genera represent extremes of specialization within their respective groups. The resulting classification, we believe, possesses the advantage of expressing both phyletic relationships and adaptive trends better than those classifications which place the cynodonts and their therapsid descendants in three infraorders (Cynodontia, Ictidosauria, and Tritylodontia). A similar sort of reclassification of other therapsid groups, notably of the therocephalian-bauriamorph assemblage, is also overdue.

INFRAORDER CYNODONTIA

SUPERFAMILY CYNOGNATHOIDEA Brink 1963.

Cynodonts in which the posterior postcanine teeth usually possess three or more cusps aligned in an anteroposterior row; a narrow lingual cingulum bearing several small cusps is frequently present, but only rarely is the cingulum expanded to form a broad lingual shelf; canines are usually well-developed; incisors are usually small and unspecialized. Most members are carnivorous. Included are primitive cynodonts of the Permian and earliest Triassic and all carnivorous cynodonts of the later Triassic.

FAMILY PROCYNOSUCHIDAE Broom 1948.

Includes: Silphedestidae Haughton and Brink 1954; Dviniidae Tatarinov 1968 a.

Primitive cynodonts with five or more incisors, small "precanine" maxillary teeth in front of the enlarged canine, and posterior postcanine teeth with a prominent lingual cingulum; the dentary is small, with a low coronoid process, no angle, and with the masseteric fossa restricted to the posterodorsal portion of the bone; palatal plates of the maxillae and palatines do not meet at the midline so that the secondary palate is incomplete; interpterygoidal vacuities usually present; ribs normal, lacking plate-like expansions.

Horizon: Upper Permian: *Daptocephalus* Zone, Beaufort Series, of South Africa; Zone IV of Russia; Kawinga Formation of Tanzania.

Genus *PROCYNOSUCHUS* Broom 1937.

Synonyms: ? *Cyrbasiodon* Broom 1931; *Paracynosuchus* Broom 1940a; *Mygalesaurus* Broom 1942; *Aelurodraco* Broom and Robinson 1948b; *Leavachia* Broom 1948; *Galeophrys* Broom 1948; *Galecranium* Broom 1948; *Silphedestes* Broom 1949; *Protocynodon* Broom 1949; *Silphedocynodon* Brink 1951; *Scalopocynodon* Brink 1961.

PROCYNOSUCHUS DELAHARPEAE Broom 1937.

Synonyms: ? *Cyrbasiodon boycei* Broom 1931; *Procynosuchus rubidgei* Broom 1938; *Paracynosuchus rubidgei* Broom 1940a; *Nanictosuchus melinodon* Broom 1940a; *Nanictosaurus robustus* Broom 1940b; *Mygalesaurus platyceps* Broom 1942; *Aelurodraco microps* Broom and Robinson 1948b; *Leavachia duvenhagei* Broom 1948; *Galeophrys kitchingi* Broom 1948; *Galecranium liorhynchus* Broom 1948; *Silphedestes polyodon* Broom 1949; *Protocynodon pricei* Broom 1949; *Silphedocynodon gymnotemporalis* Brink 1951; *Leavachia microps* Brink and Kitching 1951a; *Leavachia gracilis* Brink and Kitching 1951a; *Scalopocynodon gracilis* Brink 1961.

Horizon: Upper Permian: *Daptocephalus* Zone of South Africa.

Remarks: Many genera and species have been based on juvenile specimens of *Procynosuchus*, including all forms placed in the Family Silphedestidae by Haughton and Brink (1954). *Cyrbasiodon boycei* is probably synonymous with *P.*

delaharpeae, but in view of the poor quality of the type specimen of the former species, we have chosen to retain the latter well-established name. (See paper by Mendrez in this volume, p. 51).

Genus *DVINIA* Amalitzky 1922.

Synonyms: *Permocynodon* Woodward 1932.

DVINIA PRIMA Amalitzky 1922.

Synonyms: *Permocynodon sushkini* Woodward 1932.

Horizon: Upper Permian: Upper Tatarian deposits of Arkhangel'sk region, Russia.

Genus *PARATHRINAXODON* Parrington 1936.

PARATHRINAXODON PROOPS Parrington 1936.

Horizon: Upper Permian: Kawinga Formation of the Ruhuhu Valley, Tanzania.

PROCYNOSUCHIDAE incertae sedis:

Genus *NANOCYNODON* Tatarinov 1968b.

NANOCYNODON SEDUCTUS Tatarinov 1968b.

Horizon: Upper Permian: Upper Tatarian of Russia.

Remarks: Tatarinov placed this species in the Galesauridae, but it is more likely a juvenile procynosuchid.

FAMILY GALESAURIDAE Lydekker 1890.

Includes: Nythosauridae Watson 1917; Cynosuchidae Haughton 1924a; Cynosauridae Haughton and Brink 1954; Thrinaxodontidae Watson and Romer 1956.

Moderately advanced cynodonts with four upper and three lower incisors, no "precanine" maxillary teeth, and posterior postcanines with internal cingulum moderately developed or absent; dentary with well-developed coronoid process, incipiently-developed angular region, and masseteric fossa extending to lower border of the bone; postdentary elements slightly reduced in height from procynosuchid condition; palatal plates of the maxillae and palatines may or may not meet at the midline; interpterygoidal vacuities present only in juveniles; thoracic and lumbar ribs with plate-like expansions.

Horizon: Upper Permian to Lower Triassic: Beaufort Series (Upper *Daptocephalus* Zone to *Cynognathus* Zone, most abundant in *Lystrosaurus* Zone) of South Africa; Fremouw Formation of Antarctica.

Genus *CYNOSAURUS* Schmidt 1927.

Synonyms: *Cynosuchus* Owen 1876; *Cynosuchoides* Broom 1931; *Nanictosaurus* Broom 1936; *Mygalesuchus* Broom 1942; *Baurocynodon* Brink 1951.

CYNOSAURUS SUPPOSTUS (Owen 1876).

Synonyms: *Cynosuchus suppostus* Owen 1876; *Cynosuchus whaitsi* Haughton 1918; *Cynosaurus suppostus,* Schmidt 1927; *Cynosuchoides whaitsi* Broom 1931; *Nanictosaurus kitchingi* Broom 1936; *Mygalesuchus peggyae* Broom 1942; *Baurocynodon gracilis* Brink 1951.

Horizon: Upper Permian: Upper *Daptocephalus* Zone of South Africa.

Remarks: This is the only undoubted galesaurid from the Permian. The last three synonyms are based on small juvenile specimens.

Genus *GALESAURUS* Owen 1859.

Synonyms: *Glochinodon* van Hoepen 1916; *Glochinodontoides* Haughton 1924b.

GALESAURUS PLANICEPS Owen 1859.

Synonyms: *Glochinodon detinens* van Hoepen 1916; *Glochinodontoides gracilis* Haughton 1924b; *Notictosaurus gracilis* Broom and Robinson 1948a; *Notictosaurus trigonocephalus* Brink and Kitching 1951b.

Horizon: Lower Triassic: *Lystrosaurus* Zone of South Africa.

Remarks: Small, immature specimens have usually been

referred to the genus *Galesaurus*, large, mature specimens to *Glochinodontoides*.

Genus *THRINAXODON* Seeley 1894a.

Synonyms: ? *Nythosaurus* Owen 1876; *Ictidopsis* Broom 1912a; *Notictosaurus* Broom 1936; *Micrictodon* Broom 1937.

THRINAXODON LIORHINUS Seeley 1894a.

Synonyms: ? Nythosaurus larvatus Owen 1876, *Ictidopsis elegans* Broom 1912a; *Ictidopsis formosa* van Hoepen 1916; *Thrinaxodon putterilli* Broom 1932; *Notictosaurus luckhoffi* Broom 1936; *Micrictodon marionae* Broom 1937.

Horizon: Lower Triassic: *Lystrosaurus* Zone of South Africa; Fremouw Formation of Antarctica.

Remarks: *Nythosaurus larvatus* Owen is based on the natural mould of a skull bearing impressions of the postcanine teeth. It is probably synonymous with either *Thrinaxodon liorhinus* or *Platycraniellus elegans*. We consider it to be indeterminate at present, and retain Seeley's name for this best-known species of cynodont.

Genus *PLATYCRANIELLUS* van Hoepen 1917.

Synonyms: *Platycranion* van Hoepen 1916; *Platycranium* van Hoepen 1917.

PLATYCRANIELLUS ELEGANS (van Hoepen 1916).

Synonyms: *Platycranion elegans* van Hoepen 1916; *Platycraniellus elegans* van Hoepen 1917.

Horizon: Lower Triassic: *Lystrosaurus* Zone of South Africa.

Remarks: This species is known with certainty from the type only which comes from Harrismith, Orange Free State. A second specimen referred to this species by Brink (1954) is a *Galesaurus*.

Genus *TRIBOLODON* Seeley 1894a.

TRIBOLODON FRERENSIS Seeley 1894a.

Horizon: Lower Triassic: *Cynognathus* Zone of South Africa.

Remarks: This is the youngest species referable with certainty to the Galesauridae. Though frequently classified as a cynognathid, it is a typical galesaurid in its known features.

FAMILY CYNOGNATHIDAE Watson 1917.

Includes: Karromysidae Haughton 1924a.

Advanced carnivorous cynodonts of large size, with elongated facial region and short temporal region; zygomatic arch, postorbital bar, and occipital plate of the squamosal very broad and heavy; occipital portion of the squamosal not emarginated dorsally (as in other advanced cynodonts); dentary very large, with broad posterodorsally-directed coronoid process and distinct angle; postdentary jaw elements greatly reduced in dorsoventral dimension to form a sturdy rod; surangular forms accessory articulation with the squamosal; posterior cheek teeth laterally compressed, with three to six(?) cusps aligned anteroposteriorly, and lacking cingulum cusps except in very young individuals; lumbar ribs with overlapping expansions.

Horizon: Lower Triassic: *Cynognathus* Zone of South Africa and Lesotho (reference to Middle Triassic Molteno Beds of Lesotho is incorrect. Turner: in press); Puesto Viejo Formation of Argentina.

Genus *CYNOGNATHUS* Seeley 1895b.

Synonyms: *Karoomys* Broom 1903b; *Lycognathus* Broom 1913b; *Lycochampsa* Broom 1915b; *Cynidiognathus* Haughton 1922; *Lycaenognathus* Broom 1925; *Cynogomphius* Broom 1932; *Cistecynodon* Brink and Kitching 1953.

CYNOGNATHUS CRATERONOTUS Seeley 1895b.

Synonyms: *Cynognathus berryi* Seeley 1895b; *Cynognathus platyceps* Seeley 1895b; *Karoomys browni* Broom 1903b; *Nythosaurus browni* Broom 1912a; *Lycognathus ferox*

Broom 1913b; *Lycochampsa ferox* Broom 1915b; *Cynidiognathus longiceps* Haughton 1922; *Cynidiognathus broomi* Haughton 1922; *Lycaenognathus platyceps* Broom 1925; *Lycaenognathus kannemeyeri* Broom 1931; *Cynogomphius berryi* Broom 1932; *Cynidiognathus merenskyi* Broili and Schröder 1935b; *Cistecynodon parvus* Brink and Kitching 1953; *Cynognathus minor* Bonaparte 1967a.

Horizon: Same as for family.

Remarks: Generic and specific distinctions within the Cynognathidae have been based on characters which vary with age (tooth number and morphology, skull proportions) and are influenced by postmortem deformation. It seems best to us to recognize but a single species, pending a thorough revision of the family. *Karoomys, Cistecynodon*, and *Nythosaurus browni* are based on tiny juveniles of *Cynognathus*.

FAMILY CHINIQUODONTIDAE von Huene 1936.

Advanced carnivorous cynodonts of small to large size, in which secondary palate extends nearly to or beyond the posterior end of the tooth row (in contradistinction to all other families—except the Tritheledontidae— in which the secondary palate ends well in front of the last tooth) ; occipital portion of the squamosal emarginated dorsally; dentary very large, contacting the squamosal in at least one species; postdentary elements reduced to a narrow rod; surangular contacts the squamosal; postcanines vary greatly in morphology, in some species are sectorial with small or no cingulum cusps, in others have broad lingual shelves which contact similar shelves in the occluding dentition; this family probably contains the immediate ancestors of mammals.

Horizon: Middle and Upper Triassic: Middle Triassic Chañares Formation of Argentina, Manda Formation of Tanzania; Middle or Upper Triassic Santa Maria Formation of Brazil; Upper Triassic Ischigualasto Formation of Argentina.

Genus *CHINIQUODON* von Huene 1936.

CHINIQUODON THEOTONICUS von Huene 1936.

Horizon: Middle and Upper Triassic: Middle Triassic Chañares Formation of Argentina; Middle or Upper Triassic Santa Maria Formation of Brazil; Upper Triassic Ischigualasto Formation of Argentina.

Remarks: This species is poorly understood; possibly some of the specimens referred to it from the Chañares and Ischigualasto formations do not belong here.

Genus *BELESODON* von Huene 1936.

BELESODON MAGNIFICUS von Huene 1936.

Horizon: Middle or Upper Triassic: Santa Maria Formation of Brazil.

Remarks: *Belesodon* is not clearly separable from *Chiniquodon* except on the basis of features which may merely reflect ontogenetic differences. However, because important features of the postcanine dentition are not known for either genus, we prefer to maintain them as distinct for the present.

Genus *ALEODON* Crompton 1955.

ALEODON BRACHYRAMPHUS Crompton 1955.

Horizon: Middle Triassic: Manda Formation of Tanzania.

Remarks: Undescribed specimens being studied by Crompton indicate that this species is a chiniquodontid, the only one known from Africa.

Genus *PROBELESODON* Romer 1969.

PROBELESODON LEWISI Romer 1969.

Horizon: Middle Triassic: Chañares Formation of Argentina.

Genus *PROBAINOGNATHUS* Romer 1970.

PROBAINOGNATHUS JENSENI Romer 1970.

Horizon: Middle Triassic: Chañares Formation of Argentina.

Remarks: This species possesses a contact between dentary and squamosal bones, generally considered one of the principal diagnostic characters of mammals. Despite previous remarks to the contrary (Barghusen and Hopson, 1970), *Probainognathus* is probably very close to the line which gave rise to the Class Mammalia.

FAMILY TRITHELEDONTIDAE Broom 1912b.

Includes: Ictidosauridae Young 1947; Diarthrognathidae Crompton 1958.

Very advanced carnivorous cynodonts of small size in which incisors number two above and below; in some species the upper postcanines (and probably the lowers as well) have a transversely-oriented cutting edge, in others the uppers have an oblique and the lowers a longitudinal cutting edge; secondary palate very long (as in the Chiniquodontidae); postorbital bar absent; dentary contacts the squamosal at least in some.

Horizon: Upper Triassic: Stormberg Series (Red Beds and Cave Sandstone) of South Africa and Lesotho; Los Colorados Formation of Argentina (Bonaparte, personal communication).

Genus *TRITHELEDON* Broom 1912b.

TRITHELEDON RICONOI Broom 1912b.

Horizon: Upper Triassic: Red Beds of South Africa.

Remarks: Crompton (in Hopson and Crompton, 1969) has restudied the type and only specimen and has determined its close affinities with *Pachygenelus* and *"Diarthrognathus"*. For this reason, we use the family name Tritheledontidae Broom 1912 for all of the forms called "ictidosaurs".

Genus *PACHYGENELUS* Watson 1913.

Synonyms: *Diarthrognathus* Crompton 1958.

PACHYGENELUS MONUS Watson 1913.

Synonyms: *Diarthrognathus broomi* Crompton 1958.

Horizon: Upper Triassic: Red Beds and Cave Sandstone of South Africa and Lesotho.

Remarks: *Diarthrognathus broomi* is based on two juvenile specimens which are probably, though not certainly, referable to *P. monus*. Although a specific distinction may prove to be valid, it is doubtful that generic differences exist.

SUPERFAMILY TRITYLODONTOIDEA Simpson 1928 (New rank, erected as suborder). Cynodonts of omnivorous or herbivorous habits in which some or all of the postcanine teeth have transversely-widened crowns which meet in complex occlusion; dentary very large with large coronoid process and distinct angular region often with a true angular process; postdentary elements reduced to narrow rod; surangular contacts squamosal; occipital portion of the squamosal emarginated dorsally; lumbar ribs primitively with overlapping expansions, but rib specializations lost in later forms.

FAMILY DIADEMODONTIDAE Haughton 1924a.

Includes: Gomphognathidae Broom 1903a; Traversodontidae von Huene 1936; Gomphodontosuchidae Watson and Romer 1956; Trirachodontidae Romer 1967.

Primitive to advanced cynodonts of omnivorous to herbivorous habits in which canines are not lost, postcanine teeth are single-rooted and upper postcanines are much wider than long; postorbital bar and prefrontal and postorbital bones present; lumbar ribs with overlapping expansions except in very advanced forms.

Horizon: Lower to Upper Triassic: Lower Triassic *Cynognathus* Zone of South Africa, Puesto Viejo Formation of Argentina; Lower or Middle Triassic "*Sinokannemeyeria* Fauna Beds" of Shansi, China;

Middle Triassic Las Cabras and Chañares formations of Argentina, Ntawere Formation of Zambia, and Manda Formation of Tanzania; Middle or Upper Triassic Santa Maria Formation of Brazil, and Potrerillos Formation of Argentina; Upper Triassic Ischigualasto Formation of Argentina, and Newark Group of Nova Scotia, Canada.

SUBFAMILY DIADEMODONTINAE New Rank.

Includes: Eudiademodontinae Lehman 1961; Gomphodontoinae Lehman 1961.

Primitive omnivorous or herbivorous diademodontids in which the postcanine dentition consists of an anterior series of simple pointed teeth, a middle series of transversely-expanded "molariform" teeth, and a posterior series grading from "sub-molariform" to sectorial; upper "molariform" teeth wider than long with a large outer cusp and one or two smaller inner cusps connected by a centrally-located transverse ridge; lower "molariform" teeth nearly circular in crown view with large outer and inner cusps joined by a centrally-located transverse ridge; lumbar ribs with broad overlapping expansions.

Genus *DIADEMODON* Seeley 1894b.

Synonyms: ? *Cynochampsa* Owen 1859; *Gomphognathus* Seeley 1895a; *Octagomphus* Broom 1919; *Cyclogomphodon* Broom 1919; *Protacmon* Watson 1920; *Sysphinctostoma* Broili and Schröder 1936; *Gomphodontoides* Brink and Kitching 1951b; *Cragievarus* Brink 1965.

DIADEMODON TETRAGONUS Seeley 1894b.

Synonyms: ? *Cynochampsa laniaria* Owen 1859; *Diademodon mastacus* Seeley 1894b; *Diademodon browni* Seeley 1894b; *Gomphognathus kannemeyeri* Seeley 1895a; *Gomphognathus polyphagus* Seeley 1895a; *Diademodon entomophonus* Seeley 1908; *Gomphognathus minor* Broom 1911; *Diademodon platyrhinus* Broom 1913a; *Trirachodon browni* Broom 1915a; *Cyclogomphodon platyrhinus* Broom 1919; *Octagomphus woodi* Broom 1919; *Protacmon brachyrhinus* Watson 1920; *Gomphognathus grossarthi* Broili and Schröder 1935a; *Gomphognathus broomi* Broili and Schröder 1935a; *Sysphinctostoma smithi* Broili and Schröder 1936; *Protacmon reubsameni* Broom 1950; *Sysphinctostoma gracilis* Broom 1950; *Gomphodontoides megalops* Brink and Kitching 1951b; *Diademodon parringtoni* Brink 1955; *Diademodon laticeps* Brink 1955; *Diademodon rhodesiensis* Brink 1963; *Cragievarus kitchingi* Brink 1965.

Horizon: Lower Triassic to Middle Triassic: Lower Triassic *Cynognathus* Zone of South Africa; Middle Triassic Ntawere Formation of Zambia.

Remarks: The named species of African diademodontines have been based on dental differences and variations in skull sizes and proportions which can be attributed to ontogenetic variation and, perhaps, sexual dimorphism, as well as to postmortem distortion. In the absence of valid criteria for distinguishing species of *Diademodon*, we prefer to recognize a single species. The earliest named diademodontine, *Cynochampsa laniaria,* is based on a fragmentary snout lacking postcanine teeth; we prefer to consider it a *nomen vanum*.

DIADEMODONTINAE incertae sedis:

Genus *ORDOSIODON* Young 1961.

ORDOSIODON LINCHEYUENSIS Young 1961.

Horizon: Lower or Middle Triassic: Beds approximately equivalent to *Cynognathus* Zone of Shansi, China.

Remarks: This species is based on a small dentary probably of juvenile diademodontine.

SUBFAMILY TRIRACHODONTINAE New Rank.
Primitive omnivorous or herbivorous diademodontids in which the postcanine dentition consists of transversely-expanded "molariform" teeth, plus one or two sectorial teeth at the posterior end of the tooth row (simple anterior teeth and "sub-molariform" posterior teeth are lacking); upper and lower "molariforms" of similar morphology, crowns with three main cusps in a transverse row across the centre of the tooth with cusps connected by ridges, margins of the crowns with continuous rim of small cingulum cusps; lumbar ribs with broad overlapping expansions.

Genus *TRIRACHODON* Seeley 1894b.
Synonyms: *Trirachodontoides* Broom 1932; *Inusitatodon* Brink and Kitching 1953.
TRIRACHODON BERRYI Seeley 1894b.
Synonyms: *Trirachodon kannemeyeri* Seeley 1895a; *Trirachodon minor* Broom 1905; *Trirachodontoides berryi* Broom 1932; *Inusitatodon smithi* Brink and Kitching 1953.
Horizon: Lower Triassic: *Cynognathus* Zone of South Africa.
Remarks: The named species are based on dental and size characteristics which change ontogenetically.

Genus *CRICODON* Crompton 1955.
CRICODON METABOLUS Crompton 1955.
Horizon: Middle Triassic: Manda Formation of Tanzania.

TRIRACHODONTINAE incertae sedis:
Genus *SINOGNATHUS* Young 1959.
SINOGNATHUS GRACILIS Young 1959.
Horizon: Lower or Middle Triassic: "*Sinokannemeyeria* Fauna Beds" of Shansi, China.
Remarks: Young believed this form to be a galesaurid, but it is clearly more advanced and appears to have "molariform" postcanine teeth of diademodontid, especially triracho-dontine, appearance.

SUBFAMILY TRAVERSODONTINAE Lehman 1961.
Includes: Gomphodontosuchinae Lehman 1961.
Advanced herbivorous diademodontids in which the postcanine dentition consists of transversely-expanded "molariform" teeth, with one or two sectorial teeth occurring only in certain ontogenetic stages of the more primitive species; upper postcanines with three main cusps in a transverse row behind the centre of the crown, with the outer cusp being the largest and possessing a vertical shear surface on its inner face, and with a small to very large basin in the central portion of the crown; lower· postcanines with two main cusps oriented more or less transversely on the anterior half of the crown and a basined "heel" on the posterior half of the crown, with the outer cusp possessing a vertical shear surface on its outer face; lower canine reduced in advanced forms; lumbar ribs with broad overlapping expansions in early members, but these become progressively reduced and ultimately lost in advanced members of the group.

Genus *TRAVERSODON* von Huene 1936.
TRAVERSODON STAHLECKERI von Huene 1936.
Synonyms: ? *Traversodon major* von Huene 1936.
Horizon: Middle or Upper Triassic: Santa Maria Formation of Brazil.
Remarks: ? *Traversodon major* is based on fragments which differ from *T. stahleckeri* only in size.

Genus *GOMPHODONTOSUCHUS* von Huene 1928.
GOMPHODONTOSUCHUS BRASILIENSIS von Huene 1928.
Horizon: Middle or Upper Triassic: Santa Maria Formation of Brazil.

Genus *PASCUALGNATHUS* Bonaparte 1966.
PASCUALGNATHUS POLANSKII Bonaparte 1966.
Horizon: Lower Triassic: Puesto Viejo Formation of Argentina.
Remarks: The earliest and most primitive traversodontine, it shows many resemblances to *Diademodon* indicating a diademodontine origin of traversodontines.

Genus *ANDESCYNODON* Bonaparte 1967b.
ANDESCYNODON MENDOZENSIS Bonaparte 1967b.
Horizon: Middle Triassic: Las Cabras Formation of Argentina.
Remarks: A primitive traversodontine, slightly more advanced than *Pascualgnathus.*

Genus *SCALENODON* Crompton 1955.
SCALENODON ANGUSTIFRONS (Parrington 1946).
Synonyms: *Trirachodon angustifrons* Parrington 1946; *Scalenodon angustifrons* Crompton 1955.
Horizon: Middle Triassic: Manda Formation of Tanzania.

Genus *LUANGWA* Brink 1963.
LUANGWA DRYSDALLI Brink 1963.
Horizon: Middle Triassic: Ntawere Formation of Zambia.
Remarks: Although its postcanine morphology is not adequately known, this species seems to be distinct.

Genus *MASSETOGNATHUS* Romer 1967.
MASSETOGNATHUS PASCUALI Romer 1967.
Synonyms: *Massetognathus teruggii* Romer 1967.
Horizon: Middle Triassic: Chañares Formation of Argentina.
Remarks: The type skull of *M. teruggii* differs from that of *M. pascuali* in no significant features other than size. It is here considered to be an old individual of the latter species.

Genus *EXAERETODON* Cabrera 1943.
Synonyms: *Theropsis* Cabrera 1943; *Proexaeretodon* Bonaparte 1963b.
EXAERETODON ARGENTINUS (Cabrera 1943).
Synonyms: *Belesodon? argentinus* Cabrera 1943; *Exaeretodon frenguellii* Cabrera 1943; *Theropsis robusta* Cabrera 1943; *Exaeretodon argentinus* Bonaparte 1962; *Proexaeretodon vincei* Bonaparte 1963b.
Horizon: Upper Triassic: Ischigualasto Formation of Argentina.
Remarks: With the exception of the following form, all Ischigualasto traversodontines can be accommodated in a single species for which the name *E. argentinus* has page priority.

Genus *ISCHIGNATHUS* Bonaparte 1963a.
ISCHIGNATHUS SUDAMERICANUS Bonaparte 1963a.
Horizon: Upper Triassic: Ischigualasto Formation of Argentina.
Remarks: This species is similar to, but apparently distinct from, *Exaeretodon.*

Genus *SCALENODONTOIDES* Crompton and Ellenberger 1957.
SCALENODONTOIDES MACRODONTES Crompton and Ellenberger 1957.
Horizon: Upper Triassic: Lower part of the Red Beds, Stormberg Series, of Lesotho.
Remarks: The type specimen was said to be from the Molteno Beds, but Crompton (in Cox 1969) and Turner (in press) have since determined that it is from the overlying Red Beds. *Scalenodontoides* is very similar to *Exaeretodon* and the two may prove to be identical.

TRAVERSODONTINAE incertae sedis:

Genus *THEROPSODON* von Huene 1950.

THEROPSODON NJALILUS von Huene 1950 *nomen vanum*.

Horizon: Middle Triassic: Manda Formation of Tanzania.

Remarks: This form is based on a complete but poorly preserved skull with lower jaws in place. Because several other genera and species of traversodontines, mostly undescribed, are now known from the Manda Formation and are differentiated primarily on the basis of postcanine morphology, which is not readily available in the type specimen of *T. njalilus*, we believe it is best to consider it a *nomen vanum*.

Genus *COLBERTOSAURUS* Minoprio 1957.

Synonym: *Colbertia* Minoprio 1954.

COLBERTOSAURUS MURALIS (Minoprio 1954).

Synonyms: *Colbertia muralis* Minoprio 1954; *Colbertosaurus muralis* Minoprio 1957.

Horizon: Middle or Upper Triassic: Potrerillos Formation of Argentina.

Remarks: This species is inadequately known, being based on a fragmentary dentary. Bonaparte (1966) compares it to the traversodontines *Andescynodon* and *Pascualgnathus*.

FAMILY TRITYLODONTIDAE Cope 1884.

Includes: Bienotheriidae Young 1940.

Very advanced herbivorous cynodonts in which one pair of upper and lower incisors is greatly enlarged, canines are absent, and multiple-rooted postcanine teeth bear three (upper) or two (lower) longitudinal rows of crescentic cusps; postorbital bar and prefrontal and postorbital bones absent; lumbar ribs lack overlapping expansions.

Horizon: Upper Triassic to Middle Jurassic: Upper Triassic Red Beds and Cave Sandstone, Stormberg Series, of South Africa and Lesotho; Lufeng Series of Yunnan, China; Los Colorados Formation of Argentina; Kayenta Formation of the United States; Rhaetic of Germany; Lower Jurassic fissures of England; Middle Jurassic Stonesfield Slate of England.

Genus *TRITYLODON* Owen 1884.

Synonyms: *Likhoelia* Ginsburg 1961; *Tritylodontoideus* Fourie 1962.

TRITYLODON LONGAEVUS Owen 1884.

Synonyms: *Likhoelia ellenbergeri* Ginsburg 1961; ? *Tritylodontoideus maximus* Fourie 1962; ? *Tritylodontoides maximus* Fourie 1963;

Horizon: Upper Triassic: Red Beds and Cave Sandstone, Stormberg Series, of South Africa and Lesotho.

Remarks: The generic name *Tritylodon* should be restricted to southern African forms and should not be applied to isolated teeth from the Rhaeto-Lias of Europe (see *Tritylodon fraasi* below), as the latter are, in fact, generically indeterminate. *Likhoelia* is based on a juvenile specimen of *T. longaevus*. Kitching (ms.) believes *Tritylodontoideus* to be a large *T. longaevus*.

Genus *BIENOTHERIUM* Young 1940.

BIENOTHERIUM YUNNANENSE Young 1940.

Synonyms: *Bienotherium elegans* Young 1940.

Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.

Remarks: *B. elegans* is based on an immature *B. yunnanense*.

BIENOTHERIUM MAGNUM Chow 1962.

Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.

Remarks: *B. magnum* is recognized as a distinct species because

it comes from a higher horizon than *B. yunnanense* and is much larger.

Genus *LUFENGIA* Chow and Hu 1959.

LUFENGIA MINOR (Young 1947).

Synonyms: *Bienotherium minor* Young 1947; *Lufengia delicata* Chow and Hu 1959; *Lufengia minor* new combination.

Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.

Remarks: Hopson (ms.) believes *B. minor* Young pertains to the genus *Lufengia*.

Genus *OLIGOKYPHUS* Hennig 1922.

Synonyms: *Mucrotherium* E. von Heune 1933 *Uniserium* E. von Huene 1933.

OLIGOKYPHUS TRISERIALIS Hennig 1922.

Synonyms: *Oligokyphus biserialis* Hennig 1922; *Mucrotherium cingulatum* E. von Huene 1933; *Uniserium enigmaticum* E. von Huene 1933.

Horizon: Lower Jurassic: Liassic Bonebed of Germany.

OLIGOKYPHUS MAJOR Kühne 1956.

Synonyms: *Oligokyphus minor* Kühne 1956.

Horizon: Lower Jurassic: Lower Lias Fissures of Somerset, England.

Remarks: Kühne described two size groups of *Oligokyphus* from a single fissure to which he gave separate names. We believe it more likely that the groups represent male and female of a single species for which the name *O. major* has priority.

Genus *STEREOGNATHUS* Charlesworth 1855.

STEREOGNATHUS OOLITICUS Charlesworth 1855.

Horizon: Middle Jurassic: Stonesfield slate of Oxfordshire, England.

Remarks: This is the latest known therapsid reptile.

TRITYLODONTIDAE OF UNCERTAIN TAXONOMIC POSITION

TRITYLODON FRAASI Lydekker 1887 *nomen vanum*

Synonyms: *"Triglyphus"* O.Fraas 1866; *Tritylodon fraasi* Lydekker 1887; *Triglyphus fraasi* Hennig 1922.

Horizon: Rhaeto-Liassic Bonebed of Wurttemberg, Germany.

Remarks: The type and only specimen of this species, an isolated upper postcanine tooth, is lost. Because its crown pattern is identical to that of several genera of tritylodontids, it is not diagnostic and is best regarded as a *nomen vanum*.

CHALEPOTHERIUM PLIENINGERI (Ameghino 1903) *nomen vanum.*

Synonyms: *Microlestes plieningeri* Ameghino 1903; *Chalepotherium plieningeri* Simpson 1928.

Horizon: Rhaeto-Liassic Bonebed of Wurttemberg, Germany.

Remarks: The type and only specimen of this species consists of a damaged upper postcanine tooth which is not diagnostic as to genus or species; therefore, *C. plieningeri* is a *nomen vanum.*

CYNODONTIA incertae sedis:

Genus MICROHELODON Broom 1931.

MICROHELODON EUMERUS (Seeley 1895a) *nomen vanum.*

Synonyms: *Microgomphodon eumerus* Seeley 1895a; *Microhelodon eumerus* Broom 1931.

Horizon: Lower Triassic: *Cynognathus* Zone of South Africa.

Remarks: The type and only specimen is a damaged snout which may pertain to a bauriamorph or to a cynodont. Seeley associated a cynodont skeleton with the type, but

Broom (1931) and Brink (1955) consider this association to be incorrect.

Genus *ARCHAEODON* von Huene 1925.
ARCHAEODON REUNINGI von Huene 1925.
Horizon: Upper Triassic? : "Youngest Stormberg" equivalent? of South-West Africa.
Remarks: The type and only specimen is an isolated tooth with divided roots, but lacking the crown. It does not appear to be referable to the Tritylodontidae and is unlike any known Triassic mammal. We question the correctness of the reported Triassic age.

Genus *DROMATHERIUM* Emmons 1857.
DROMATHERIUM SYLVESTRE Emmons 1857.
Horizon: Upper Triassic: Cumnock Formation, Newark Group, of North Carolina, United States.
Remarks: This incomplete dentary with damaged postcanine teeth may belong to a cynodont or to a mammal. Its affinities are at present indeterminate.

Genus *MICROCONODON* Osborn 1886.
Synonyms: *Tytthoconus* Palmer 1903.
MICROCONODON TENUIROSTRIS Osborn 1886.
Synonyms: *Tytthoconus tenuirostris* Palmer 1903.
Horizon: Upper Triassic: Cumnock Formation, Newark Group, of North Carolina, United States.
Remarks: This tiny dentary is possibly a mammal, or it may be a cynodont, most likely a chiniquodontid, close to the reptile-mammal class boundary.

Genus *KUNMINIA* Young 1947.
KUNMINIA MINIMA Young 1947 *nomen vanum.*
Horizon: Upper Triassic: Lower Lufeng Series of Yunnan, China.
Remarks: This poorly-preserved little skull may be that of a mammal, possibly the same as *Morganucodon oehleri* from the same beds. The specimen as now known is indeterminate and the name is best considered a *nomen vanum.*

Genus *TRICUSPES* E. von Huene 1933.
TRICUSPES TUBINGENSIS E. von Huene 1933.
Horizon: Lower Jurassic: Liassic Bonebed of Germany.
Remarks: This isolated tooth may pertain to a cynodont, to a mammal, or to some unknown reptilian type.

Genus *EORAETIA* Dietrich 1937.
EORAETIA SIEGERTI Dietrich 1937.
Horizon: Upper Triassic or Lower Jurassic: Rhaeto-Lias of Halberstadt, Germany.
Remarks: The affinities of this isolated ulna are uncertain.

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