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A COMPREHENSIVE TAXONOMIC REVISION OF *DICYNODON* (THERAPSIDA, ANOMODONTIA) AND ITS IMPLICATIONS FOR DICYNODONT PHYLOGENY, BIOGEOGRAPHY, AND BIOSTRATIGRAPHY

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ABSTRACT—The dicynodont wastebasket genus *Dicynodon* is revised following a comprehensive review of nominal species. Most nominal species of *Dicynodon* pertain to other well-known dicynodont genera, especially *Oudenodon* and *Diictodon*. Of the Karoo Permian species that are referable to "*Dicynodon*" sensu lato, we recognize four common, valid morphospecies: *Dicynodon lacerticeps*, *D. leoniceps*, *D. woodwardi*, and *Dinanomodon gilli*, comb. nov. Eleven additional species of "*Dicynodon*" are recognized worldwide: *D. alticeps*, *D. amalitzkii*, *D. bathyrhynchus*, *D. benjamini*, *D. bogdaensis*, *D. huenei*, *D. limbus*, *D. sinkianensis*, *D. traquairi*, *D. trautscholdi*, and *D. vanhoepeni*. Morphometric analysis of *D. lacerticeps* and *D. leoniceps* specimens recovers statistically significant separation between these species in snout profile and squamosal shape, supporting their distinction. A new phylogenetic analysis of Anomodontia reveals that "*Dicynodon*" is polyphyletic, necessitating taxonomic revision at the generic level. *D. benjamini* and *D. limbus* are basal cryptodonts, whereas the other valid "*Dicynodon*" species are basal dicynodontoids. The genus *Dicynodon* is restricted to *D. lacerticeps* and *D. huenei*. We reinstate use of *Daptocephalus*, *Sintocephalus*, *Turfanodon*, *Daqingshanodon*, *Jimusaria*, and *Gordonia* for other species. We synonymize *Vivaxosaurus permirus* and *Dicynodon trautscholdi* (as *V. trautscholdi*, comb. nov.) We establish new generic names for several species formerly included in *Dicynodon*: *Peramodon amalitzkii*, comb. nov., *Keyseria benjamini*, comb. nov., *Euptychognathus bathyrhynchus*, comb. nov., *Syops vanhoepeni*, comb. nov., and *Basilodon woodwardi*, comb. nov. Of the main Karoo Permian taxa, *Dicynodon*, *Basilodon*, and *Dinanomodon* range throughout the *Cistecephalus* and *Dicynodon* assemblage zones, but *Daptocephalus* is restricted to the *Dicynodon* Assemblage Zone.

Broom (1911:1081):

> "*Dicynodon* is the most troublesome genus we have to deal with. Specimens differ so greatly in size and shape that one hardly knows what to do unless one does as was practically done by Owen, make every specimen the type of a distinct species. For many years to come the genus *Dicynodon* must remain in utter confusion, and will be useless for stratigraphic work."

Haughton (1917:127):

> "The genus *Dicynodon* is an exceedingly troublesome one to work, on account of the large variety of forms which have been assigned to it, forms the types of which are now deposited in collections in widely separated parts of the world, which types are occasionally rather fragmentary and not particularly well defined."

Sushkin (1926:325):

> "A natural arrangement of the species within the enormous genus *Dicynodon* has never been attempted, most species being well characterised by a peculiar combination of characters of which the genetical value and the lines of radiation are obscure."

Watson (1948:875–876):

> "In these circumstances, it is evident that only a study of a large series of completely prepared skulls of *Dicynodon* would make it possible to disentangle the lines of descent amongst the Anomodonts and allow the great group of species of *Dicynodon* to be divided amongst a soundly based series of genera."

INTRODUCTION

Dicynodon is one of the canonical figures from the early days of vertebrate paleontology. It was the first fossil vertebrate described from South Africa and provided the first evidence of mammal-like features in a taxon outside of Mammalia. It is enshrined with the likes of *Ichthyosaurus*, *Iguanodon*, *Megalosaurus*, and *Plesiosaurus* in the Crystal Palace gardens near London (Fig. 1), where it has inspired generations as an emblem of the prehistoric world. Like its Crystal Palace companions, by virtue of being the first representative discovered of a major fossil group, it served for many decades as a taxonomic dumping ground for generalized members of that group. But whereas those other venerable genera have been subject to extensive revision in recent years (all but *Ichthyosaurus* have since been restricted to the type species) (Storrs, 1997; Großmann, 2007; Benson, 2010; Maisch, 2010; McDonald et al., 2010; Norman, 2010), *Dicynodon* has languished in a state of taxonomic inflation greater today than in the 19th century. In part, this is because the sheer number of nominal species of *Dicynodon* (168) makes this a daunting taxon to work on. This problem is aggravated by the poor preparation of many *Dicynodon* type specimens and the minor differences originally used to separate its species. In the century since Broom's (1911) pessimistic (but accurate) comments on the state of *Dicynodon* research quoted above, extensive progress has been made in resolving dicynodont

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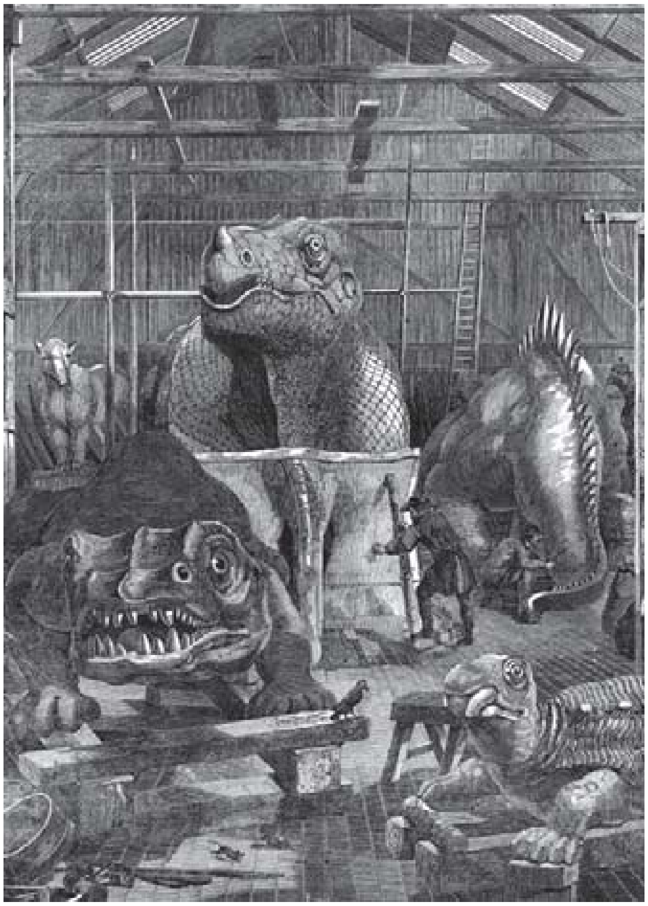

FIGURE 1. *Dicynodon* then—an illustration of Benjamin Waterhouse Hawkins' Sydenham worskshop, showing *Palaeotherium* (top left), *Iguanodon* (top center), *Hylaeosaurus* (top right), *Labyrinthodon* (bottom left), and *Dicynodon* (bottom right) under construction. The Crystal Palace *Dicynodon* specimens were restored as tusked turtle-like creatures with complete carapaces, scaly integument, and sprawling limbs.

alpha taxonomy and systematics (Cox, 1959, 1964; Cruickshank, 1967; Keyser, 1973, 1975, 1993; Keyser and Cruickshank, 1979; Cluver and Hotton, 1981; Tollman et al., 1981; Cluver and King, 1983; King, 1988, 1990; King and Rubidge, 1993; Angielczyk 2001, 2002a, 2004; Maisch 2002a, 2002b; Angielczyk and Kurkin, 2003a; Modesto et al., 2003; Maisch and Gebauer, 2005; Sullivan and Reisz, 2005; Grine et al., 2006; Fröbisch, 2007; Angielczyk and Sullivan, 2008; Fröbisch and Reisz, 2008; Angielczyk et al., 2009; Kammerer and Angielczyk, 2009), but *Dicynodon* itself has remained problematic, speciose, and vaguely defined. To understand why this problem has persisted to the present day, a brief history of *Dicynodon* research is warranted.

Anomodontia and its major subclade Dicynodontia were among the most species-rich and abundant tetrapod clades of the Permian and Triassic (for a recent review, see Fröbisch, 2009). Anomodonts were the dominant herbivores of their time and exhibited enormous ecological diversity, including large browsing (Fig. 2), small burrowing, and even climbing forms (Cox, 1972; Hotton, 1986; Fröbisch and Reisz, 2009). Owen (1845) initially described *Dicynodon* based on a set of skulls collected by A. G. Bain near Fort Beaufort in the Karoo Basin of South Africa, which were made the type specimens of *Dicynodon lacerticeps* (the type species), *D. bainii* (= *Aulacephalodon bainii*), and *D. strigiceps* (indeterminate, but potentially a specimen of *Oudenodon bainii*). *Dicynodon* was the first 'mammal-like reptile' to be described as such: Kutorga (1838) described the Russian dinocephalians *Syodon*, *Brithopus*, and *Orthopus* several years earlier, but considered these taxa to be extinct representatives of modern mammalian groups. Owen, however, recognized that although *Dicynodon* was clearly of a 'reptilian' grade, its skeleton exhibited a set of characters otherwise known only in mammals. In the following years Owen described additional species of *Dicynodon* (Owen, 1855) and new genera of dicynodonts (*Ptychognathus* Owen, 1859, and *Oudenodon* Owen, 1860b), culminating in his monographic catalogue of South African fossil reptiles (Owen, 1876). The Catalogue introduced a number of new *Dicynodon* species and solidified the wastebasket composition of the genus (essentially, all tusked dicynodonts lacking postcanine teeth), because Owen's species included specimens currently placed in *Aulacephalodon*, *Dicynodontoides*, *Diictodon*, *Lystrosaurus*, and *Tropidostoma*.

Lydekker (1890) referred extensive additional Karoo material in the collections of the Natural History Museum (London) to Owen's species and tentatively synonymized some of them (e.g., he suggested that *Dicynodon recurvidens* could represent the juvenile of *Dicynodon leoniceps*). Seeley (1898) made the first attempt to divide *Dicynodon* and *Oudenodon* into subgenera, breaking them into *Rhachicephalodon* and *Aulacephalodon* (for *Dicynodon*) and *Rhachiocephalus* and *Aulacocephalus* (for *Oudenodon*) based on degree of prognathism (high in *Rhachicephalodon* and *Rhachiocephalus*). Broom (1903) broke from the earlier Dicynodontia (tusked dicynodonts)-Cryptodontia (tuskless dicynodonts) split, recognizing a close relationship between *Dicynodon* and *Oudenodon* and placing both in Dicynodontidae. Instead, he separated the more clearly aberrant dicynodont genera into separate families: Endothiodontidae (containing *Endothiodon*, *Esoterodon*, *Cryptocynodon*, and *Pristerodon*), Lystrosauridae (containing *Lystrosaurus* and tentatively the Scottish taxa *Gordonia* and *Geikia*), and Cistecephalidae (monotypic, *Cistecephalus*).

Broom made several advances reigning in the unwieldy, wastebasket composition of 19th century *Dicynodon*: he solidified the distinction between *Dicynodon* and *Lystrosaurus* (*Lystrosaurus declivis* was recognized as distinct from *Dicynodon* by Owen, but various other species, including *L. curvatus* and *L. murrayi*, were originally named as species of *Dicynodon*), removed the large Middle Triassic species of "*Dicynodon*" and transferred them to Seeley's (1909) genus *Kannemeyeria*, and recognized the distinct nature of the broad-skulled "*Dicynodon*" species with massive nasal bosses (first by creating a new genus, *Bainia* [Broom, 1921], but later [Broom, 1932] recognizing the priority of Seeley's [1898] name *Aulacephalodon* for these species, albeit misspelling it as '*Aulacocephalodon*'). Unfortunately, these forward steps in revising *Dicynodon* taxonomy were outweighed by a massive step backwards: Broom's decision that *Oudenodon*, recognized as a separate taxon since Owen's (1860b) initial description, represented the tuskless female of *Dicynodon*. To be fair, this idea did not originate with Broom: 19th century diagnoses of *Dicynodon* and *Oudenodon* strongly emphasized the presence/absence of tusks in distinguishing these genera, and Lydekker (1890) mentioned (although he did not agree with) the possibility that they could represent sexual dimorphs of a single taxon. Thus, when Broom (1912a) discovered evidence for tusk dimorphism in the small dicynodont *Diaelurodon whaitsi* (= *Pristerodon mackayi*), with nearly half the specimens at a locality being tuskless but otherwise identical to their tusked counterparts, the realization that dicynodonts could have tusk dimorphism cast sufficient doubt on tusklessness as a unique character of *Oudenodon* to permit

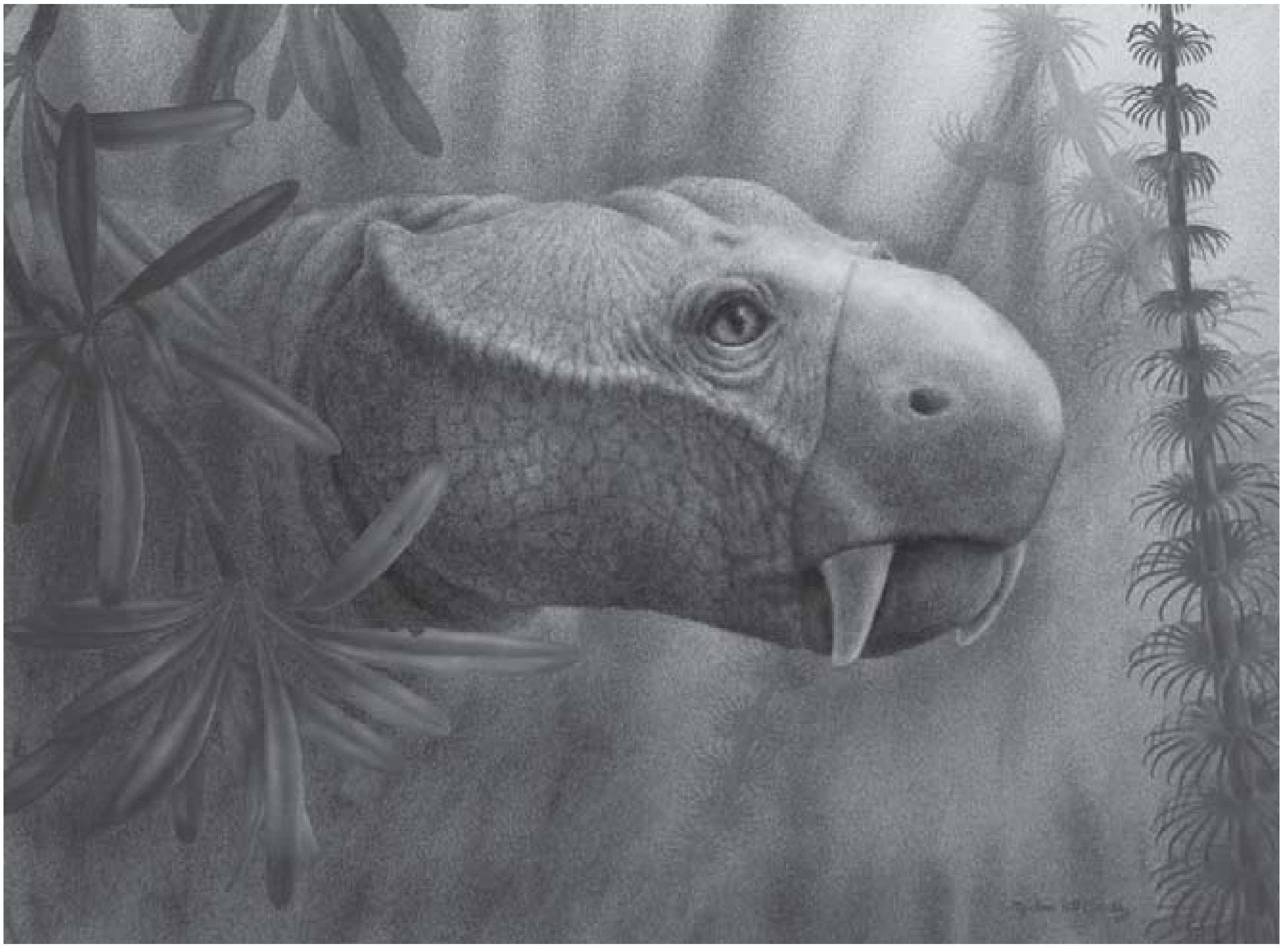

FIGURE 2. *Dicynodon* now—a study of the head of *Dicynodon lacerticeps* emerging from a Late Permian thicket, restoring the taxon with a keratinous beak covering the tip of the snout and fleshy, glandular skin befitting its position as a stem member of the mammalian lineage. Art by Marlene Donnelly.

synonymy with *Dicynodon*. Broom (1913a) transferred all nominal species of *Oudenodon* (except for *Oudenodon rugosus*, a Russian anteosaurid dinocephalian; see Efremov, 1954; Kammerer, 2011) to *Dicynodon*, nearly doubling the size of the latter. Although Broom synonymized *Oudenodon* with *Dicynodon*, all the species of *Oudenodon* were retained as valid in new combinations, i.e., no species of *Oudenodon* were considered to represent females of known species of *Dicynodon*. This may seem like an unusual double standard from a modern taxonomic standpoint, but it follows Broomian taxonomic logic, in which minor proportional differences or stratigraphic and/or geographic separation were sufficient to recognize specific distinction, but generic distinction necessitated either major morphological differences or different tooth counts (hence the dozens of species of *Dicynodon* but different genera for nearly every theriodont specimen Broom described). Under this system, most species were known only from the holotype, so it makes sense that there should be a 50/50 chance that any given species of "*Dicynodon*" should be represented only by a tusked (*Dicynodon*) or tuskless (*Oudenodon*) specimen. In subsequent years Broom, Boonstra, Haughton, and Watson went on to name 26 species of *Dicynodon* based on tuskless *Oudenodon*-morph holotypes, all of which are currently considered synonyms of *Oudenodon bainii* (see Keyser [1975] and the Species Accounts below). Eventually, the discovery of *Oudenodon* bone beds, with no tusked dicynodonts mixed in, led Broom (1940a) to concede that that some species of *Dicynodon* (e.g., *D. platyceps*) must have been tuskless in males and females, but this realization did not prompt him to reconsider the synonymy of *Oudenodon* and *Dicynodon*.

For the most part, other treatments of dicynodont systematics in the first half of the 20th century followed Broom's taxonomic scheme, and the broadly inclusive *Dicynodon* (including *Oudenodon* as well as species currently referred to *Aulacephalodon*, *Dicynodontoides*, *Diictodon*, *Emydops*, *Odontocyclops*, *Pelanomodon*, *Pristerodon*, *Rhachiocephalus*, and *Tropidostoma*) was maintained (e.g., Haughton, 1917, 1924; Watson, 1917; Haughton and Brink, 1954). Two systematic reviews of dicynodonts during this period merit particular attention, however, for their foresight and focus on characters of phylogenetic import: those of van Hoepen (1934) and Toerien (1953). Van Hoepen (1934) included a review of dicynodont systematics in his description of the new taxa *Compsodon helmoedi* and *Oudenodon margaritae*; both this review and *Compsodon* itself unfortunately received relatively little attention in subsequent years, in part because of harsh criticism by Broom (1938). Van Hoepen (1934) divided non-endothiodont dicynodonts into Compsodontidae (nearly equivalent in composition to the modern Emydopoidea, and including *Emydops*, *Cistecephalus*, and *Myosaurus*) and Dicynodontidae. He split Dicynodontidae into five subfamilies, each containing species of *Dicynodon* sensu Broom: Dicynodontinae (including *Dicynodon*, *Daptocephalus*, and *Kannemeyeria*), Pylaecephalinae (including *Pylaecephalus* and *Diictodon*), Oudenodontinae (including *Oudenodon* and *Aulacocephalodon* [sic]), Pelorocyclopinae (including *Rachiocephalus* [sic], *Eocyclops*, *Megacyclops*, *Pelorocyclops*, and *Platycyclops*), and Orophicephalinae (including *Orophicephalus* and *Palemydops*). Van Hoepen (1934) named *Daptocephalus* to house species of *Dicynodon* characterized by an extremely narrow, elongate intertemporal bar in which the postorbitals meet on the midline. Two of the species included in *Daptocephalus* have subsequently been demonstrated to represent very different dicynodonts (*D. recurvidens* has been transferred to *Dicynodontoides* [Angielczyk et al., 2009] and *D. lutriceps* has been synonymized with *Oudenodon bainii* [Keyser, 1975]), but the rest form a coherent morphotype. Additionally, van Hoepen (1934) was the first to recognize the distinction between the taxa now known as *Dicynodon* and *Diictodon*. Broom (1913c) erected the new genus *Diictodon* based solely on the apparent confinement of the pineal foramen within the preparietal (a condition now known to be variable within *Diictodon feliceps*), whereas van Hoepen (1934) recognized that several nominal species of *Dicynodon* were very similar to *Diictodon* in a number of respects, particularly intertemporal morphology. These species (*D. ictidops*, *D. macrorhynchus*, *D. rubidgei*, *D. sollasi*, and *D. testudirostris*) were placed in the new genus *Pylaecephalus*, and along with *Diictodon* made up the Pylaecephalinae. Currently, all of these species are considered synonyms of *Diictodon feliceps* (Sullivan and Reisz, 2005) and Pylaecephalinae has been resurrected (as Pylaecephalidae) to refer to the clade containing *Diictodon* and its closest relatives (Kammerer and Angielczyk, 2009; Angielczyk and Rubidge, 2010). Oddly, van Hoepen retained *D. psittacops* and *D. feliceps* itself in *Dicynodon* (as the only valid species other than *D. lacerticeps*), but it should be noted that the holotypes of both species are somewhat aberrant for *Diictodon* (that of *D. psittacops* is highly distorted and that of *D. feliceps* is unusually large, with massive tusks). Finally, van Hoepen (1934) continued to recognize *Oudenodon* as a distinct genus, and considered *Aulacephalodon* and *Rhachiocephalus* to be its closest relatives (indicated in his fig. 19, an early evolutionary tree of dicynodonts), a notable precursor to the current conception of Cryptodontia.

Toerien (1953) focused on dicynodont palatal morphology. He recognized consistent differences between the palates of *Dicynodon* and *Oudenodon*, and treated the latter genus as valid. Toerien (1953) followed several aspects of van Hoepen's (1934) systematic arrangement, including restricting Dicynodontidae to *Dicynodon*, *Daptocephalus*, and *Kannemeyeria* and placing *Oudenodon* in a separate group (in this case by resurrecting Owen's [1860a] Cryptodontia for *Oudenodon*, *Kitchingia* and *Platycylops* [= *Rhachiocephalus*], and *Pelanomodon*; unlike van Hoepen [1934], Toerien [1953] did not consider *Aulacephalodon* to belong to this group because it had tusks). Toerien (1953) explicitly considered *Dicynodon* to be a paraphyletic genus, the species of which (including species currently considered synonymous with *Diictodon feliceps*; Toerien [1953] did not recognize van Hoepen's [1934] Pylaecephalinae) made up an evolutionary series ancestral to *Aulacephalodon*, *Daptocephalus*, *Lystrosaurus*, and *Kannemeyeria*. Excepting the inclusion of *Aulacephalodon*, this arrangement is very similar to the modern conception of Dicynodontoidea, with *Dicynodon* basal to the two major Triassic dicynodont clades.

Although occasional synonymies between *Dicynodon* species had been tentatively proposed since Lydekker's (1890) day, the first major alpha taxonomic revisions of *Dicynodon* were produced by Keyser (1973, 1975), who demonstrated that many nominal species of the genus were instead referable to *Tropidostoma microtrema* or *Oudenodon bainii*. Keyser (1975) recognized that much of the variation in skull shape between different nominal species of "*Dicynodon*" was attributable to taphonomic deformation and ontogenetic variation. The next major revision was that of Cluver and Hotton (1981), who distinguished the cranial morphologies of *Dicynodon*, *Oudenodon*, *Kingoria*, and *Diictodon*, and referred many former *Dicynodon* species to the latter two genera. Although this work removed many species from *Dicynodon*, it did not synonymize them within genera, so *Dicynodon*, *Diictodon*, and *Kingoria* remained speciose. Broad, sweeping synonymies of Permian dicynodont taxa were proposed in species lists by Brink (1986), but not supported in his text. More recently, reviews of the species compositions of *Diictodon* (King, 1993; Sullivan and Reisz, 2005; Angielczyk and Sullivan, 2008) and *Kingoria* (= *Dicynodontoides*) (Angielczyk et al., 2009) have greatly reduced the number of valid species within these genera (one in *Diictodon*, two in *Dicynodontoides*).

Even with the advances made in distinguishing distantly related dicynodonts such as *Diictodon* and *Oudenodon* from *Dicynodon* proper, there remain more than 30 currently accepted species of *Dicynodon* in the Late Permian of South Africa alone (King, 1988), and many more worldwide. Furthermore, some previous synonymies (e.g., several species listed as probable synonyms of *Diictodon feliceps* by Sullivan and Reisz [2005]) were noted at the time as being tentative, and some previous referrals have already been contested (e.g., Cox's [1965] referral of *Dicynodon galecephalus* to *Kingoria*—Angielczyk et al. [2009] argued that this species does indeed represent *Dicynodon*). Here we present a comprehensive revision of *Dicynodon*, reexamining every nominal species in order to recognize consistent, biologically meaningful morphospecies that can be used in phylogenetic and biostratigraphic studies.

ALPHA TAXONOMIC REVISION OF *DICYNODON*

Materials and Methods

We personally examined the holotypes of every nominal *Dicynodon* species, except in those cases in which the type specimen is lost, in which case we took information from the original description (Owen, 1876; Broom, 1907, 1932, 1937b, 1940a, 1940b; Repelin, 1923; Boonstra, 1948). Our alpha taxonomic review of these species went through three major phases: first, we determined whether a holotype was referable to 'core *Dicynodon*,' i.e., represented a Permian dicynodontoid (Fig. 3), or whether it could be referred to a known non-dicynodontoid taxon such as *Diictodon feliceps* or *Oudenodon bainii*. In the case of the latter, we made referrals based on comparisons with holotypes, well-preserved referred specimens, and recent descriptions of the taxa in question (Sullivan and Reisz, 2005; Botha and Angielczyk, 2007; Angielczyk et al., 2009). For the 'core *Dicynodon*' species, we first examined South African specimens, because they represent the bulk of nominal species. We binned these specimens into morphotypes diagnosed by discrete characters and consistent proportional differences observed across a range of sizes and styles of taphonomic deformation, and thus unlikely to be the result of ontogenetic variation or distortion. The vast majority of South African species could be referred to one of four morphotypes: (1) Morphotype A, including *Dicynodon lacerticeps* as the oldest nominal species; (2) Morphotype B, including *Dicynodon leoniceps* as the oldest nominal species; (3) Morphotype C, including *Dicynodon woodwardi* as the oldest nominal species; (4) and Morphotype D, including *Dicynodon gilli* as the oldest nominal species. Extrabasinal Permian dicynodontoid species were

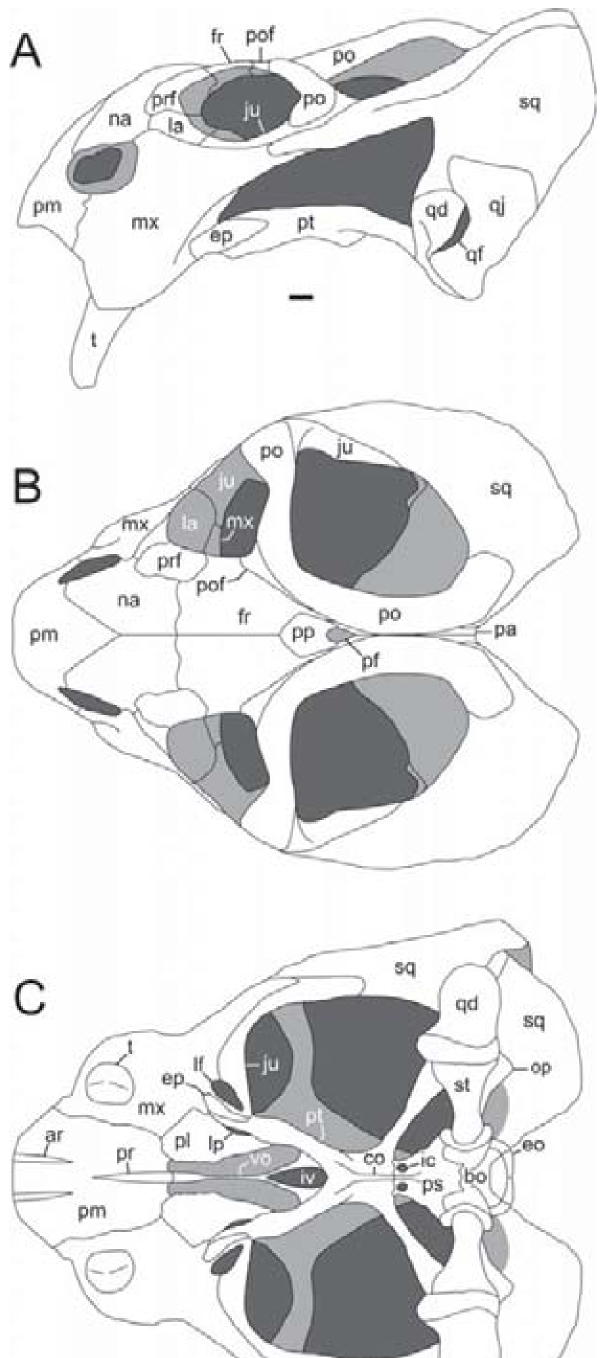

FIGURE 3. Cranial anatomy of a representative Permian dicynodontoid, *Dicynodon lacerticeps*, in (**A**) left lateral, (**B**) dorsal, and (**C**) palatal views. **Abbreviations**: **ar**, anterior palatal ridge; **bo**, basioccipital; **co**, crista oesophagea; **eo**, exoccipital; **ep**, ectopterygoid; **fr**, frontal; **ic**, opening for internal carotid artery; **iv**, interpterygoid vacuity; **ju**, jugal; **la**, lacrimal; **lf**, labial fossa; **lp**, lateral palatal fenestra; **mx**, maxilla; **na**, nasal; **op**, opisthotic; **pa**, parietal; **pf**, pineal foramen; **pl**, palatine; **pm**, premaxilla; **po**, postorbital; **pof**, postfrontal; **pp**, preparietal; **pr**, median palatal ridge; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **qd**, quadrate; **qf**, quadratojugal foramen; **qj**, quadratojugal; **sq**, squamosal; **st**, stapes; **t**, caniniform tusk; **vo**, vomer. Scale bar equals 2 cm.

then compared to these four morphotypes and to each other to determine their possible validity—in all cases the extrabasinal 'core *Dicynodon*' species possessed combinations of characters distinguishing them from the Karoo representatives of the genus.

Institutional Abbreviations—**AMG**, Albany Museum, Grahamstown, South Africa; **AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **ANSP**, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.; **BGS GSE**, British Geological Survey, Murchison House Museum, Edinburgh, Scotland, U.K.; **BP**, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa; **BSP**, Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, Germany; **CAMZM**, University Museum of Zoology, Cambridge, England, U.K.; **CGP**, Council for Geosciences, Pretoria, South Africa; **ELGNM**, Elgin Museum, Elgin, Scotland, U.K.; **ELM**, East London Museum, East London, South Africa; **FMNH**, The Field Museum of Natural History, Chicago, Illinois, U.S.A.; **GPIT**, Institut und Museum für Geologie und Paläontologie der Eberhard-Karls-Universität Tübingen, Germany; **GSI**, Curatorial Division, Geological Survey of India, Kolkata, India; **IGCAGS**, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; **LM**, Livingstone Museum, Livingstone, Zambia; **MMK**, McGregor Museum, Kimberley, South Africa; **MNHN**, Muséum national d'Histoire naturelle, Paris, France; **NHMUK**, The Natural History Museum, London, England, U.K.; **NMQR**, National Museum, Bloemfontein, South Africa; **NMW**, Naturhistorisches Museum Wien, Vienna, Austria; **OXFUM**, Oxford University Museum of Natural History, Oxford, U.K.; **PEM**, Port Elizabeth Museum, Port Elizabeth, South Africa; **PIN**, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **RC**, Rubidge Collection, Wellwood, Graaff-Reinet, South Africa; **ROZ**, Roy Oosthuizen Collection, currently housed in Iziko, The South African Museum, Cape Town, South Africa; **SAM**, Iziko, The South African Museum, Cape Town, South Africa; **SGU**, Scientific Research Institute of Saratov State University, Moscow, Russia; **SMFNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **TM**, Ditsong, the National Museum of Natural History, Pretoria, South Africa; **TSK**, Zambian specimens currently in the collection of Prof. Thomas Kemp, Oxford University Museum of Natural History, Oxford, U.K.; **UCMP**, University of California Museum of Paleontology, Berkeley, California, U.S.A.; **USNM**, National Museum of Natural History, Washington, D.C., U.S.A.

Species Accounts

Dicynodon acutirostris Broom, 1935

Holotype—TM 250, a partial skull missing the right zygomatic arch and temporal region (Fig. 4).

Locus Typicus—Leeukloof, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Tropidostoma dubium* (Owen, 1876).

Remarks—Broom (1935:71) described *Dicynodon acutirostris* on the basis of a partial skull from Leeukloof, "at an horizon a little higher than that which yields the abundant specimens of *D. grimbeeki*" (= *Diictodon feliceps*). Broom considered this taxon to be most closely related to *Dicynodon dubius*, *Dicynodon cavifrons*, *Dicynodon rogersi* (all considered to represent *Tropidostoma dubium* herein) and *Dicynodon mustoi* (= *Oudenodon bainii*), but differentiated it on the basis of a more pointed snout, shorter postorbital, larger pineal foramen, shorter, broader preparietal, and wider parietals. Keyser (1973) argued that TM 250 represents a specimen of *Tropidostoma*, a conclusion

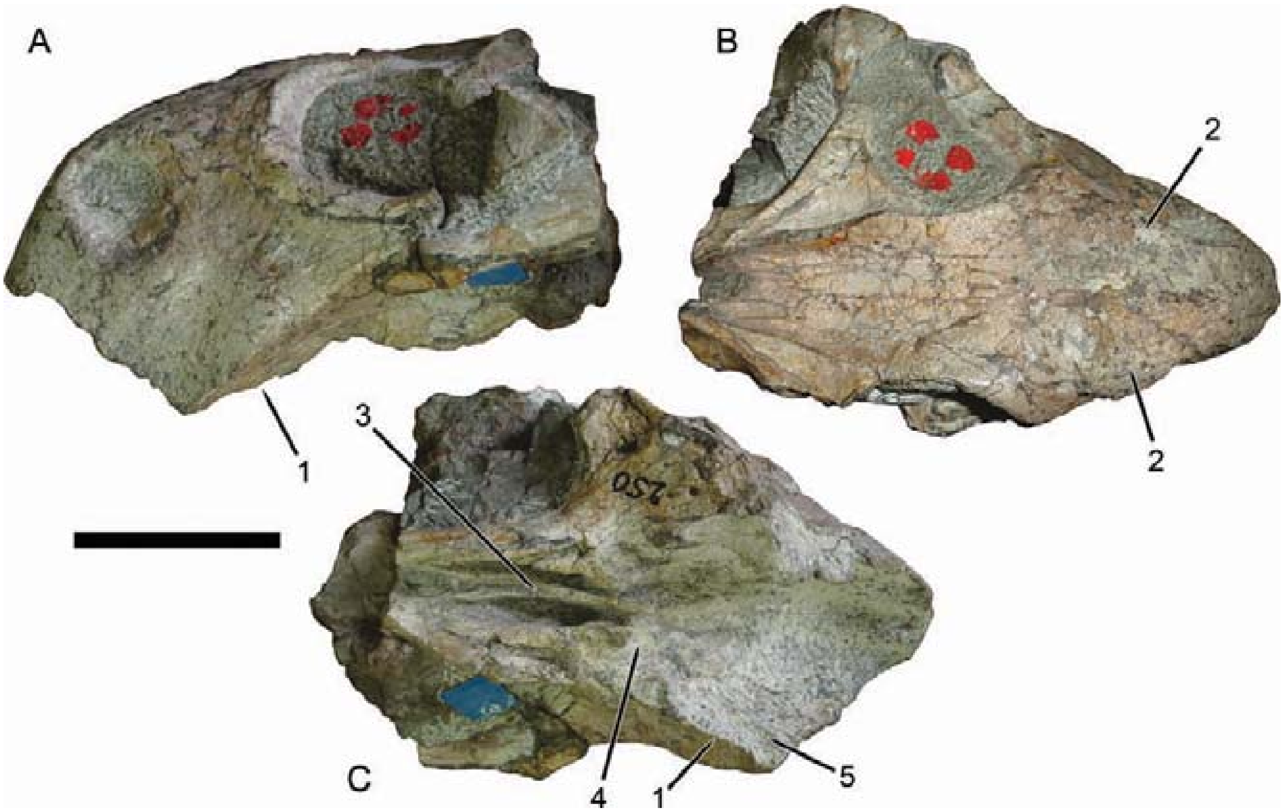

FIGURE 4. TM 250, the holotype of *Dicynodon acutirostris* (= *Tropidostoma dubium*), in left lateral (**A**), dorsal (**B**), and palatal (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses on the posterodorsal margins of the external nares, and as an oudenodontid on the basis of the (3) lengthy interpterygoid vacuity reaching the level of the palatal exposure of the palatines. Additionally, the (4) palatal surface of the palatine with a smooth anterior section flush with the secondary palate and a rugose, raised posterior section indicates that this specimen is not a dicynodontoid. This specimen can be identified as *Tropidostoma* rather than *Oudenodon* on the basis of the relatively long, low snout and small external naris, even though it (5) lacks tusks. Scale bar equals 5 cm.

supported by Botha and Angielczyk (2007) based on morphometric analysis and maintained here. Broom (1935) and Keyser (1973) both noted that TM 250 lacks tusks, which is atypical for *Tropidostoma*. However, variable development of the tusks in *Tropidostoma* is well documented (Keyser, 1973; Botha and Angielczyk, 2007), and specimens with only one or no tusks are known. The characters listed by Broom (1935) to justify specific separation of *D. acutirostris* are highly variable in dicynodonts, and morphometric analysis has demonstrated that TM 250 does not differ significantly from other specimens of *Tropidostoma* in these features (Botha and Angielczyk, 2007).

Dicynodon aetorhamphus Broom, 1948

Holotype—RC 85, a complete, well-preserved skull (Fig. 5).

Locus Typicus—Hoeksplaas, Murraysburg, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodon lacerticeps* Owen, 1845.

Remarks—Broom (1948) described *Dicynodon aetorhamphus* as a new species differentiated from its presumed nearest relative *Dicynodon kitchingi* (here considered a synonym of *Dicynodon lacerticeps*) by a smaller pineal foramen and broader preparietal. He further distinguished this species from *Dicynodon trigonocephalus* (= *D. lacerticeps*) by the narrower temporal region of the skull and from the Zambian *Dicynodon roberti* (= "*Dicynodon*" *vanhoepeni*) by a greater ratio of interorbital-to-intertemporal width. Haughton and Brink (1954), Cluver and Hotton (1981), and King (1988) retained *D. aetorhamphus* as a valid species of *Dicynodon*, but Brink (1986) considered it a junior synonym of *Diictodon feliceps*. RC 85 is clearly not a specimen of *Diictodon*; it lacks pylaecephalid synapomorphies and the presence of a labial fossa allows RC 85 to be identified as a dicynodontoid. This specimen exhibits the full suite of characters diagnosing the *Dicynodon lacerticeps* morphotype: short, narrow intertemporal region with overlap of parietals by postorbitals, premaxilla squared-off in palatal view, gradually sloping snout profile, caniniform process and tusk angled forwards, and squamosal rami acutely angled in lateral view. The shape of the preparietal, which Broom (1948) used to diagnose *D. aetorhamphus*, is notoriously variable within dicynodonts (Toerien, 1953) and is insufficient to separate this species from *D. lacerticeps*.

Dicynodon alfredi (Owen, 1862)

Holotype—NHMUK 47342, a skull (missing the temporal arches) and mandible with the left caniniform tusk exposed in section (Fig. 6).

Locus Typicus—Rhenosterberg, Middelburg, South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Junior subjective synonym of *Lystrosaurus declivis* (Owen, 1859).

Remarks—Owen (1862) initially described this taxon as a species of *Ptychognathus* (= *Lystrosaurus*), but it was variously

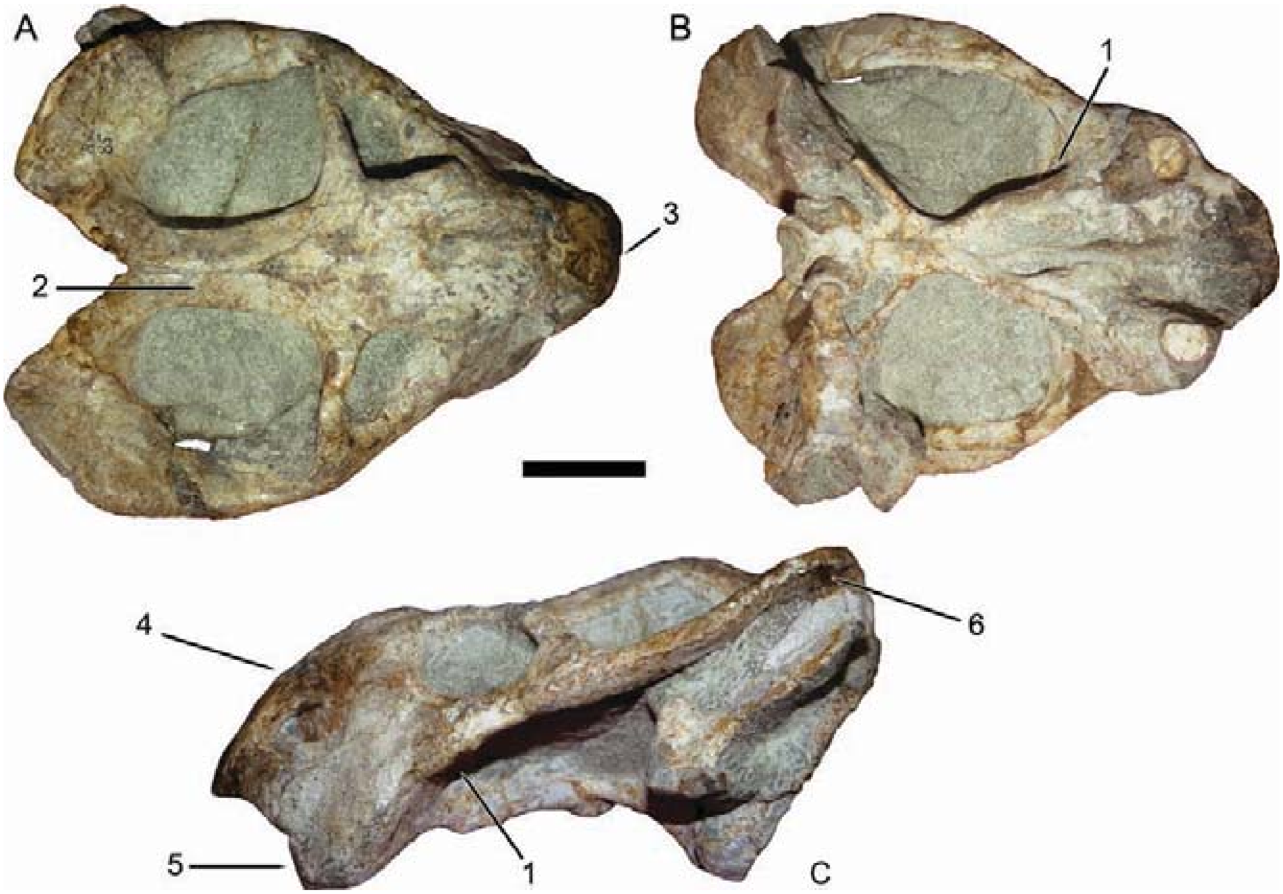

FIGURE 5. RC 85, the holotype of *Dicynodon aetorhamphus* (= *Dicynodon lacerticeps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa, and as *D. lacerticeps* on the basis of the (2) short intertemporal bar with nearly complete postorbital-parietal overlap, (3) squared-off premaxillary tip, (4) gradually sloping snout, (5) anteriorly directed caniniform process, and (6) acutely angled squamosal rami in lateral view. Scale bar equals 5 cm.

included either directly within *Dicynodon* or within *Ptychognathus* as a subgenus of *Dicynodon* throughout the 19th century. Lydekker (1890) considered this species to be a junior synonym of *Ptychosiagum* (= *Lystrosaurus*) *latirostris*, but von Huene (1931) resurrected it in the combination *Lystrosaurus alfredi*. Cluver (1971) synonymized *L. alfredi* with *Lystrosaurus declivis*, a conclusion more recently borne out by morphometric analysis (Grine et al., 2006).

Dicynodon allani Broom, 1940b

Holotype—RC 37, a somewhat weathered complete skull, lower jaws, and anterior cervical vertebrae (Fig. 7).

Locus Typicus—Wimbledon, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1940b) diagnosed *Dicynodon allani* based on its short, wide pineal foramen, significant contribution of the postfrontal to the orbital margin, short nasals, and lack of tusks, and considered it to be most closely related to *Dicynodon robustus* (= *Oudenodon bainii*). Keyser (1975) argued that RC 37 falls within the range of variation for *Oudenodon bainii* and synonymized *D. allani* with that taxon, a position maintained by Brink (1986) and King (1988) and supported here. RC 37 exhibits a postcaniniform crest, elongate interpterygoid vacuity, and postparietal contribution to the skull roof indicating oudenodontid affinities, and has the characteristic snout morphology (Botha and Angielczyk, 2007) of *Oudenodon bainii*.

Dicynodon alticeps Broom and Haughton, 1913

Holotype—SAM-PK-2347, a nearly complete skull missing portions of the temporal bars (Fig. 8).

Locus Typicus—One mile west of Oudeberg, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Valid as *Sintocephalus alticeps* (Broom and Haughton, 1913).

Remarks—Broom and Haughton (1913) described *Dicynodon alticeps* as a new species similar to the giant *Dicynodon leoniceps*. In addition to the smaller size of *D. alticeps*, Broom and Haughton distinguished the new species based on the angulation of the snout (50° to the plane of the dorsal surface of the interorbital region), slightly anteriorly directed tusks, relatively large orbits, broad intertemporal region, and elongate postorbitals. Van Hoepen (1934) removed *D. alticeps* from *Dicynodon*, making it

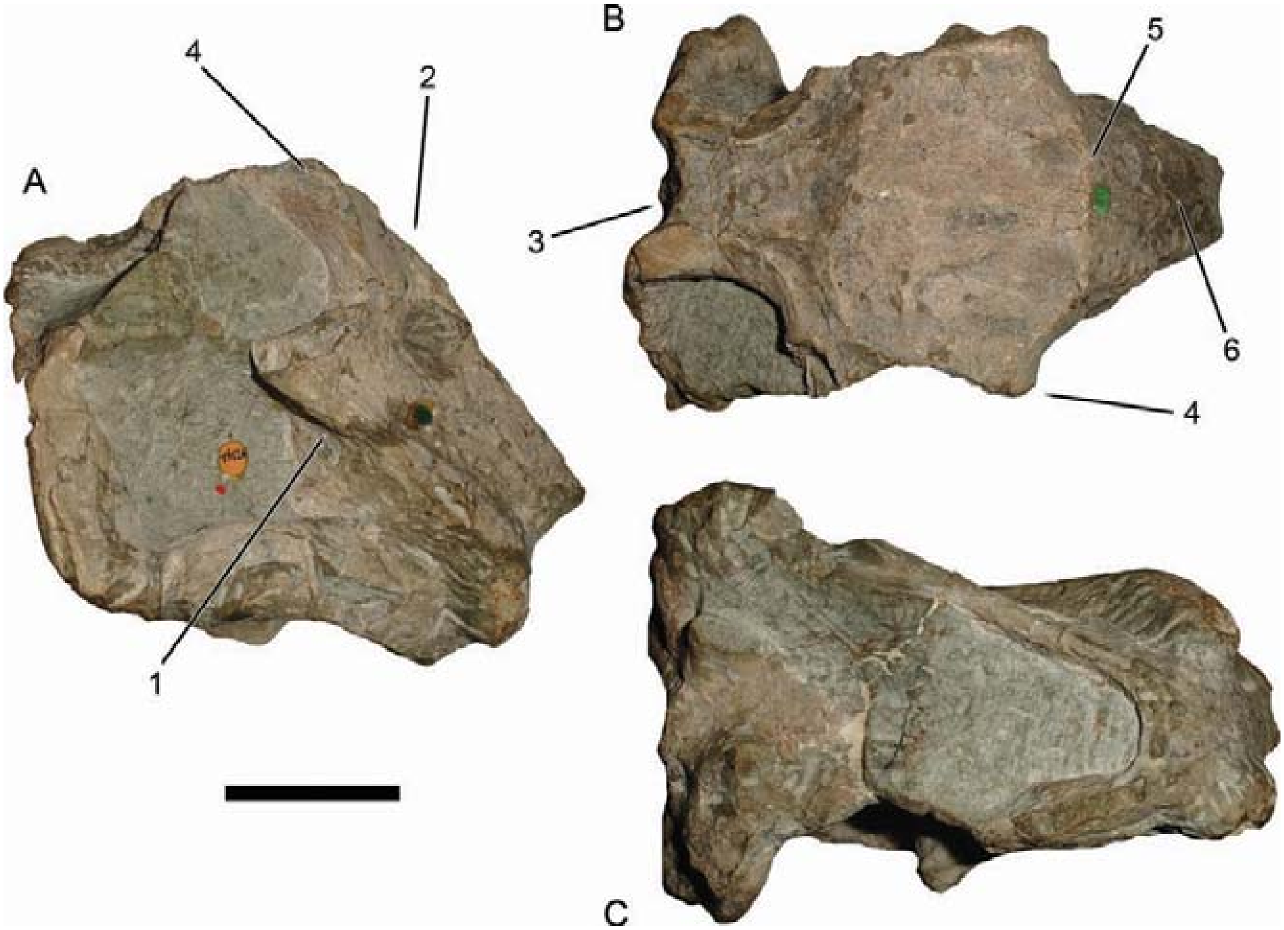

FIGURE 6. NHMUK 47342, the holotype of *Dicynodon alfredi* (= *Lystrosaurus declivis*), in right lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa, as a lystrosaurid on the basis of the (2) strongly deflected snout, as *Lystrosaurus* on the basis of the (3) very short intertemporal bar with broad exposure of the parietals, and as *L. declivis* on the basis of the combination of the (4) prominent prefrontal bosses, (5) ridge running between the prefrontals, splitting the snout into fronto-nasal and nasal-premaxillary planes, and (6) a median ridge on the dorsal surface of the premaxilla. Scale bar equals 5 cm.

the type species of his new genus *Sintocephalus*. Haughton and Brink (1954), Cluver and Hotton (1981), and King (1988) retained *D. alticeps* as a valid species, but Brink (1986) considered it a junior synonym of *Dicynodon lacerticeps* (although he still used the genus *Sintocephalus* for *D. gilli* and *D. gracilis*, disregarding type status). SAM-PK-2347 is an unusual specimen. The rugose palatine surface and presence of a labial fossa indicate that it is a dicynodontoid, and it is superficially similar to specimens of *D. lacerticeps*. However, it differs from the standard *D. lacerticeps* morphotype in several important characters. Most notable is the breadth of the intertemporal region, which is equivalent to that of the interorbital region until the level of the pineal foramen. Posterior to the pineal foramen, although the intertemporal region is constricted (with a narrow trough on the dorsal surface at the posterior end), at no point is there dorsal overlap of the parietals by the postorbitals. The intertemporal rami of the postorbitals are angled more vertically than horizontally, and the narrow trough at the end of the intertemporal bar is rimmed on both sides by the parietals. Although relative breadth and degree of postorbital-parietal overlap on the intertemporal bar is highly variable within dicynodont species, especially ontogenetically, the condition in SAM-PK-2347 falls outside of the observed range for *D. lacerticeps*. In all specimens of the *D. lacerticeps* morphotype, the intertemporal bar is significantly less wide than the interorbital region by the level of the pineal foramen and there is extensive overlap of the parietals by the postorbitals, with nearly complete overlap posteriorly. This is true even in very small (presumed juvenile) *D. lacerticeps* (as well as *D. leoniceps* and *Dinanomodon*) skulls, so this distinction cannot be attributed to ontogeny (also because SAM-PK-2347 is equal in size to most 'typical' *D. lacerticeps* skulls). SAM-PK-2347 also differs from the *D. lacerticeps* morphotype in its extremely steep snout profile, which is more similar to the condition in *D. leoniceps*. SAM-PK-2347 is further distinguished from *D. lacerticeps*, *D. leoniceps*, and *Dinanomodon* by the morphology of the temporal arch, which has a convex ventral edge anteriorly (as seen in lateral view), immediately posterior to the level of the postorbital bar. This morphology is preserved on both sides of SAM-PK-2347, suggesting that this is a real feature, distinct from the uniformly straight ventral arch edges in other Permian dicynodontoids. Based on the combination of features listed above, we recognize *D. alticeps* as a valid species. For the resurrection of the genus *Sintocephalus* for this species, refer to the Phylogenetic Analysis.

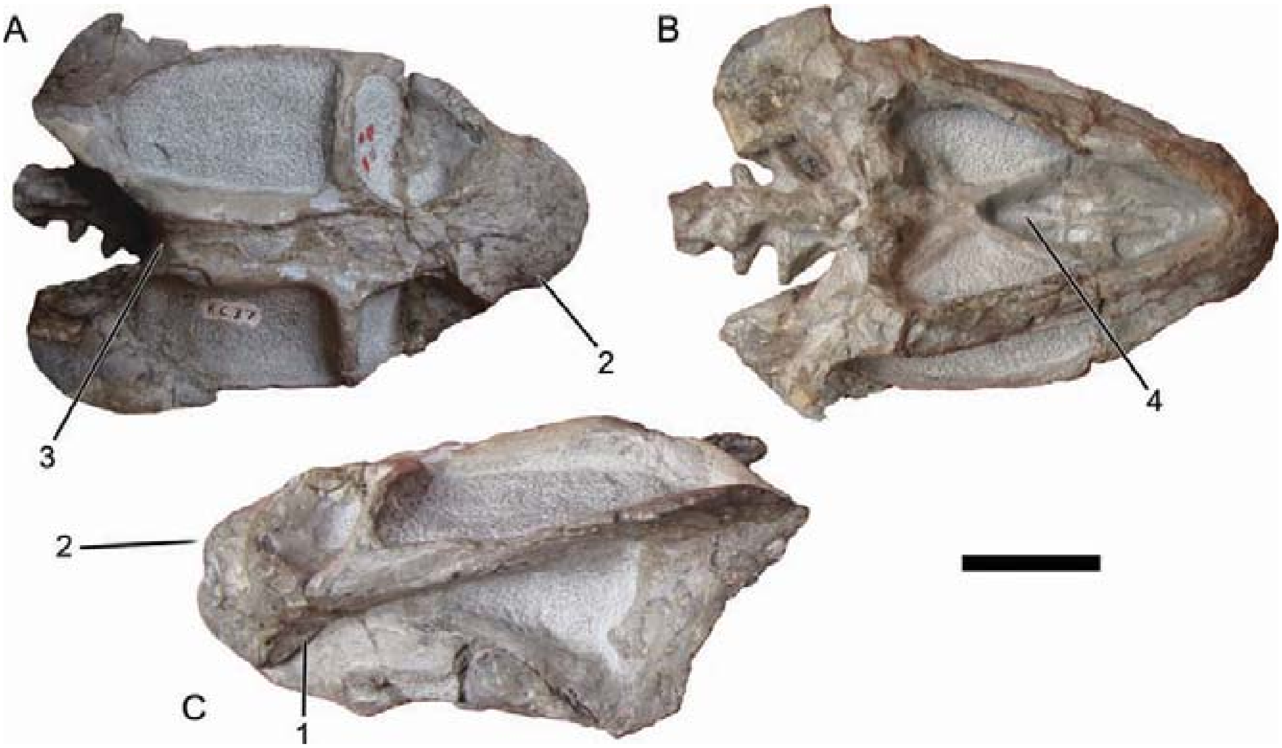

FIGURE 7. RC 37, the holotype of *Dicynodon allani* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

Dicynodon amalitzkii Sushkin, 1926

Holotype—PIN 2005/38, a well-preserved complete skull and lower jaws (Fig. 9), axial column (missing the caudal region), pectoral girdle, and fragmentary pelvic girdle.

Locus Typicus—Sokolki, Arkhangelsk Region, Kotlasskii District, Russia.

Horizon—Upper Vyatkian substage, Tatarian series (Upper Permian).

Status—Valid as *Peramodon amalitzkii* (Sushkin, 1926), comb. nov.

Remarks—Sushkin (1926) distinguished *Dicynodon amalitzkii* from the other North Dvina dicynodonts (of which he recognized only *Dicynodon annae* and *Dicynodon trautscholdi* as valid) by its smaller skull size, proportionally taller snout, massive mandibular symphysis, larger preparietal, elongate anterior processes of the parietals, and broader, less anteriorly directed caniniform process. He further distinguished the new species from *D. trautscholdi* by the larger septomaxilla and from *D. annae* by the narrower parietal region. Efremov (1940) synonymized *D. amalitzkii* (as well as *D. annae*) with *D. trautscholdi*, an approach followed in most subsequent studies (e.g., King, 1988; Ivakhnenko et al., 1997; Battail and Surkov, 2000). However, Angielczyk and Kurkin (2003a) noted a number of morphological dissimilarities between the holotypes of *D. amalitzkii* and *D. trautscholdi* and tested this distinction in a phylogenetic analysis. They found that *D. amalitzkii* and *D. trautscholdi* did not form a clade, supporting specific separation. Subsequently, this species was treated as valid by Ivakhnenko (2003, 2008). *Dicynodon amalitzkii* has a suite of features that allow it to be distinguished from other Permian dicynodontoid species. *Dicynodon amalitzkii* can be distinguished from all Permian dicynodontoids other than *Dinanomodon gilli* and *D. trautscholdi* by the presence of an elongate anterior process of the frontals along their midline suture. Unlike *Dinanomodon* and *D. trautscholdi*, however, *D. amalitzkii* lacks an elongate ascending process of the premaxilla extending posteriorly to meet the anterior process of the frontals. The snout of *D. amalitzkii* is strongly pitted, and this sculpturing is present on the premaxillary, nasal, and prefrontal. The general snout morphology of *D. amalitzkii* is most similar to that of *D. leoniceps* (tall, steeply sloping snout, short but well-developed ‘hook’ tip to the premaxilla, ventrally directed canine), but *D. amalitzkii* has a much shorter, broader intertemporal bar than *D. leoniceps*, as well as a shorter, more broadly rounded caniniform process. For placement of this species in the new genus *Peramodon*, refer to the Phylogenetic Analysis.

Dicynodon andrewsi Broom, 1921

Holotype—MMK 4169, a strongly laterally sheared skull missing the left squamosal and portions of both temporal arches (Fig. 10).

Locus Typicus—Biesjiespoort, Victoria West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Based on the broad exposure of the parietals, Broom (1921) described *Dicynodon andrewsi* as a possible ancestor of *Dicynodon tigriceps* (= *Aulacephalodon bainii*). Keyser (1975) disagreed (given the lack of tusks in MMK 4169), and instead argued that this specimen is referable to *Oudenodon bainii*, a position maintained by Kitching (1977), Brink (1986), and King

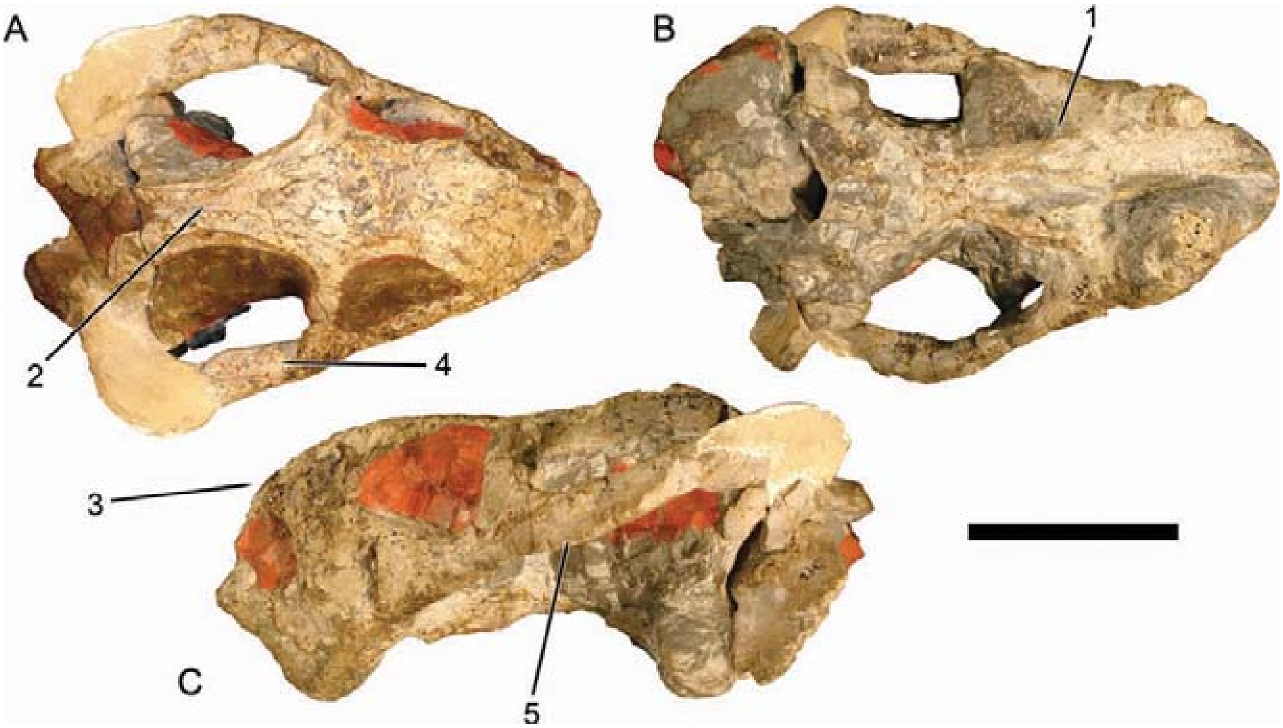

FIGURE 8. SAM-PK-2347, the holotype of *Dicynodon alticeps* (= *Sintocephalus alticeps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. *Sintocephalus alticeps* can be distinguished from other dicynodontoids by the combination of a (2) broad intertemporal bar (especially at the level of the pineal foramen) with extensive exposure of the parietals, even in a constricted posterior trough, (3) sharply sloping snout profile, and (4) transversely thickened temporal arch with an (5) expanded region immediately posterior to the postorbital bar with a convex ventral margin. Scale bar equals 10 cm.

(1988). The right side of the snout in MMK 4169 is incomplete and poorly preserved, but the left side is mostly intact and shows a postcaniniform crest (indicating that this is a cryptodont) and the snout morphology Botha and Angielczyk (2007) described as diagnostic for *O. bainii*.

Dicynodon annae (Amalitzky, 1922)

Holotype—PIN 2005/5, a poorly preserved but nearly complete skull missing portions of the squamosals (Fig. 11).

Locus Typicus—Sokolki, Arkhangelsk Region, Kotlasskii District, Russia.

Horizon—Upper Vyatkian substage, Tatarian series (Upper Permian).

Status—Junior subjective synonym of *Vivaxosaurus trautscholdi* (Amalitzky, 1922).

Remarks—Amalitzky (1922) described two new species of the otherwise Scottish dicynodont genus *Gordonia* from the Late Permian of Russia: *G. annae* and *G. rossica*. Sushkin (1926) argued that *G. annae* lacked the characteristic features of *Gordonia* (large size of the posttemporal foramina) and transferred this species to the more inclusive genus *Dicynodon*. Sushkin (1926) considered *Dicynodon annae* (including another of Amalitzky's [1922] North Dvina dicynodont species, *Oudenodon venyukovi*, as a junior synonym) to be distinguishable from *Dicynodon trautscholdi* (including *G. rossica* as a junior synonym) by its broader intertemporal region. Efremov (1940) argued that this distinction could be attributed to deformation or intraspecific variation, and synonymized *D. annae* with *D. trautscholdi*. All subsequent studies (e.g., King, 1988; Ivakhnenko et al., 1997; Ivakhnenko, 2003; Angielczyk and Kurkin, 2003a) have followed Efremov (1940) in treating *D. annae* (as well as *O. venyukovi* and *G. rossica*) as a junior synonym of *D. trautscholdi*. PIN 2005/5 shares *D. trautscholdi*'s (based on the holotype, PIN 2005/1) relatively thin, anteroventrally directed snout morphology, unique caniniform process morphology (narrow and anteroventrally directed with a rounded lobe anterior to the tusk), depressed preparietal, and apparently a near contact between the dorsal process of the premaxilla and anterior process of the frontals (the existence of the frontal process is somewhat uncertain because of poor preservation in this area on PIN 2005/5, but an elongate posterior extension of the premaxilla is evident).

Dicynodon anneae Broom, 1940b

Holotype—RC 42, a dorsoventrally crushed skull with a poorly preserved ventral surface (Fig. 12).

Locus Typicus—Wellwood, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dinanomodon gilli* (Broom, 1932).

Remarks—Broom (1940b) distinguished *Dicynodon anneae* from its presumed nearest relative, *Dicynodon lissops*, by its proportionally smaller orbits and larger temporal fenestrae. It was further distinguished from *Dicynodon venteri* by its shorter snout and differently sloping occiput. Toerien (1954) proposed the replacement name *Dicynodon whitsonae* for this species, incorrectly believing it to be preoccipied by the similarly named *Dicynodon annae* (Amalitzky, 1922). Haughton and Brink (1954) and Kitching (1977) treated *D. whitsonae* as a valid species of *Dicynodon*, but Cluver and Hotton (1981) transferred it to *Diictodon*. King (1988) listed *Diictodon whitsonae* as a valid species, but

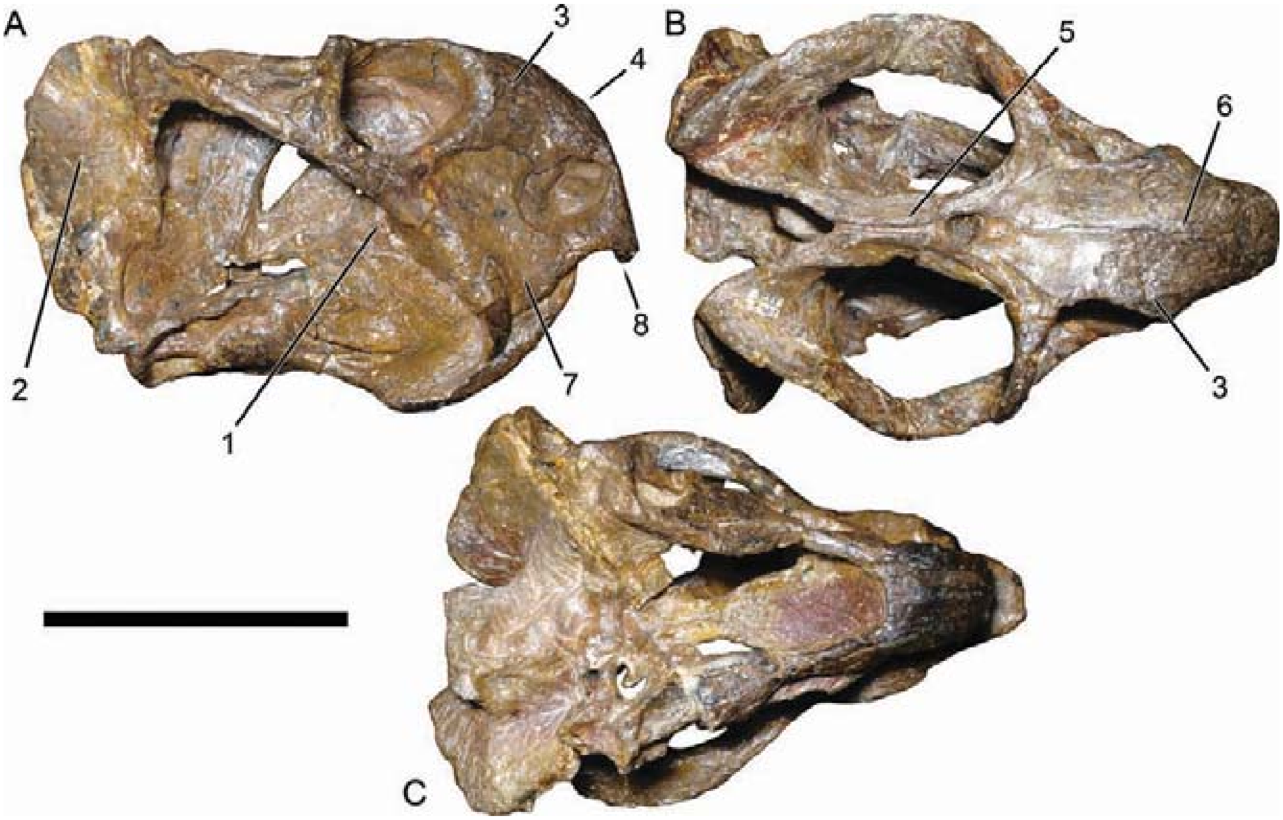

FIGURE 9. PIN 2005/38, the holotype of *Dicynodon amalitzkii* (= *Peramodon amalitzkii*), in right lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. *Peramodon amalitzkii* can be distinguished from other dicynodontoids by the combination of a (2) squamosal with a broadly rounded dorsal margin in lateral view, (3) densely pitted prefrontal, nasal, and premaxilla, (4) sharply sloping snout profile, (5) short intertemporal bar with nearly complete postorbital-parietal overlap, (6) anterior process of the frontals, but no elongate dorsal process of the premaxilla, (7) short, broadly rounded caniniform process, and (8) short but prominently hooked premaxillary tip. Scale bar equals 10 cm.

Brink (1986) and Sullivan and Reisz (2005) considered it a junior synonym of *Diictodon feliceps*. RC 42 is a very small skull that is superficially similar to *Diictodon* in its large preparietal and short intertemporal bar with a brief region of complete postorbital overlap of the parietals. However, the very thin postfrontals and large palatine pads in this specimen indicate that it is not *Diictodon*, but rather a "*Dicynodon*"-grade dicynodontoid. The highly distorted, juvenile nature of RC 42 makes it impossible to accurately determine snout and temporal arch shape in this specimen. That said, the presence of an elongate anterior process of the frontals nearly contacting an elongate posterior dorsal process of the premaxilla in RC 42 is sufficient to identify it as a juvenile specimen of *Dinanomodon gilli*.

Dicynodon antjiesfonteinensis Toerien, 1953

Holotype—BP/1/277, a very poorly preserved skull and lower jaws (missing large portions of the temporal arches, snout, and postdentary regions) (Fig. 13).

Locus Typicus—Antjiesfontein, Prince Albert, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Toerien (1953) described *Dicynodon antjiesfonteinensis* as a new species of *Tapinocephalus* Assemblage Zone (AZ) *Dicynodon*. Cluver and Hotton (1981) transferred *D. antjiesfonteinensis* to *Diictodon* but retained it as a valid species. King (1988) synonymized *D. antjiesfonteinensis* with another *Tapinocephalus* AZ-restricted species, *Diictodon* (formerly *Dicynodon*) *vanderhorsti*, whereas Brink (1986) and Sullivan and Reisz (2005) included it within the expansive *Diictodon feliceps*. We agree with referral of this specimen to *D. feliceps*: although BP/1/277 is very poorly preserved, the right side of the skull shows a clear precaniniform notch, and the short intertemporal region with broad postorbital-parietal overlap is typical of *Diictodon* among pylaecephalids.

Dicynodon bainii Owen, 1845

Holotype—NHMUK 36228, a complete but poorly preserved, poorly prepared dorsoventrally crushed skull (Fig. 14).

Locus Typicus—Fort Beaufort, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Valid as *Aulacephalodon bainii* (Owen, 1845).

Remarks—*Dicynodon bainii* was one of the original species of *Dicynodon* named by Owen (1845) and was distinguished from the type species *D. lacerticeps* by the generally more massive skull, presence of large nasal bosses, and wider intertemporal region. Although Seeley (1898) made *D. bainii* the type species of his new subgenus *Aulacephalodon*, this species was ignored for much of the 19th and early 20th centuries in favor of

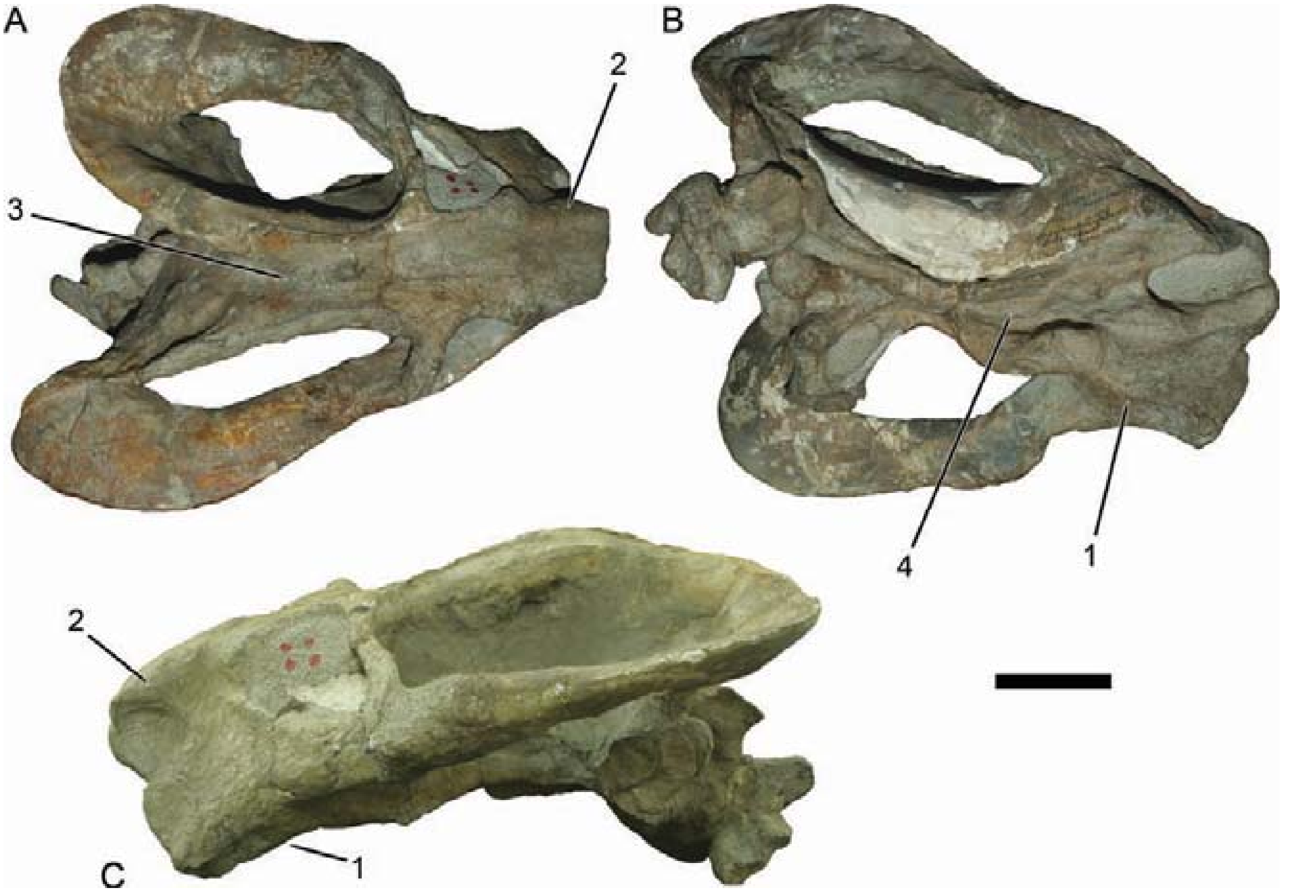

FIGURE 10. MMK 4169, the holotype of *Dicynodon andrewsi* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

Dicynodon tigriceps (represented by a better type skull) to refer to the 'broad-skulled *Dicynodon*' morphotype. Broom (1921) overlooked *Dicynodon* (*Aulacephalodon*) *bainii* entirely and made *D. tigriceps* the type species of his new genus *Bainia*, although he later corrected this oversight (Broom, 1932). It should be noted that although at this time Broom considered *Oudenodon* to represent the female of *Dicynodon* and transferred all nominal *Oudenodon* species to *Dicynodon*, he explicitly did not utilize the combination *Dicynodon bainii* (Owen, 1860b) for the type species of *Oudenodon* because of concerns with preoccupation by *D. bainii* Owen, 1845. In reestablishing Seeley's *Aulacephalodon* for *A. bainii* and similar nominal species, Broom (1932) misspelled the genus as *Aulacocephalodon*, which remained in use for much of the later 20th century. Keyser (1972) and Tollman et al. (1981) revised the nominal species of *Aulacephalodon* and argued that there is a single diagnosable species, *A. bainii*. All subsequent authors have recognized *A. bainii* as the only valid species of *Aulacephalodon*.

Dicynodon bathyrhynchus von Huene, 1942

Holotype—GPIT/RE/7104, a well-preserved skull missing the left zygomatic arch and a broad section running the length of the skull at a level immediately below the naris (Fig. 15).

Locus Typicus—Kingori locality, Ruhuhu Basin, Tanzania.

Horizon—Lower Bone Bed, Upper Usili Formation (Upper Permian).

Status—Valid as *Euptychognathus bathyrhynchus* (von Huene, 1942), comb. nov.

Remarks—Von Huene (1942) named *Dicynodon bathyrhynchus* for its unusually deep, ventrally directed snout, more similar to the condition in *Lystrosaurus* than typical "*Dicynodon*" specimens. Haughton and Brink (1954) and King (1988) considered *D. bathyrhynchus* to be a valid species, but Brink (1986) synonymized it with *Dicynodon lacerticeps*. Although the general proportions of GPIT/RE/7104 are strikingly dissimilar from those of other *Dicynodon* species, we were initially loath to consider *D. bathyrhynchus* valid because of the heavily reconstructed nature of the holotype, making the reality of these differences uncertain. Recently, however, two well-preserved, intact South African specimens (CGP AF107-83 and CGP/1/310) matching the *D. bathyrhynchus* morphotype were identified during a search of the CGP collections. An additional South African skull with this morphology (UCMP 42714) is housed in the collections at the University of California, Berkeley. These specimens support the separation of *D. bathyrhynchus* as a valid species and indicate its presence in both the Tanzanian and South African basins, albeit as a very rare

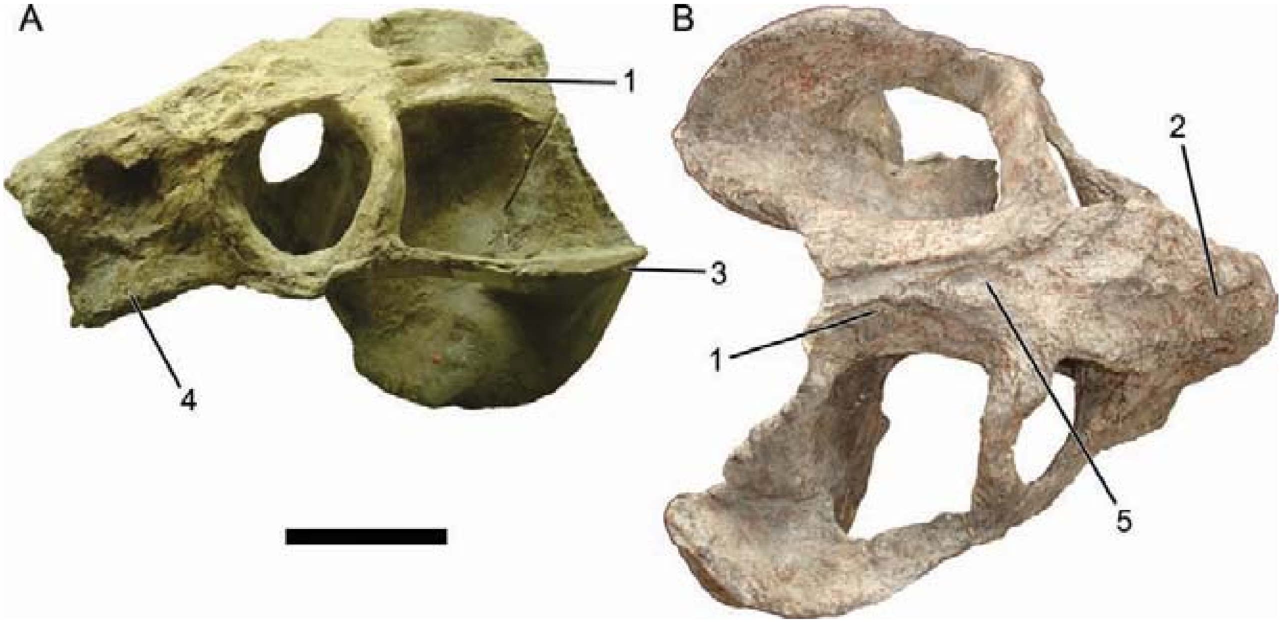

FIGURE 11. PIN 2005/5, the holotype of *Dicynodon annae* (= *Vivaxosaurus trautscholdi*), in oblique left lateral view (**A**) and NHMUK R4039, a cast of the holotype, in dorsal view (**B**). This specimen can be identified as *Vivaxosaurus trautscholdi* on the basis of the combination of the (1) short intertemporal bar with broad but incomplete postorbital-parietal overlap, (2) an elongate dorsal process of the premaxilla, (3) acutely angled squamosal rami in lateral view, (4) thin, anteriorly directed caniniform process with rounded edge anterior to tusk, and (5) depressed surface of the preparietal anterior to the pineal foramen. Scale bar equals 10 cm.

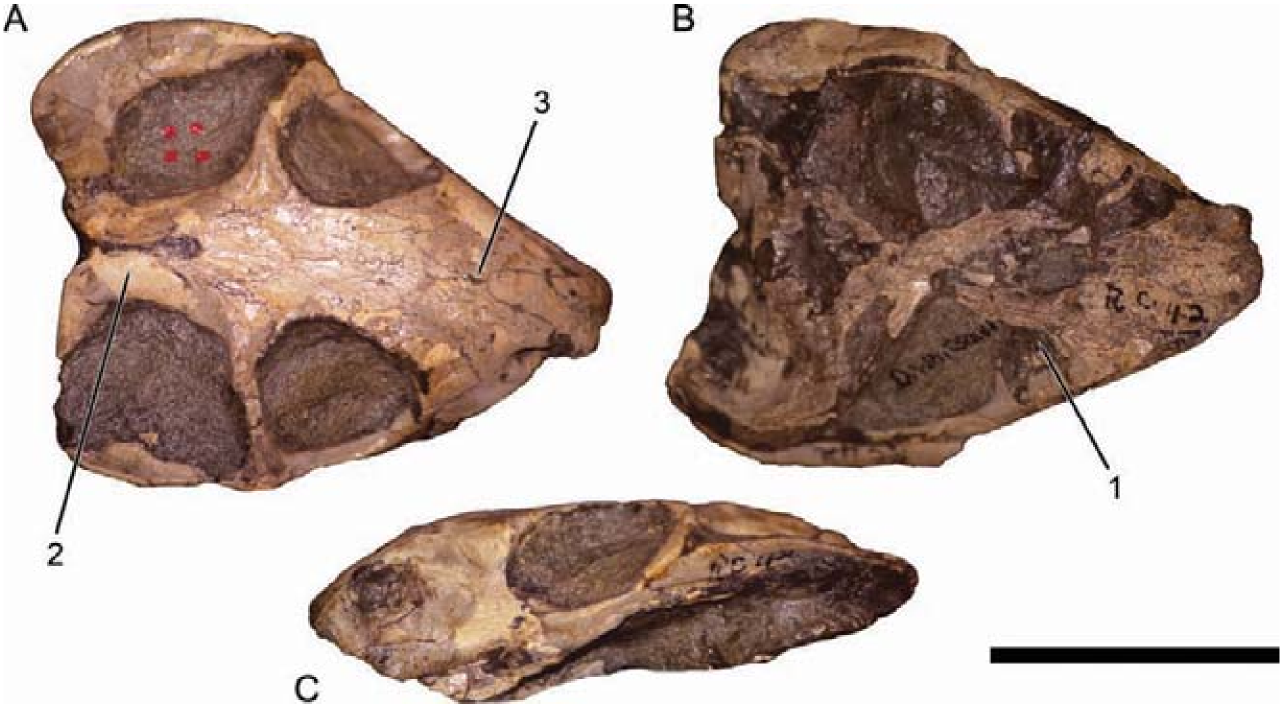

FIGURE 12. RC 42, the holotype of *Dicynodon anneae* (= *Dinanomodon gilli*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid rather than *Diictodon* by the (1) labial fossa and (2) complete overlap of the parietals by the postorbitals. This specimen is a juvenile, as indicated by the relatively small temporal fenestrae, very short intertemporal bar, small tusks, and large preparietal, but can be identified as *Dinanomodon gilli* by the (3) elongate anterior processes of the frontals nearly meeting an elongate dorsal process of the premaxilla. Scale bar equals 5 cm.

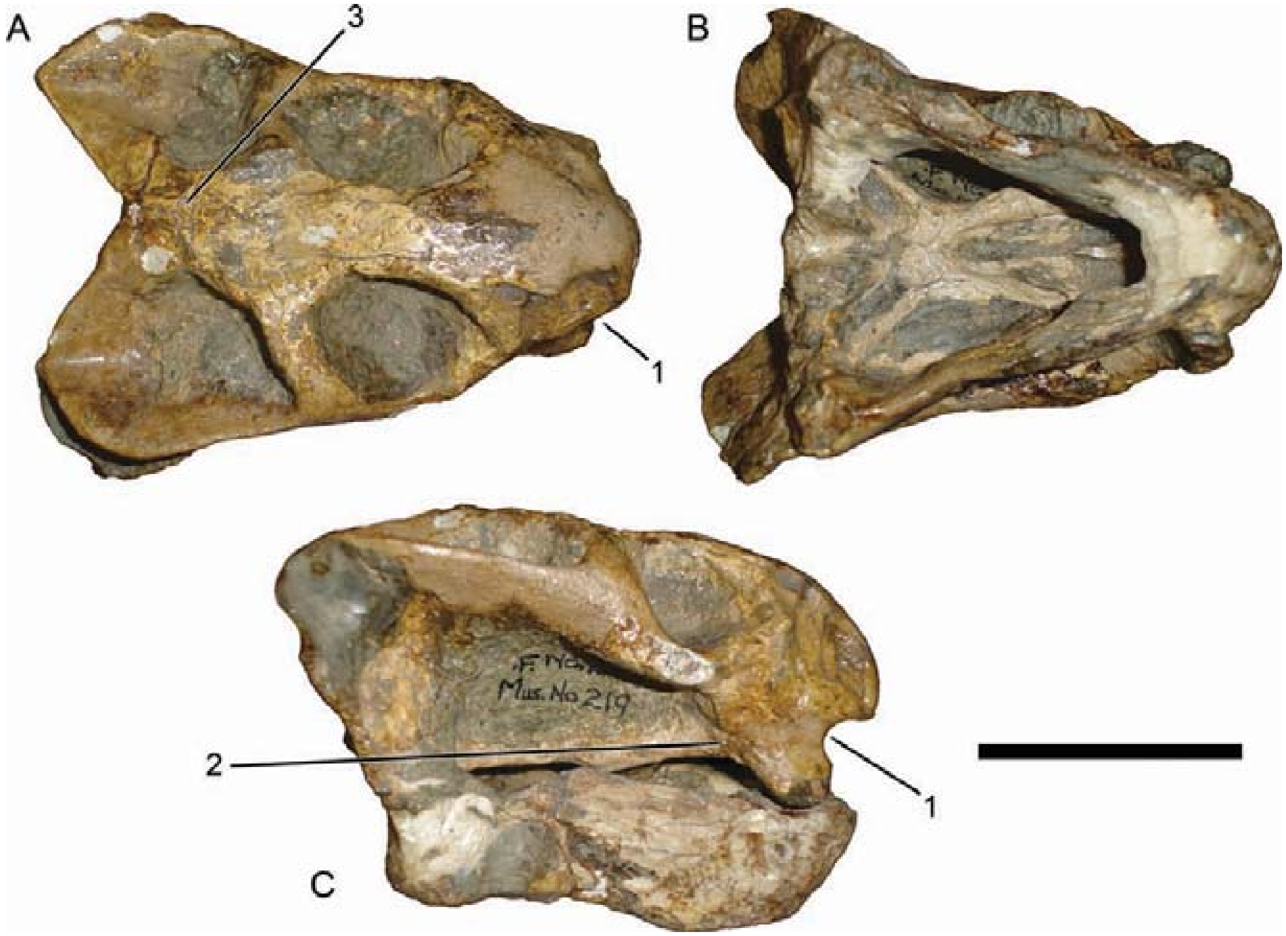

FIGURE 13. BP/1/277, the holotype of *Dicynodon antjiesfonteinensis* (= *Diictodon feliceps*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch and (2) posterior edge of the caniniform process at the level of the anterior edge of the orbits and as *D. feliceps* on the basis of the (3) broad postorbital-parietal overlap and lack of postcanines. Scale bar equals 5 cm.

taxon. *Dicynodon bathyrhynchus* can be distinguished from all other Permian dicynodontoids by its anteroposteriorly short, dorsoventrally tall, ventrally deflected snout, thin, horizontal lateral dentary shelf dorsal to the mandibular fenestra, extremely short intetemporal bar but with complete postorbital-parietal overlap, tall, broadly rounded temporal arch in lateral view, and prominent prefrontal bosses with an arcuate ridge extending between them on the dorsal surface of the snout. For placement of this species in the new genus *Euptychognathus*, refer to the Phylogenetic Analysis.

Dicynodon benjamini Broom, 1948

Holotype—RC 63, a complete, somewhat laterally compressed skull (Fig. 16).

Locus Typicus—Brookfield, Murraysburg, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Valid as *Keyseria benjamini* (Broom, 1948), comb. nov.

Remarks—Broom (1948) described *Dicynodon benjamini* as a new species of *Dicynodon* characterized by an unusally broad parietal region. He compared *D. benjamini* to a disparate array of other *Dicynodon* species, and distinguished it from *D. grimbeeki* (= *Diictodon feliceps*), *D. halli* (= *Oudenodon bainii*), and *D. hartzenbergi* (= ?*Pelanomodon*) on the basis of a narrower snout. Haughton and Brink (1954), Kitching (1977), and King (1988) listed *D. benjamini* as a valid species. Cluver and Hotton (1981) did not address the position of this taxon, but Brink (1986) listed it as a synonym of *Dicynodontoides parringtoni*. RC 63 is not referable to *Dicynodontoides*: it has paired nasal bosses, postfrontals, broad exposure of the parietals for the entire length of the intertemporal bar, a pineal foramen without a raised rim, and a long interpterygoid vacuity reaching the level of the palatine pads. RC 63 represents a remarkably generalized dicynodont. This specimen cannot be referred to any other nominal species of dicynodont and possesses a unique combination of characters (broad intertemporal region, with wider exposure of parietal than postorbital, postfrontal makes up posterior half of dorsal margin of orbit but is exposed as only a thin strip posteriorly, paired nasal bosses overhanging external nares, prominent embayment anterior to caniniform process, well-developed ridge along lateral premaxillary-maxillary suture), but displays no clear autapomorphies, rendering it a metataxon. In addition to the holotype, another specimen (CGP S125b) exhibiting this combination of characters can be referred to *D. benjamini*. For placement of this

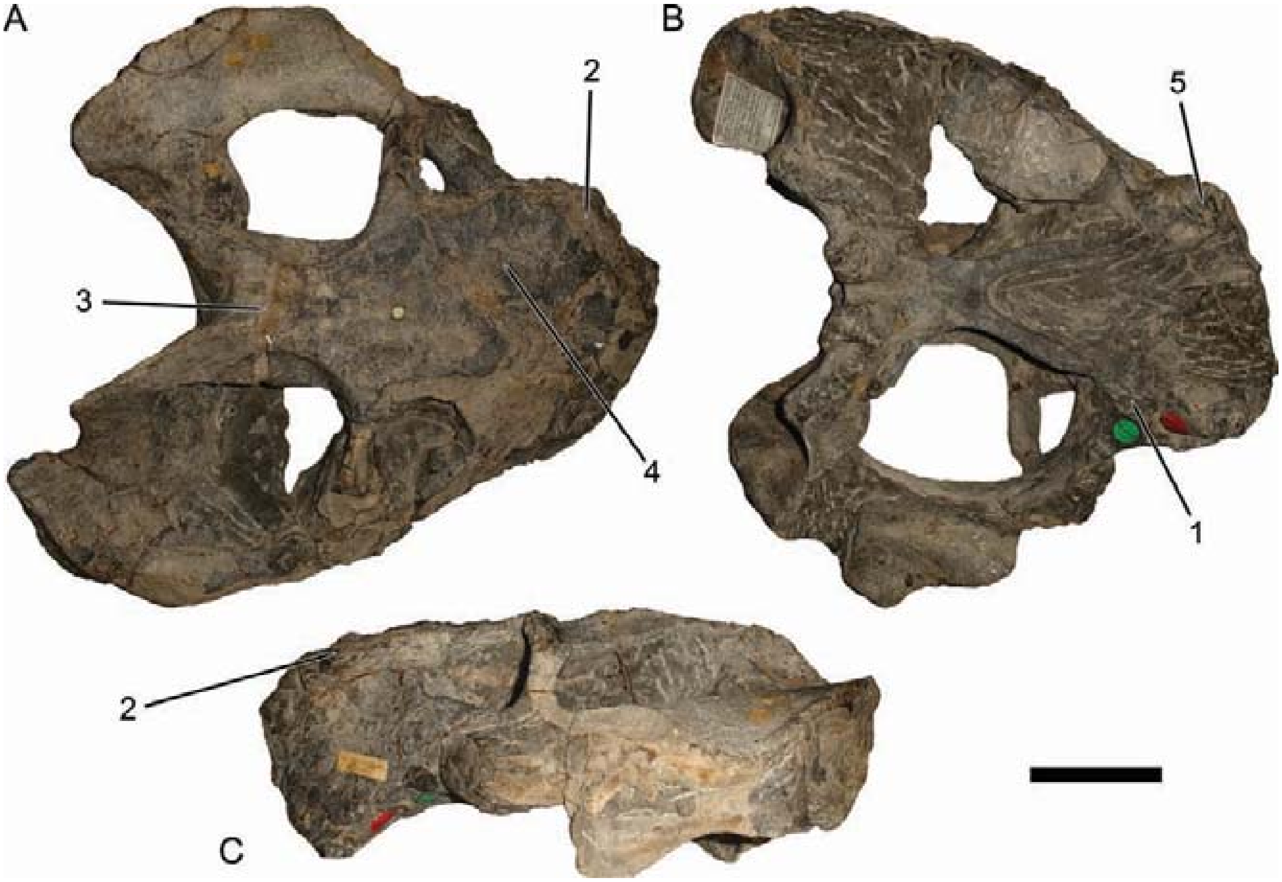

FIGURE 14. NHMUK 36228, the holotype of *Dicynodon bainii* (= *Aulacephalodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as a geikiid on the basis of the (2) robust nasal and prefrontal bosses, (3) broad intertemporal region with extensive exposure of the parietals, and (4) transverse snout ridge at the level of the prefrontals, and as *A. bainii* on the basis of the (5) massive tusks. Scale bar equals 10 cm.

species in the new genus *Keyseria*, refer to the Phylogenetic Analysis.

Dicynodon bogdaensis (Sun, 1973)

Holotype—IVPP V3241, a well-preserved skull missing the left zygomatic arch, portions of the braincase, and the tip of the snout (Fig. 17).

Locus Typicus—Taoshuyuan, Turpan Basin, Xinjiang, China.

Horizon—Guodikeng Formation (Upper Permian).

Status—Valid as *Turfanodon bogdaensis* Sun, 1973.

Remarks—Sun (1973) described *Turfanodon bogdaensis* as a new taxon of dicynodont distinguished from the similar *Dicynodon* by a broader interorbital region. King (1988) placed this species in *Dicynodon*, a referral supported by Lucas (1998a, 2001). IVPP V3241 is similar in general appearance to *Daptocephalus leoniceps*, with a steeply sloping snout and broadly rounded squamosal in lateral view. However, IVPP V3241 differs from *D. leoniceps* in its shorter intertemporal bar (compared to *D. leoniceps* specimens of equivalent size), intensely sculptured palate, broader and taller zygomatic portion of the squamosal, presence of a trough-like fossa anterior to the pineal foramen, absence of thin, strap-like dorsal exposure of the postfrontals, and presence of an anterior process of the frontals. For resurrection of the genus *Turfanodon* for this species, refer to the Phylogenetic Analysis.

Dicynodon bolorhinoides Watson, 1960

Holotype—CAMZM T606, a weathered, nearly complete skull (partially acid prepared and currently broken into several pieces, but with the pretemporal region mostly intact) and lower jaws (Fig. 18).

Locus Typicus—Kuilspoort, Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Aulacephalodon bainii* (Owen, 1845).

Remarks—Watson (1960) distinguished *Dicynodon bolorhinoides* from its presumed nearest relative, *Dicynodon bolorhinus* (here considered a synonym of *Oudenodon bainii*), by a greater distance between the external naris and orbit and the presence of a midline nasal suture (supposedly absent in *D. bolorhinus*). It was further distinguished from *Dicynodon halli* (= *Oudenodon bainii*) by a wider snout and interorbital region and from other dicynodonts in general on the basis of supposedly unique nasal boss morphology. *Dicynodon bolorhinoides* has received little attention since its description, and was not discussed in any subsequent reviews of *Dicynodon* (i.e., Cluver and Hotton, 1981; King, 1988, 1990). Brink (1986) listed this species as a junior synonym of *Diictodon feliceps* without comment. Poor preservation

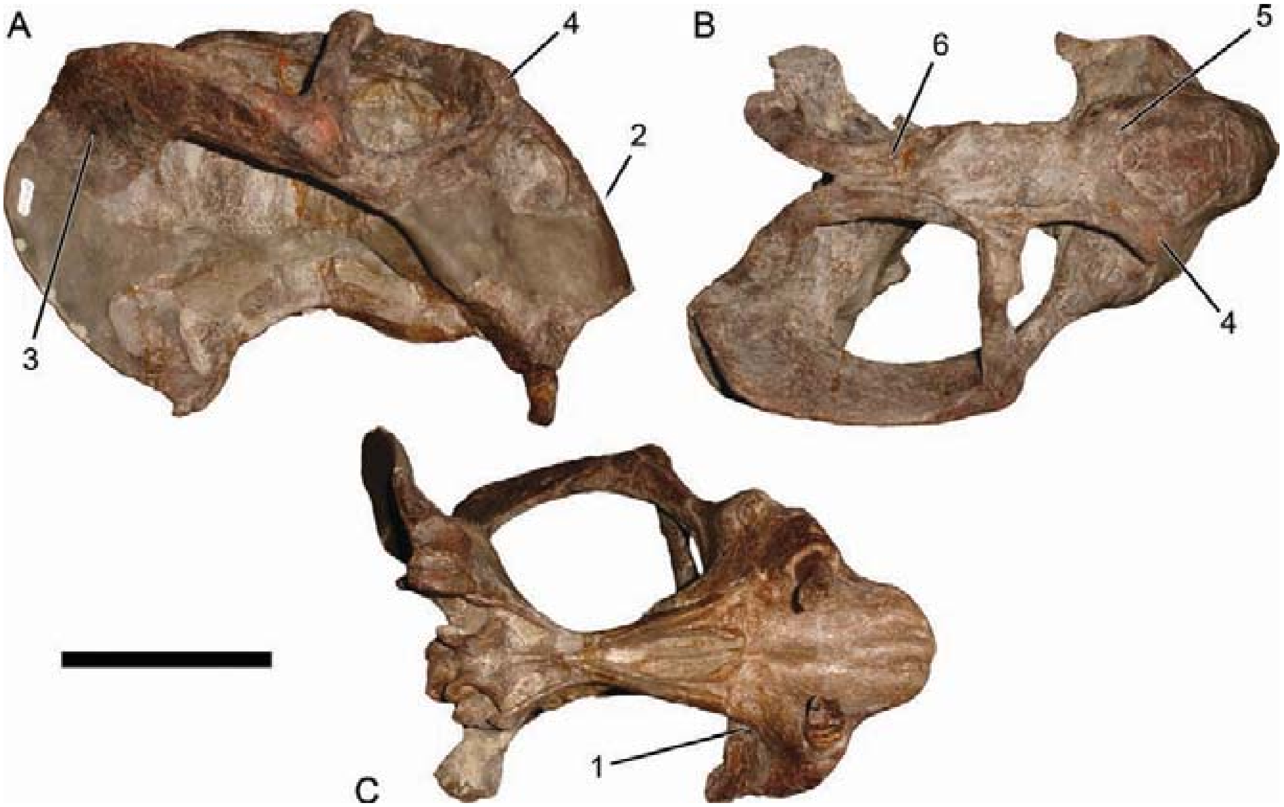

FIGURE 15. GPIT/RE/7104, the holotype of *Dicynodon bathyrhynchus* (= *Euptychognathus bathyrhynchus*), in right lateral (**A**), dorsal (**B**), and palatal (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as a lystrosaurid on the basis of the (2) tall, strongly deflected snout. *Euptychognathus bathyrhynchus* can be distinguished from other lystrosaurids by the combination of a (3) squamosal with a broadly rounded dorsal margin in lateral view, (4) prominent prefrontal bosses, (5) arcuate ridge curving between the prefrontal bosses, and (6) short intertemporal bar with nearly complete postorbital-parietal overlap. Scale bar equals 10 cm.

of the caniniform process renders identification of a labial fossa or postcaniniform crest in this specimen impossible, but several other features indicate that this specimen represents a cryptodont rather than a dicynodontoid or *Diictodon*. Characteristic features of Cryptodontia present in CAMZM T606 include paired nasal bosses located at the posterolateral margins of the external nares. The pineal boss of CAMZM T606 is prominently raised and directed dorsally, unlike in rhachiocephalids in which it is directed anteriorly. Although this specimen bears some superficial similarities to *Tropidostoma* and *Odontocyclops*, we identify CAMZM T606 as a subadult specimen of *Aulacephalodon bainii*. The characteristic geikiine transverse crest across the snout at the level of the prefrontals is present, albeit weakly developed, in this specimen. The nasal bosses are also weakly developed compared to large *Aulacephalodon* skulls, but are similar to those of *Aulacephalodon* skulls of comparable size (e.g., AMG 5730). Further supporting identification as *Aulacephalodon*, the tusks of CAMZM T606 are massive by comparison to most specimens of *Tropidostoma* and the caniniform process is anteroposteriorly wider and more ventrally directed than in *Tropidostoma* or *Odontocyclops* (in which the caniniform is angled anteriorly).

Dicynodon bolorhinus (Broom, 1911)

Holotype—AMNH FARB 5505, a badly weathered partial snout (Fig. 19).

Locus Typicus—Kuilspoort, Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1911) considered *Oudenodon bolorhinus* to be most similar to *O. strigiceps* (here considered a nomen dubium, although most probably a very poor specimen of *Oudenodon bainii*) among species of *Oudenodon*, but distinguished *O. bolorhinus* on the basis of its larger naris and more posteriorly positioned caniniform process. Following his belief that *Oudenodon* represents the tuskless female of *Dicynodon*, Broom (1913a) transferred *O. bolorhinus* and other species of the genus to *Dicynodon*, but retained them as valid species in new combinations. Haughton and Brink (1954), Kitching (1977), and King (1988) listed *D. bolorhinus* as a valid species of *Dicynodon*, but Brink (1986) considered it (albeit questionably) a junior synonym of *Oudenodon bainii*. We agree with Brink's referral—although AMNH FARB 5505 is a very poor specimen, it is tuskless, has small, ovoid nasal bosses over the nares as in *Oudenodon*, and exhibits the short, tall snout morphology recognized as diagnostic for *Oudenodon* by Botha and Angielczyk (2007).

Dicynodon brachyrhynchus Broom, 1948

Holotype—RC 86, a slightly anteroposteriorly crushed, nearly complete skull (Fig. 20).

Locus Typicus—Ferndale, Graaff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

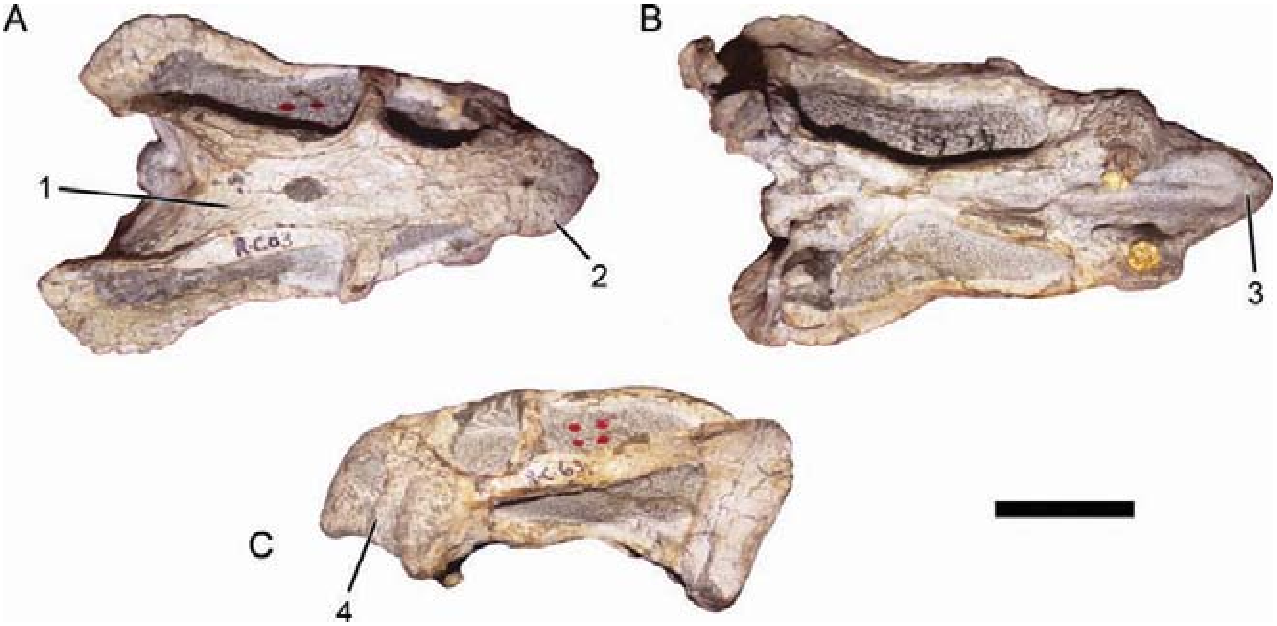

FIGURE 16. RC 63, the holotype of *Dicynodon benjamini* (= *Keyseria benjamini*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. *Keyseria benjamini* can be distinguished from other dicynodonts by the combination of (1) a long, broad intertemporal bar with extensive exposure of the parietals, (2) poorly developed nasal bosses, (3) an elongate, triangular premaxillary portion of the palate, and (4) a well-developed ridge on the premaxillary-maxillary suture. Scale bar equals 5 cm.

FIGURE 17. IVPP V3241, the holotype of *Dicynodon bogdaensis* (= *Turfanodon bogdaensis*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. *Turfanodon bogdaensis* can be distinguished from other dicynodontoids by the combination of a (2) short, narrow intertemporal bar with nearly complete postorbital-parietal overlap, (3) a depression on the preparietal anterior to the pineal foramen, (4) a wide skull at the level of the prefrontals, (5) a squamosal with a broadly rounded dorsal margin in lateral view, and (6) a sharply sloping snout profile. Scale bar equals 10 cm.

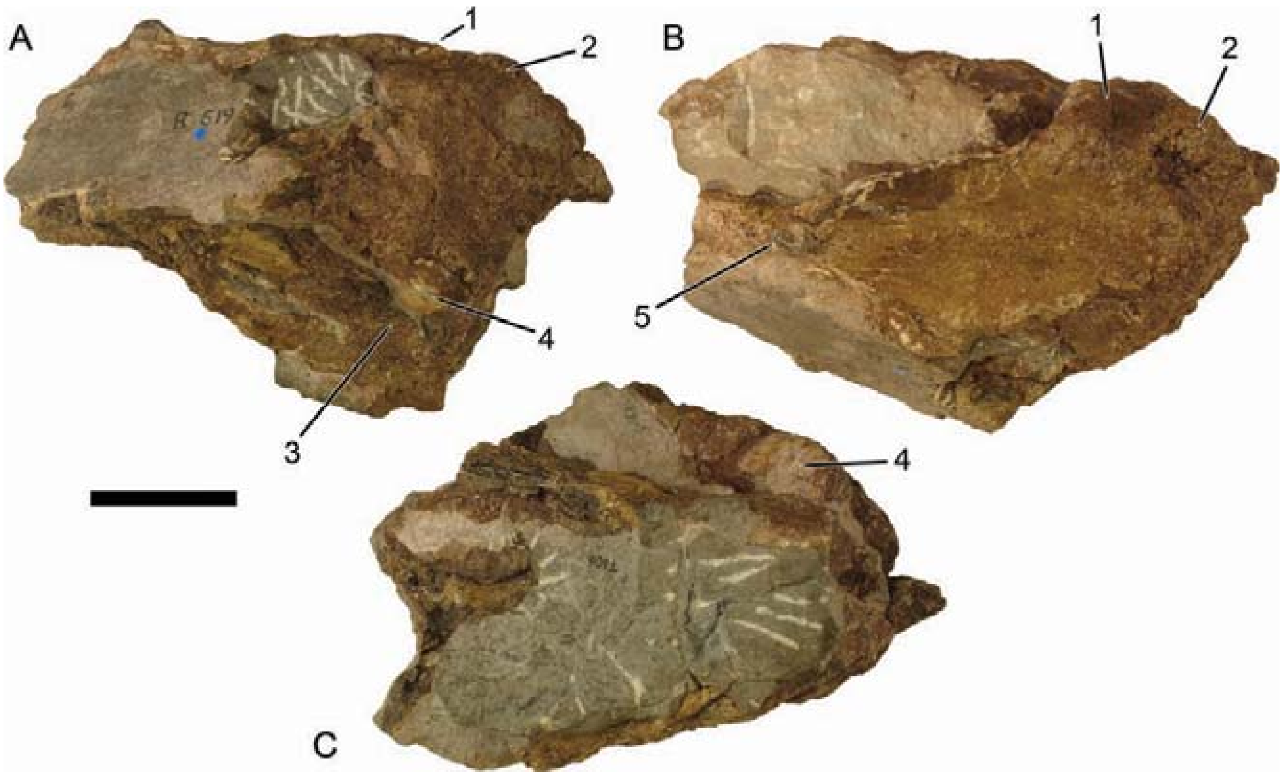

FIGURE 18. CAMZM T606, the holotype of *Dicynodon bolorhinoides* (= *Aulacephalodon bainii*), in right lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (2) paired nasal bosses on the posterodorsal margins of the external nares, and as a geikiine on the basis of the (1) transverse snout ridge at the level of the prefrontals and (5) dorsally directed, 'collar-like' pineal boss. This specimen can be identified as *Aulacephalodon* rather than *Pelanomodon* or *Geikia* on the basis of the (4) large tusks. A (3) prominent swelling in front of the lateral dentary shelf is present in various cryptodonts as well as *Dicynodon* (sensu lato), but in *Dicynodon* this swelling is usually elongate rather than broadly rounded as in this specimen. Scale bar equals 5 cm.

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1948) diagnosed *Dicynodon brachyrhynchus* primarily on the basis of its extremely short snout. He distinguished *D. brachyrhynchus* from other short-snouted *Dicynodon* species by the greater development of the nasal bosses (relative to *D. strigiceps*) and broader preparietal (relative to *D. schwarzi*). Keyser (1975) argued that the proportional differences in this skull relative to other specimens of *Oudenodon bainii* can be attributed to anteroposterior deformation, and synonymized the species, a position followed by Kitching (1977), Brink (1986), and King (1988). RC 86 is a typical specimen of *O. bainii* in all characters: it has well-developed postcaniniform crests, lengthy interpterygoid vacuity, postparietal contribution to the skull roof, lacks tusks, and exhibits the standard *Oudenodon* snout morphology.

Dicynodon breviceps Haughton, 1915

Holotype—SAM-PK-2366, a badly weathered, anteroposteriorly crushed partial skull (missing the right zygomatic arch) and lower jaws (Fig. 21).

Locus Typicus—Voetpad, Murraysburg, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Haughton (1915) diagnosed *Dicynodon breviceps* by its extreme skull breadth, nearly equal to length. Keyser (1975) argued that these proportions were due to deformation and synonymized this species with *Oudenodon bainii* (see also Brink, 1986; King, 1988). SAM-PK-2366 is an extremely poor specimen, rendering accurate determination of most taxonomically important dicynodont characters impossible, but this specimen does exhibit a postcaniniform crest (indicating it is a cryptodont), and the lack of tusks and snout morphology are in accordance with identification as *Oudenodon*.

Dicynodon brevirostris (Owen, 1876)

Holotype—NHMUK R1649a, a badly weathered skull (missing much of the snout) and lower jaws, now lost.

Locus Typicus—Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Owen (1876) diagnosed *Oudenodon brevirostris* (later transferred to *Dicynodon* by Broom [1913a]) by its extremely short snout, a feature that, as Keyser (1975) noted, is mostly due to erosion of this region on the specimen. Although he could not find the type specimen in the Natural History Museum (further search by the current authors has also been unable to locate it, and it must be presumed lost), Keyser (1975) argued that, as figured by Owen (1876), this specimen shows no features that allow it to be distinguished from *Oudenodon bainii*. We concur—

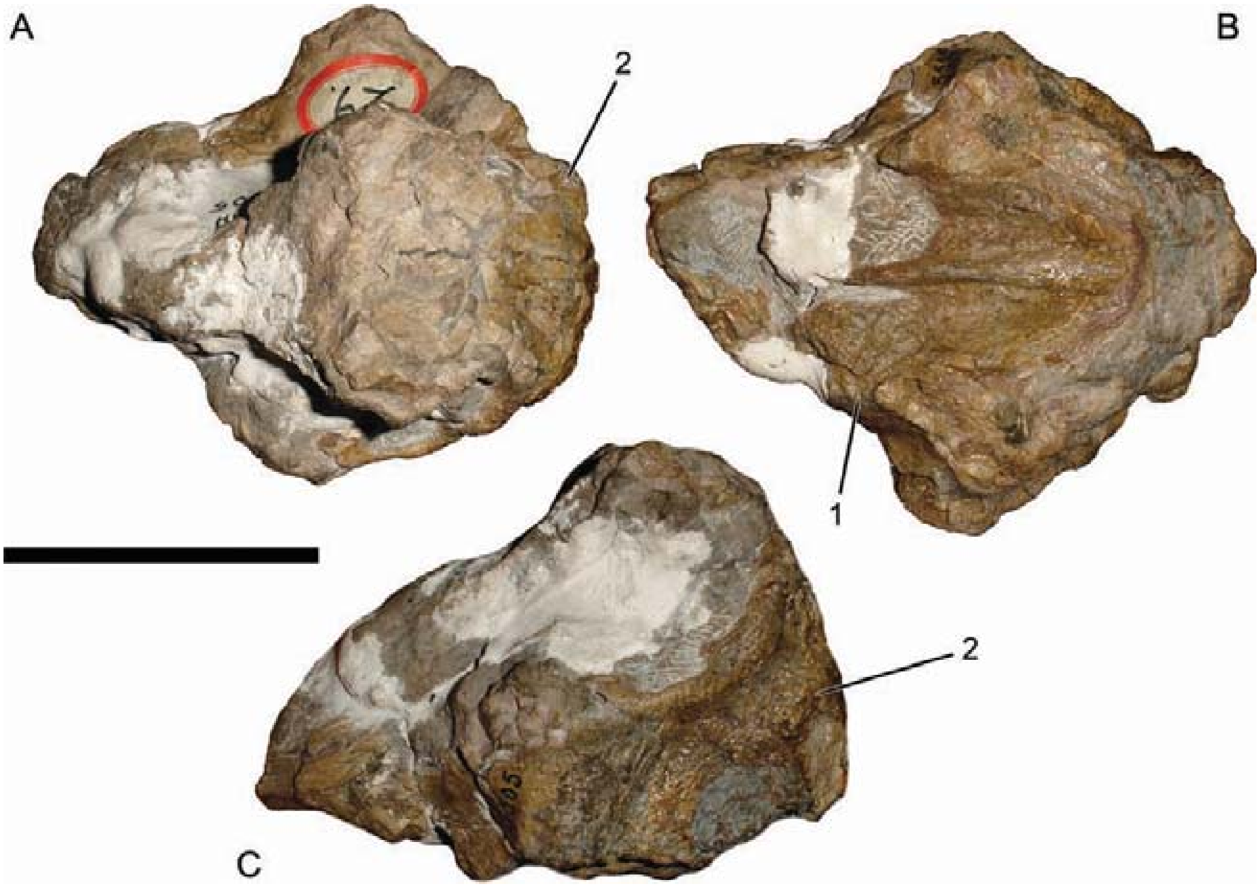

FIGURE 19. AMNH FARB 5505, the holotype of *Dicynodon bolorhinus* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares. This specimen can be identified as *Oudenodon* on the basis of the lack of tusks, small, ovoid nasal bosses, and relatively tall, short snout. Scale bar equals 5 cm.

Owen's plates show that this was a tuskless skull with a clear postcaniniform crest, and the snout morphology is typical of *O. bainii*.

Dicynodon broomi Broili and Schröder, 1937

Holotype—BSP 1934 VIII 47a, a complete, well-prepared skull and lower jaws (Fig. 22).

Locus Typicus—La-de-da, Beaufort West, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broili and Schröder (1937) named *Dicynodon broomi* for a small, well-preserved dicynodont skull with proportionally large tusks. Cluver and Hotton (1981) transferred this species to *Diictodon*. King (1988) listed *D. broomi* as a valid species of *Diictodon*, and noted that it may represent a senior synonym of the other *Tapinocephalus* AZ species *D. vanderhorsti*, based on the shared presence of a ring of bone around the pineal foramen. Brink (1986) and Sullivan and Reisz (2005) considered *D. broomi* to be synonymous with *Diictodon feliceps*, a position maintained here. The two skulls of *D. broomi* (BSP 1934 VIII 47a and 47b, one tusked and one tuskless) exhibit the precaniniform notch, median snout boss, short intertemporal region with extensive postorbital-parietal overlap, and tusk dimorphism typical of *D. feliceps*.

Dicynodon broilii Boonstra, 1948

Holotype—BSP 1934 VII 46, a complete skull.

Locus Typicus—La-de-da, Beaufort West, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Boonstra (1948) named *Dicynodon broilii* as a replacement name for *Dicynodon huenei* Broili and Schröder, 1937, preoccupied by *D. huenei* Haughton, 1932. See entry on *D. huenei* Broili and Schröder, 1937, for further information.

Dicynodon cadlei Broom, 1940a

Holotype—RC 23, a skull missing the right temporal arch (Fig. 23).

Locus Typicus—Hoeksplaas, Murraysburg, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodon lacerticeps* Owen, 1845.

Remarks—Broom (1940a) considered the intertemporal bar of this species to be narrower than any other *Dicynodon* but *D. leontops*, but distinguished it from *D. leontops* by being wider across the orbital region and in the tusks being directed forwards rather than downwards. Haughton and Brink (1954), Kitching

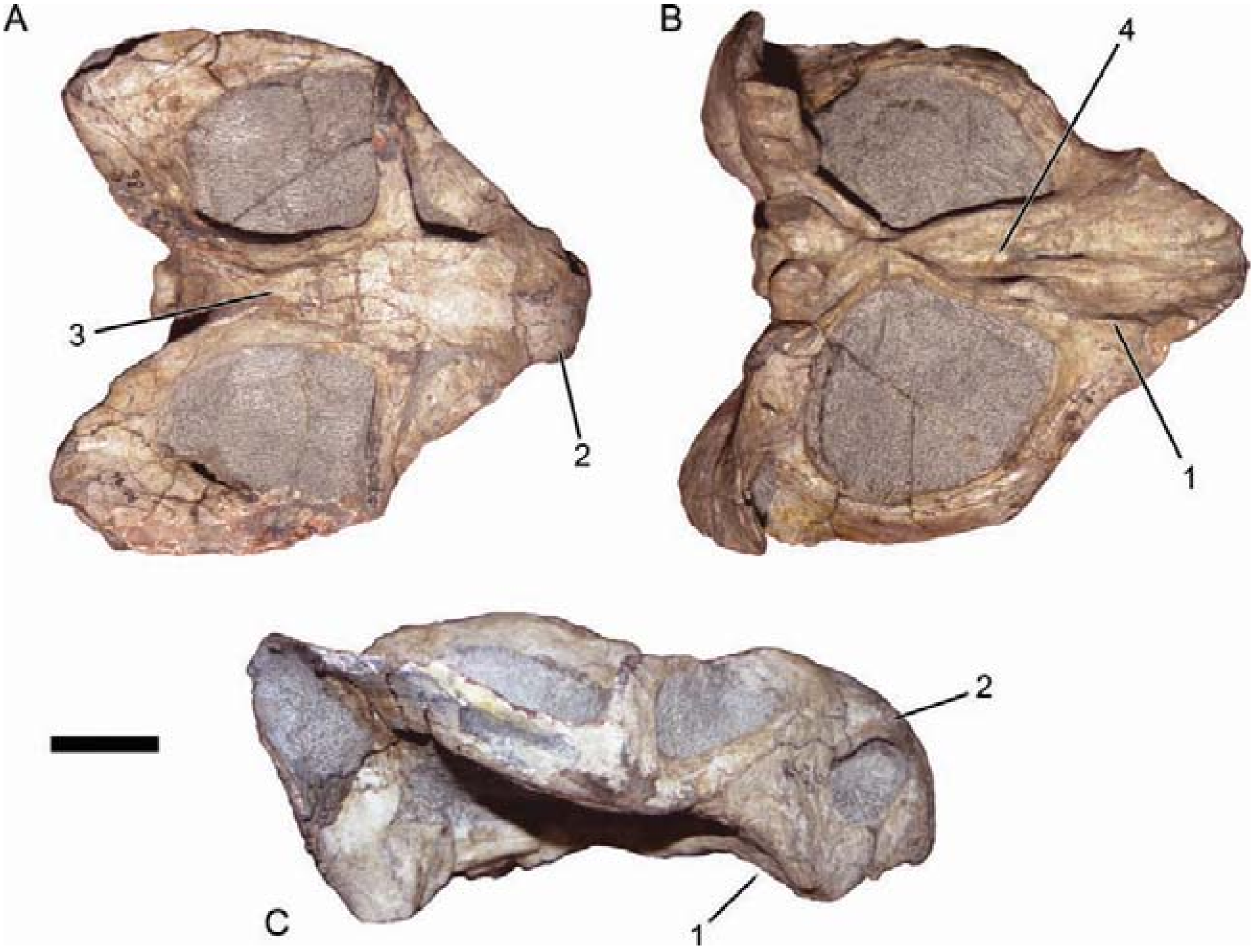

FIGURE 20. RC 86, the holotype of *Dicynodon brachyrhynchus* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

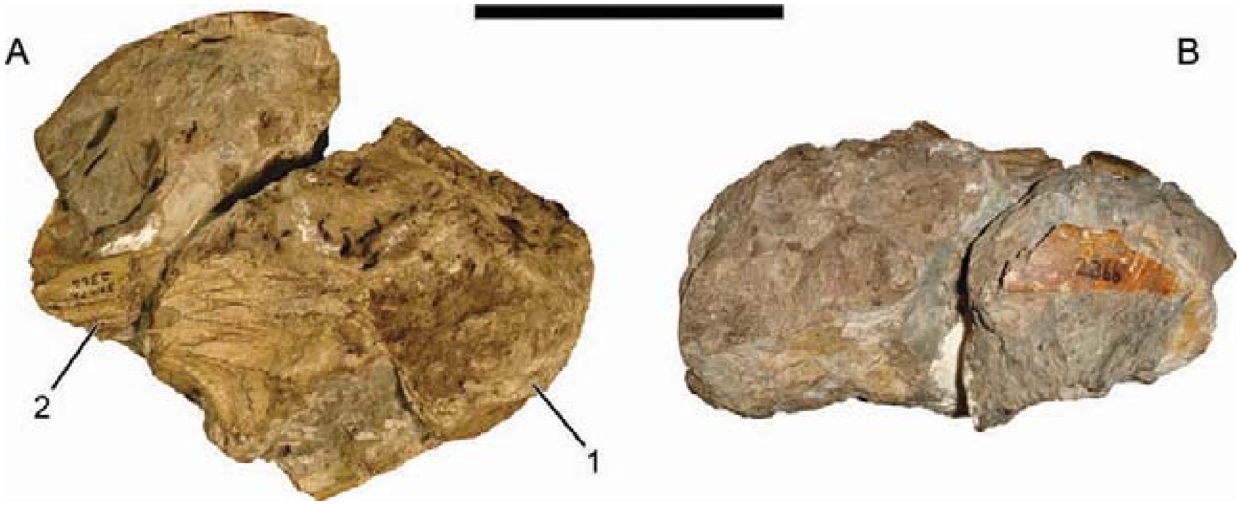

FIGURE 21. SAM-PK-2366, the holotype of *Dicynodon breviceps* (= *Oudenodon bainii*), in dorsal (**A**) and left lateral (**B**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 10 cm.

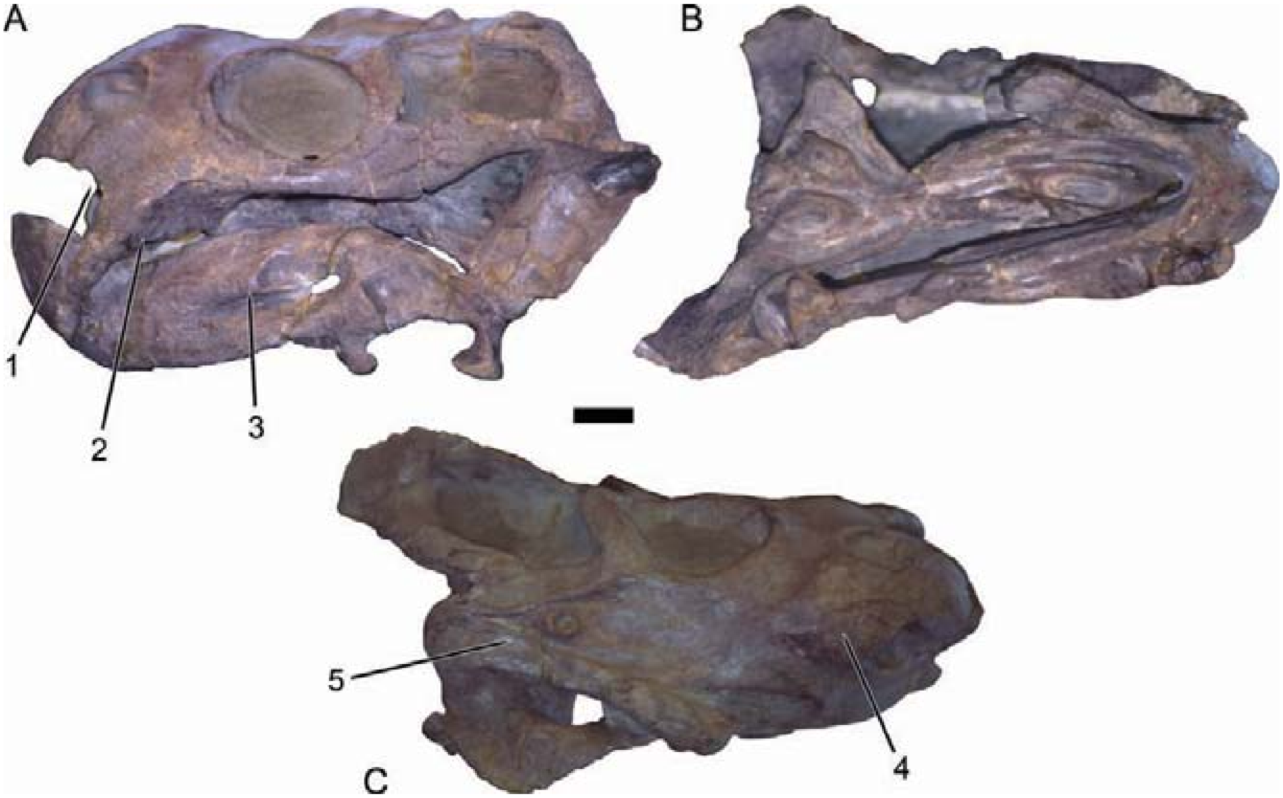

FIGURE 22. BSP 1934 VIII 47a, the holotype of *Dicynodon broomi* (= *Diictodon feliceps*), in left lateral (**A**), ventral (**B**), and dorsal (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch, (2) ventral edge of the caniniform process at same level of anterior margin of orbits, (3) sharp lateral dentary shelf, and (4) median snout boss. *Diictodon feliceps* can be distinguished from other pylaecephalids by the absence of postcanine teeth and the (5) relatively narrow intertemporal bar, with extensive but incomplete overlap of the parietals by the postorbitals. Scale bar equals 1 cm.

(1977), Cluver and Hotton (1981), and King (1988) listed this as a valid species of *Dicynodon*, but Brink (1986) considered it to be synonymous with *D. lacerticeps*. We agree with Brink's (1986) referral—RC 23 exhibits the suite of characters typical of the *Dicynodon lacerticeps* morphotype, including a short, narrow intertemporal region with nearly complete overlap of parietals by postorbitals, premaxilla squared-off in palatal view, gradually sloping snout profile, caniniform process and tusk angled forwards, and squamosal rami acutely angled in lateral view.

Dicynodon calverleyi Broom, 1940b

Holotype—RC 39, a slightly dorsoventrally crushed skull missing portions of the zygomatic arches (Fig. 24).

Locus Typicus—Klipfontein, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Basilodon woodwardi* (Broom, 1921).

Remarks—Broom (1940b) diagnosed *Dicynodon calverleyi* by its nearly circular pineal foramen, apparent lack of contribution of the postfrontal to the skull roof, and triangular depression on the postorbital. Haughton and Brink (1954), Kitching (1977), Cluver and Hotton (1981), and King (1988) listed *D. calverleyi* as a valid species of *Dicynodon*, and Brink (1986) considered it a synonym of *D. lacerticeps* despite the fact that it lacks tusks and a narrow intertemporal bar. In some proportional respects RC 39 is similar to *Tropidostoma*, but lacks a postcaniniform crest and postparietal contribution to the skull roof. RC 39 is extremely similar to the holotype of *Dicynodon microdon* (TM 267, here considered to represent a specimen of *Basilodon woodwardi*), albeit with proportionally smaller orbits. These two specimens share the same intertemporal proportions (short intertemporal region with narrow exposure of parietals but never completely overlapped by postorbitals), the prominent triangular depressions on the postorbital portion of the postorbital bar, and a lack of ornamentation on the snout (no median ridges and very weakly developed nasal bosses, which may be absent entirely in RC 39).

Dicynodon cavifrons Broom and Haughton, 1917

Holotype—SAM-PK-747, a partial skull missing the temporal arches and the left side of the occiput (Fig. 25).

Locus Typicus—Fraserburg, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Tropidostoma dubium* (Owen, 1876).

Remarks—Broom and Haughton (1917) originally diagnosed *Dicynodon cavifrons* on the basis of its triangular (in dorsal view) orbits, downward-projecting tusks, narrow, sunken frontals, short snout, large postorbitals, elongate, triangular postfrontals, and extensive squamosal contribution to the occipital plate. They did not compare *D. cavifrons* to any other species of *Dicynodon*, so it is unclear which characters of the holotype were the basis for recognizing a new species. Van Hoepen (1934) and Brink (1986) placed this species in *Oudenodon* (the latter considering

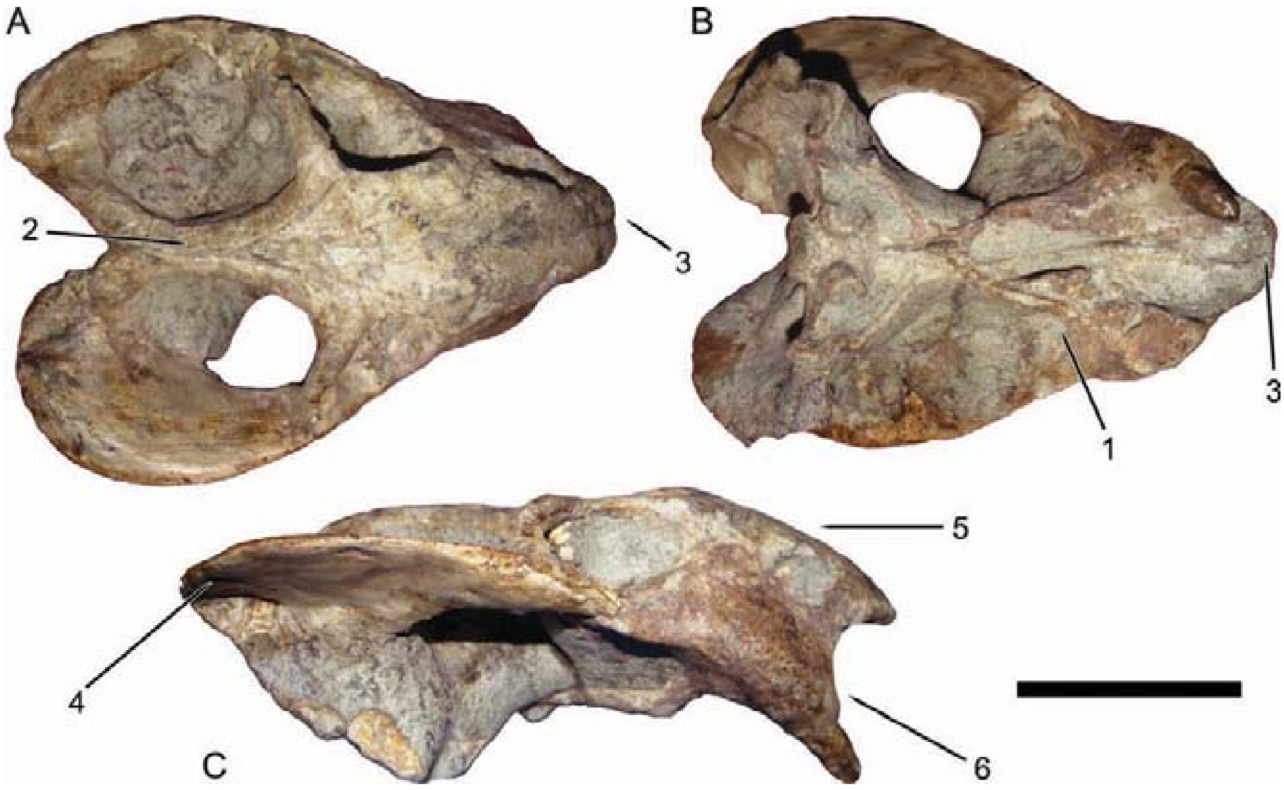

FIGURE 23. RC 23, the holotype of *Dicynodon cadlei* (= *Dicynodon lacerticeps*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa, and as *D. lacerticeps* on the basis of the (2) short intertemporal bar with nearly complete postorbital-parietal overlap, (3) squared-off premaxillary tip, (4) acutely angled squamosal rami in lateral view, (5) gradually sloping snout, and (6) anteriorly directed caniniform process. Scale bar equals 10 cm.

it a synonym of *O. bainii*), despite the presence of large tusks. Keyser (1973) synonymized *D. cavifrons* with *Tropidostoma microtrema*, a referral supported by subsequent morphometric analysis (Botha and Angielczyk, 2007).

Dicynodon clarencei Broom, 1950

Holotype—RC 97, a nearly complete but dorsoventrally crushed skull and lower jaws, with broken temporal arches (Fig. 26).

Locus Typicus—20 miles south of Hanover, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodontoides recurvidens* (Owen, 1876).

Remarks—Broom (1950) diagnosed *Dicynodon clarencei* by its narrow, elongate skull and particularly narrow intertemporal region. Haughton and Brink (1954), Kitching (1977), Cluver and Hotton (1981), and King (1988) listed *D. clarencei* as a valid species of *Dicynodon*, but Brink (1986) recognized the close similarity of RC 97 to *Dicynodontoides* and synonymized it with *Dicynodontoides parringtoni*. Angielczyk et al. (2009) recently synonymized *D. clarencei* with *Dicynodontoides recurvidens*, a referral maintained here.

Dicynodon copei Seeley, 1889

Holotype—NHMUK 47074, a very poorly preserved skull (missing the right temporal arch and much of the snout), lower jaws, and postcranial fragments (Fig. 27).

Locus Typicus—'Cape Colony,' South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Junior subjective synonym of *Lystrosaurus murrayi* (Huxley, 1859).

Remarks—Seeley (1889) described *Dicynodon copei* as being very similar to *Dicynodon murrayi* Huxley, 1859, and indeed shortly thereafter Lydekker (1890) synonymized these species in the combination *Ptychosiagum murrayi* (*Ptychosiagum* Lydekker, 1889, was named as a replacement for Owen's preoccupied *Ptychognathus*, and later superceded by *Lystrosaurus* Cope, 1870a). More recent studies (Cluver, 1971; Grine et al., 2006) have affirmed the synonymy of *D. copei* with *Lystrosaurus murrayi*.

Dicynodon cordylus (Seeley, 1888)

Holotype—NHMUK 49413, a slab containing a semi-articulated skull, lower jaw, and forelimbs (Fig. 28).

Locus Typicus—Klipfontein, Fraserburg, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontia indet.).

Remarks—Seeley (1888) described *Keirognathus cordylus* based on predominantly postcranial characters, rendering comparisons with other dicynodont taxa (mostly described based on isolated skulls) difficult. A clearly dicynodontian skull is preserved (unlike other problematic Seeley postcranial taxa such as *Theromus* and *Theriodesmus*), which led Lydekker (1889) to refer this species to *Dicynodon*, a position maintained by most subsequent authors (e.g., King, 1988). Although NHMUK 49413 comprises the essentially complete anterior half of a small dicynodont skeleton in articulation, because all of the bones are

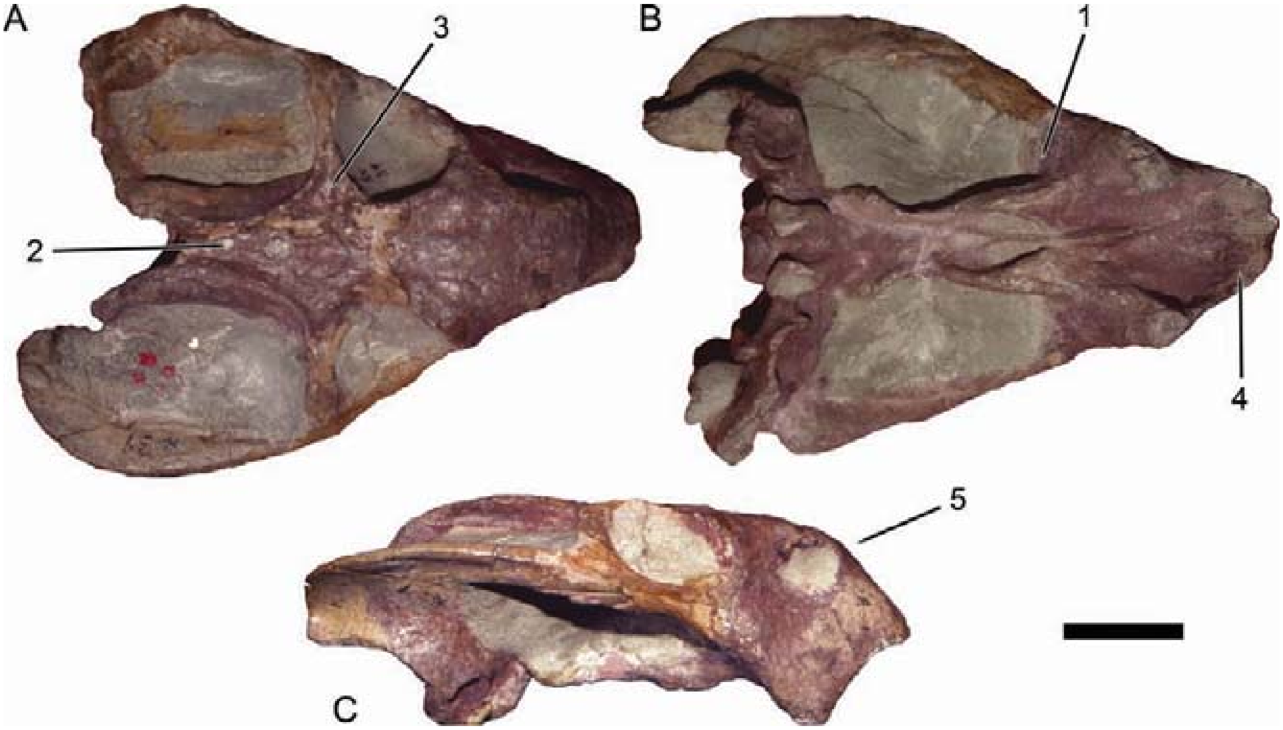

FIGURE 24. RC 39, the holotype of *Dicynodon calverleyi* (= *Basilodon woodwardi*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa, and as *B*. *woodwardi* on the basis of the (2) short, broad intertemporal bar with extensive exposure of the parietals, (3) triangular depression on the dorsal surface of the postorbital bar, (4) long premaxillary region with a distinct embayment anterior to the caniniform, and (5) slightly biplanar snout with break in slope above external naris. Scale bar equals 5 cm.

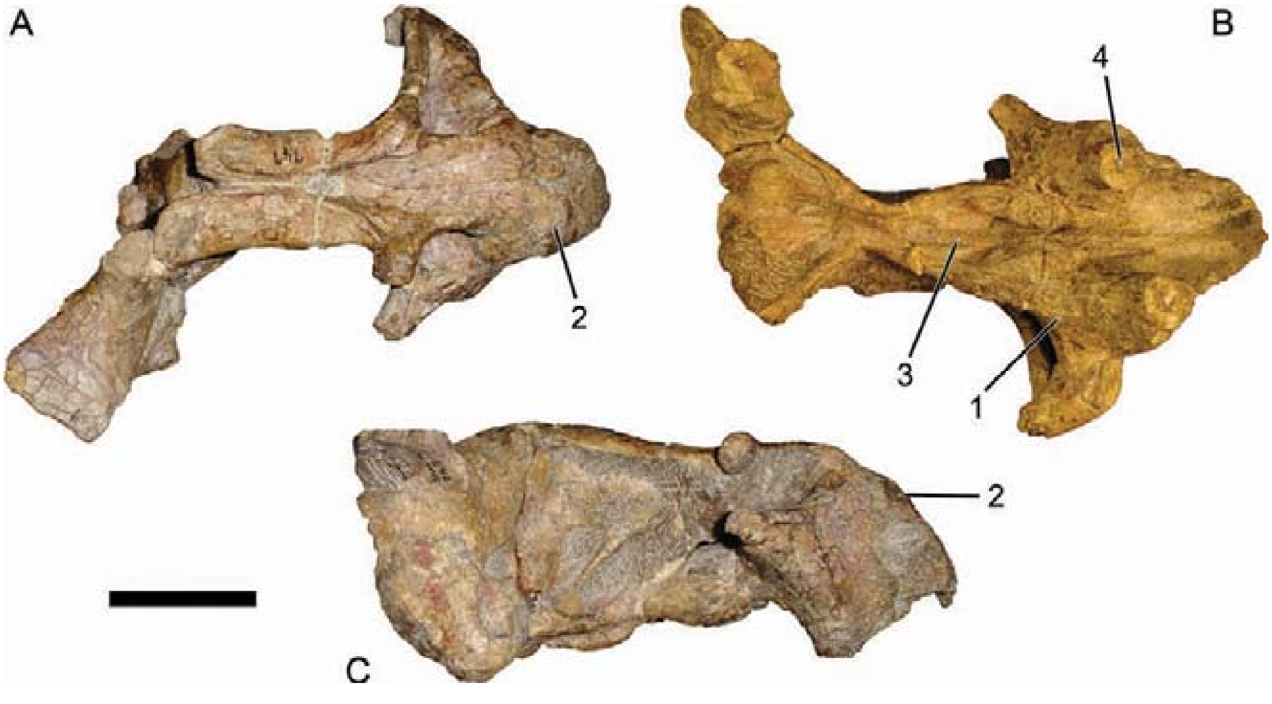

FIGURE 25. SAM-PK-747, the holotype of *Dicynodon cavifrons* (= *Tropidostoma dubium*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses on the posterodorsal margins of the external nares, as an oudenodontid on the basis of the (3) lengthy interpterygoid vacuity reaching the level of the palatal exposure of the palatines, and as *Tropidostoma* on the basis of (4) tusks and snout proportions. Scale bar equals 5 cm.

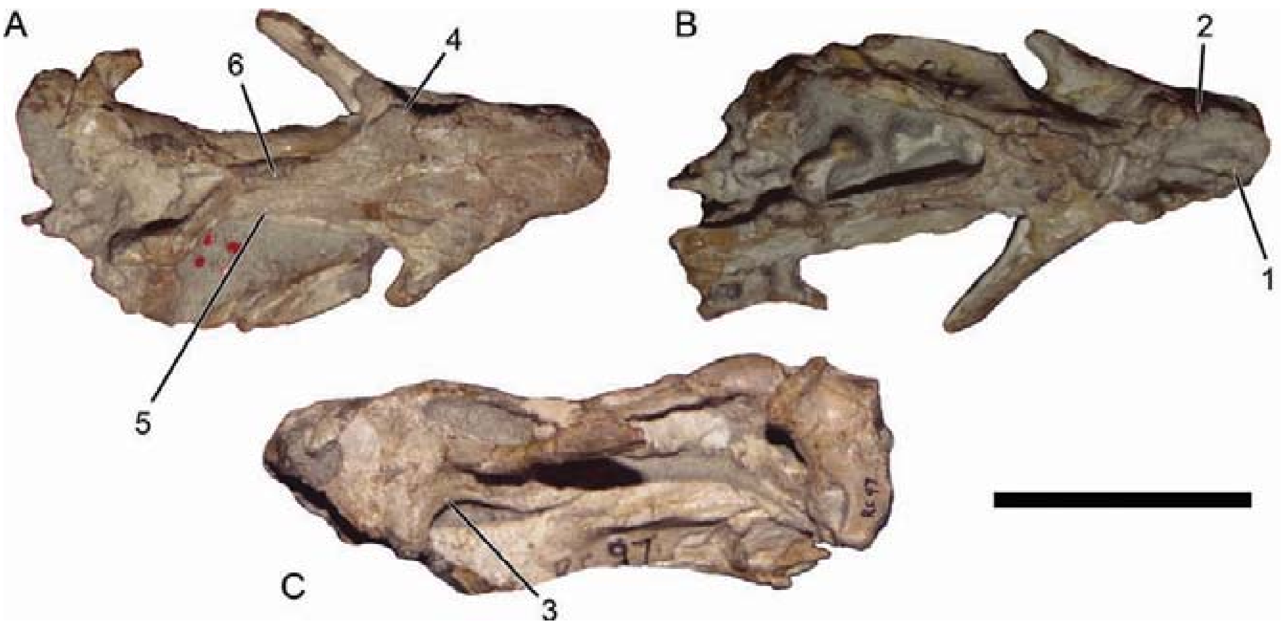

FIGURE 26. RC 97, the holotype of *Dicynodon clarencei* (= *Dicynodontoides recurvidens*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) palatal surface of the premaxilla with a groove-like depression with a rounded anterior end, (2) embayment of the palatal rim anterior to the caniniform process, and a (3) postcaniniform keel, as a kistecephalian on the basis of the (4) absence of the postfrontal, and as a kingoriid on the basis of the (5) postorbitals sloping slightly ventrolaterally, overlapping the parietals except for a narrow exposure of the latter as a sagittal crest. This specimen can be identified as *Dicynodontoides* rather than *Kombuisia* based on the (6) elongate, well-developed pineal foramen. Scale bar equals 5 cm.

exposed in section (at varying angles, so that assorted degrees of internal bone surface are exposed) and otherwise still embedded in the slab, very little morphological detail can be determined. Only the interclavicle (exposed ventrally) presents actual bone surface rather than a section. The skull section is indicative of a generalized tusked dicynodont. This specimen may represent an individual of *Diictodon feliceps*—there may be a precaniniform notch, but it is uncertain whether this is a real feature of the skull or an artifact of its having been sheared and split in half. No other pylaecephalid synapomorphies are visible in the skull, and unfortunately the postcranium is not well preserved enough to determine whether there was a cleithrum or an entepicondylar foramen on the humerus. The T-shaped interclavicle is consistent with but not diagnostic for *Diictodon*, as this morphology is present in several dicynodont taxa. In the absence of any diagnostic features beyond those general for dicynodonts, NHMUK 49413 should be considered Dicynodontia indet. and *D. cordylus* a nomen dubium.

Dicynodon corstorphinei Broom and Haughton, 1917

Holotype—SAM-PK-3337, a partial skull (missing the zygomatic arches) and lower jaws (Fig. 29).

Locus Typicus—Heuningneskrans, Camdeboo, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom and Haughton (1917) described *Dicynodon corstorphinei* based on a skull very similar to that of *Dicynodon lutriceps* and *Dicynodon mustoi*, and distinguished only by minor proportional differences of the interorbital and intertemporal regions. They further noted that the new skull's closest resemblance was to the holotype (NHMUK 36232) of *Oudenodon bainii* and indeed that these specimens agree in all salient features. Broom and Haughton (1917), however, justified the erection of a new species through the following tortuous taxonomic logic: following Broom's (1913a) synonymization of *Oudenodon* with *Dicynodon*, *Oudenodon bainii* Owen, 1860b, would become *Dicynodon bainii*, rendering it a secondary junior homonym of *Dicynodon* (= *Aulacephalodon*) *bainii* Owen, 1845, which Broom and Haughton considered to be a synonym of *Dicynodon tigriceps* (neglecting the fact that *D. bainii* Owen, 1845, has priority over *D. tigriceps* Owen, 1855). Rather than explicitly proposing a replacement name for the (under their taxonomic scheme) preoccupied *D.* (formerly *Oudenodon*) *bainii* and referring SAM-PK-3337 to this taxon, Broom and Haughton chose the opposite course: create a new species (*D. corstorphinei*) with SAM-PK-3337 as the holotype and refer NHMUK 36232 (the holotype of *O. bainii*) to it. Unsurprisingly, Keyser (1975) regarded this species as a junior synonym of *Oudenodon bainii*. However, Keyser (1975) expressed some reservations about this referral, particularly because SAM-PK-3337 appeared to exhibit confluent bosses on nasal and prefrontal, whereas these bosses are typically separate in *Oudenodon bainii*. Examination of SAM-PK-3337 by the current authors reveals that the apparent confluence between these bosses is an artifact of erosion in the snout of this specimen and not a real feature, and *D. corstorphinei* should indeed be treated as a synonym of *O. bainii*.

Dicynodon curtus Broom, 1921

Holotype—SAM-PK-7850, a distorted skull missing the left zygomatic arch and with a disarticulated lower jaw (Fig. 30).

Locus Typicus—Biesjespoort, Victoria West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

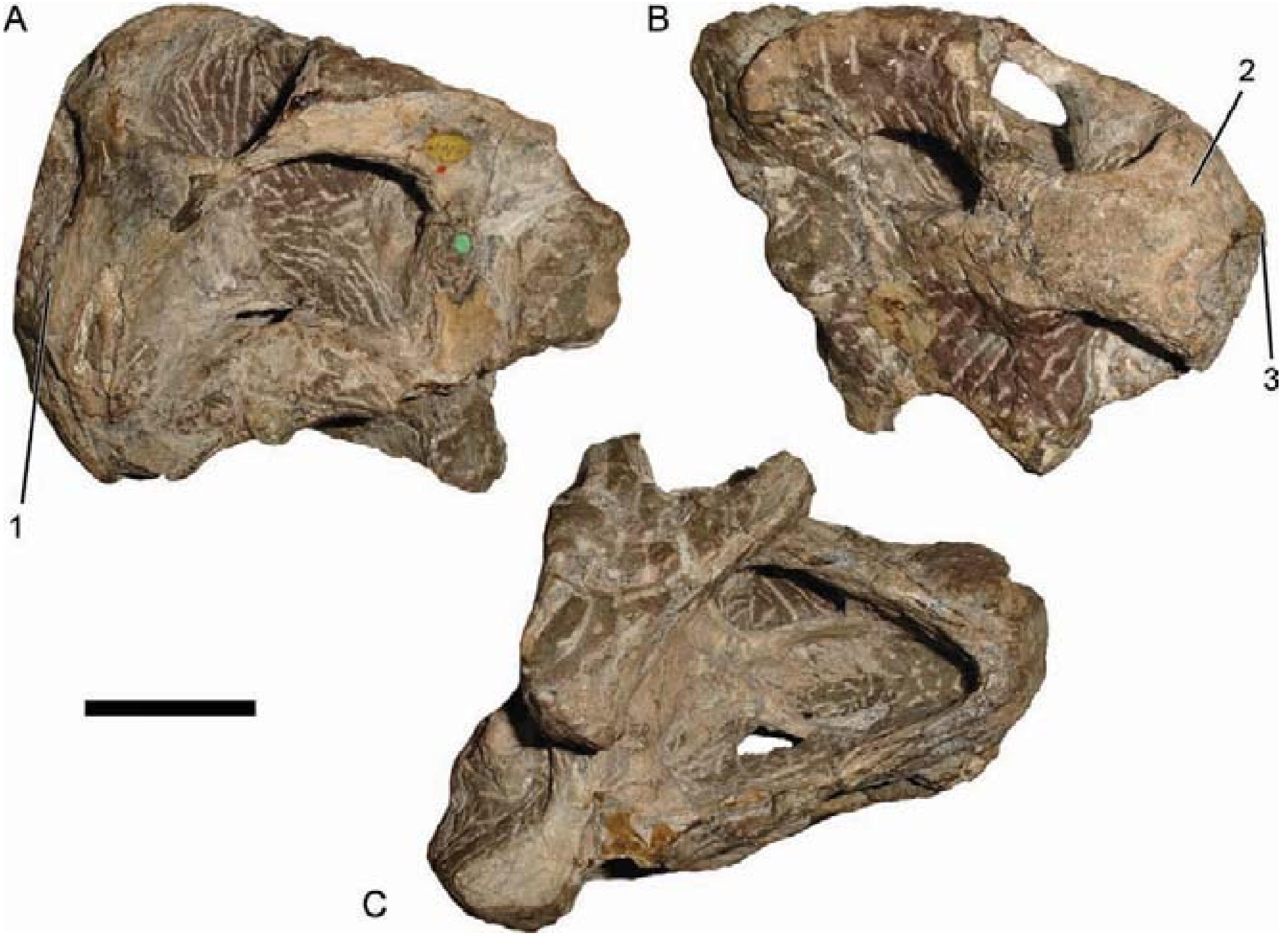

FIGURE 27. NHMUK 47074, the holotype of *Dicynodon copei* (= *Lystrosaurus murrayi*), in left lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a lystrosaurid on the basis of the (1) tall, strongly deflected snout and as *L. murrayi* based on the combination of a (2) triplanar skull profile and (3) median ridge on the dorsal surface of the premaxilla. Scale bar equals 5 cm.

Remarks—Broom (1921) described *Dicynodon curtus* as being most closely related to *Dicynodon dubius*, but differing in the shortness of the parietals and skull proportions in general. Keyser (1975) synonymized *D. curtus* with *Oudenodon bainii*, a referral maintained by King (1988) and tentatively Brink (1986). SAM-PK-7850 is well preserved but highly deformed, making it appear anteroposteriorly shorter than it would have been in life. Discrete characters support referral of this specimen to *O. bainii*: a post-caniniform crest is present, tusks are absent, and the postparietal contributes to the skull roof.

Dicynodon curvatus Owen, 1876

Holotype—NHMUK R3792, a laterally crushed skull with most of the right side eroded off (Fig. 31).

Locus Typicus—Elandsburg, Cradock, South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Valid as *Lystrosaurus curvatus* (Owen, 1876).

Remarks—Owen (1876) described *Dicynodon curvatus* as a member of *Dicynodon*, rather than *Ptychognathus* (= *Lystrosaurus*), and this species was not referred to *Lystrosaurus* until work by Broom (1932). Revisions of *Lystrosaurus* (Cluver, 1971; Colbert, 1974; Grine et al., 2006) have consistently recognized *L. curvatus* as a valid species. This species can be recognized by its rounded skull profile (without clear breaks into multiple planes), lack of ornamentation (snout ridges, furrows, or postfrontal bosses), and relatively large orbits, even at large skull size.

Dicynodon cyclops Haughton, 1917

Holotype—SAM-PK-3447, a poorly prepared partial skull missing the temporal arches and part of the post-caniniform portion of the palate (Fig. 32).

Locus Typicus—Dalham, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Haughton (1917) considered *Dicynodon cyclops* to be most similar to *Dicynodon platyceps* and *Dicynodon lutriceps*, but differentiated it based on its equal interorbital and intertemporal widths (however, Haughton admitted to having never seen the type of *D. lutriceps*, and concluded his description with the caveat that *D. cyclops* might not be a distinct species). Van Hoepen (1934) included this species in *Oudenodon*, and Keyser (1975) synonymized it with *O. bainii* (see also King, 1988). SAM-PK-3447 is very incompletely prepared, with only the dorsal skull roof adequately exposed. Contribution of the postparietal to the dorsal skull roof is evident, indicating oudenodontid affinities. No

FIGURE 28. NHMUK 49413, the holotype of *Dicynodon cordylus* (*Keirognathus cordylus*). This specimen is too poor to allow identification beyond Dicynodontia indet. Scale bar equals 5 cm.

tusks appear to be present, and although somewhat distorted, the snout profile is also in accordance with identification as *O. bainii*.

Dicynodon daptocephaloides Toerien, 1955

Holotype—BP/1/555, a nearly complete, dorsally sheared skull missing portions of the temporal arches and the right prefrontal (Fig. 33).

Locus Typicus—Groot Driefontein, Murraysburg, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Daptocephalus leoniceps* (Owen, 1876).

Remarks—Toerien (1955) described *Dicynodon daptocephaloides* as a species similar to *Dicynodon leoniceps* (van Hoepen's *Daptocephalus*), but diagnosed by the shorter, broader skull in general and intertemporal region in particular. This species was not addressed by Cluver and Hotton (1981) or King (1988); Brink (1986) listed it as tentatively valid. Kitching (1977) argued that this species could not be distinguished from *Daptocephalus leoniceps*, and considered BP/1/555 to represent a juvenile of that taxon. We agree with this referral—BPI/1/555 exhibits the sharply sloping snout and ventrally directed caniniform process of the *Daptocephalus leoniceps* morphotype, and the relative shortness and breadth of the intertemporal bar can be attributed to the juvenile status of this specimen.

Dicynodon declivis (Owen, 1859)

Holotype—NHMUK 36221, a complete and well-preserved but dorsoventrally crushed skull (Fig. 34).

Locus Typicus—Rhenosterberg, South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Valid as *Lystrosaurus declivis* (Owen, 1859).

Remarks—Owen (1859) initially described this taxon as the type species of a new genus, *Ptychognathus*, named for dicynodonts with anteroposteriorly short skulls with tall, strongly deflected snouts. In subsequent papers Owen variously treated *Ptychognathus* as a distinct genus (e.g., Owen, 1876) or a subgenus of *Dicynodon* (e.g., Owen, 1860b). Although *P. declivis* was the first-named species of *Lystrosaurus*, it was not combined in that genus until work by Brink (1951), who recognized the validity of the species over *L. latirostris* (Owen, 1860b), which was previously in wide use for the exceptionally tall-snouted species of *Lystrosaurus*. Subsequent revisions of *Lystrosaurus* (Cluver, 1971; Colbert, 1974; Grine et al., 2006) have all recognized the validity of *L. declivis*.

Dicynodon depressus (Owen, 1876)

Holotype—NHMUK 47064, a badly weathered, dorsoventrally crushed skull (missing the temporal arches) and lower jaws (Fig. 35).

Locus Typicus—Listed as Steilkrans (Stylkrantz), South Africa, but as noted by Kitching (1977), this locality contains only *Cistecephalus* AZ sediments, and so this specimen was probably collected in the Kompassberg or Rhenosterberg ranges to the northeast.

Horizon—Probably *Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Junior subjective synonym of *Lystrosaurus declivis* (Owen, 1859).

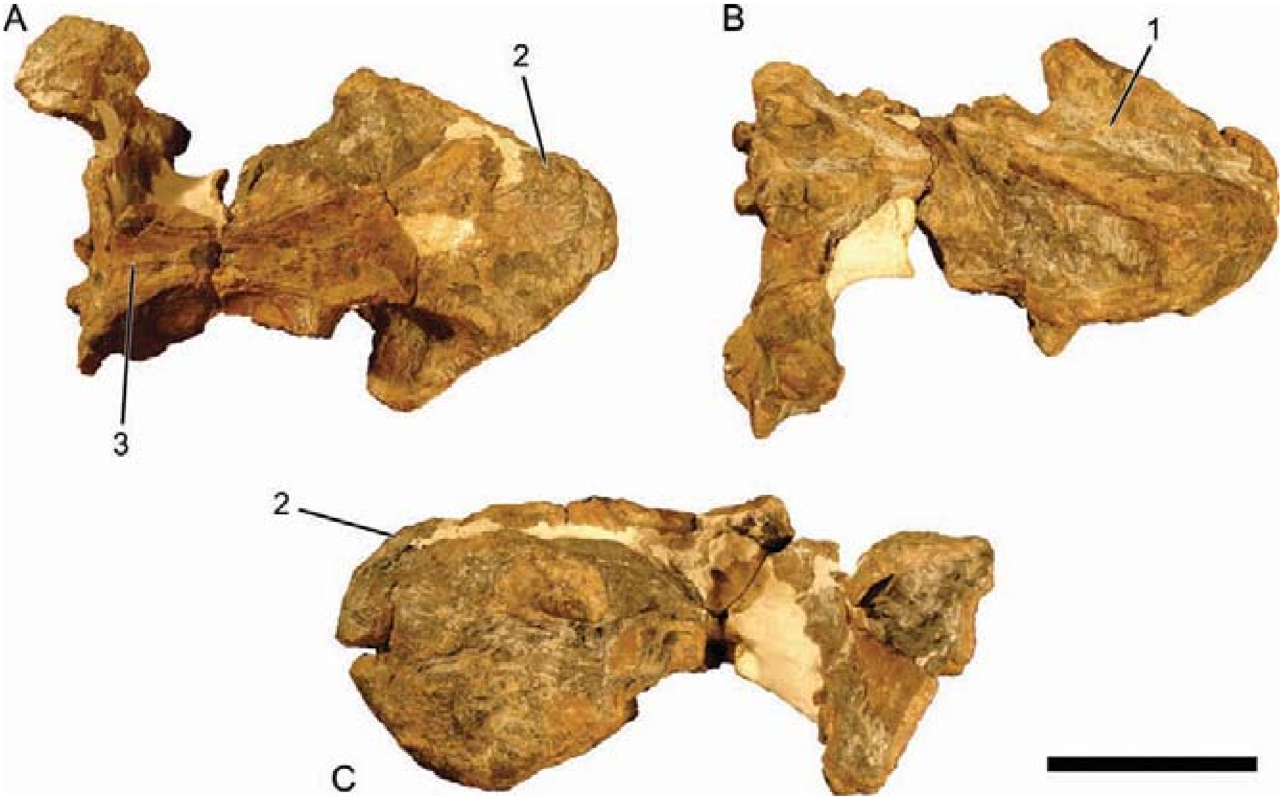

FIGURE 29. SAM-PK-3337, the holotype of *Dicynodon corstorphinei* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

Remarks—Owen (1876) diagnosed *Ptychognathus depressus* by its extremely narrow lateral profile and flattened dorsal surface. Von Huene (1931) considered this to be a valid species of *Lystrosaurus*, but Cluver (1971) synonymized it with *L. declivis*, an identification supported by subsequent work (Colbert, 1974; King, 1988; Grine et al., 2006). The apparent differences between NHMUK 47064 and *L. declivis* are entirely deformational, because this skull has suffered severe dorsoventral compression.

Dicynodon dubius Owen, 1876

Holotype—NHMUK 47051, a partial skull (missing the zygomatic arches) and lower jaws (Fig. 36).

Locus Typicus—Rinoster Kop, Graaff-Reinet, South Africa.

Horizon—?*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Valid as *Tropidostoma dubium* (Owen, 1876), comb. nov.

Remarks—Owen (1876) diagnosed *Dicynodon dubius* based on the narrow snout and relatively small tusks of the type and only known specimen. Haughton and Brink (1954), Brink (1986), and King (1988) listed *D. dubius* as a valid species of *Dicynodon*, and van Hoepen (1934) included it in *Oudenodon*, but as a valid species. NHMUK 47051 is incompletely prepared, with matrix still covering the palatal surface of the skull, ventral surface of the jaws, and lateral surfaces of the braincase. The snout is low and gently sloping and the caniniform processes are angled anteroventrally. The canines are relatively small compared to those of a *Diictodon*, *Dicynodon lacerticeps*, *Daptocephalus leoniceps*, or *Aulacephalodon* skull of similar size. The left caniniform process has been ground down to produce a medial section through the canine tusk. Enough of the matrix between the skull and lower jaw has been removed on the left side of the skull to show the presence of a well-developed postcaniniform crest. The dorsal surface of the snout was damaged during preparation, but paired nasal bosses at the dorsal margins of the external nares are present. No prefrontal bosses are present. The pineal foramen is large and circular and bordered anteriorly by a large preparietal. The intertemporal region is short (3.5 cm relative to 10.5 cm dorsal skull length) and broad (3.1 cm wide at midpoint of pineal foramen), with wide exposure of the parietals throughout. The dorsal surface of the postorbitals is nearly horizontal and the postparietal contributes to the dorsal surface of the intertemporal bar posteriorly, forming a thin wedge between the parietals. The dentary is of roughly equal height throughout its length, but has a sharply upward-hooked process at the tip of the symphysis. The paired nasal bosses on the dorsal margin of the external nares and the postcaniniform crest indicate that this specimen is a cryptodont. Among cryptodonts, only in oudenodontids does the postparietal contribute to the intertemporal skull roof (although this condition is also present in *Pristerodon*, *Cistecephalus*, and some derived dicynodontoids among dicynodonts in general [Angielczyk and Kurkin, 2003a]). The relatively long, low snout, small external naris, and presence of tusks allow NHMUK 47051 to be identified as *Tropidostoma* rather than *Oudenodon*, following the diagnosis of Botha and Angielczyk (2007). Because *Dicynodon dubius* Owen, 1876, predates *Dicynodon microtrema* Seeley, 1889, *D. dubius* becomes the valid specific name for

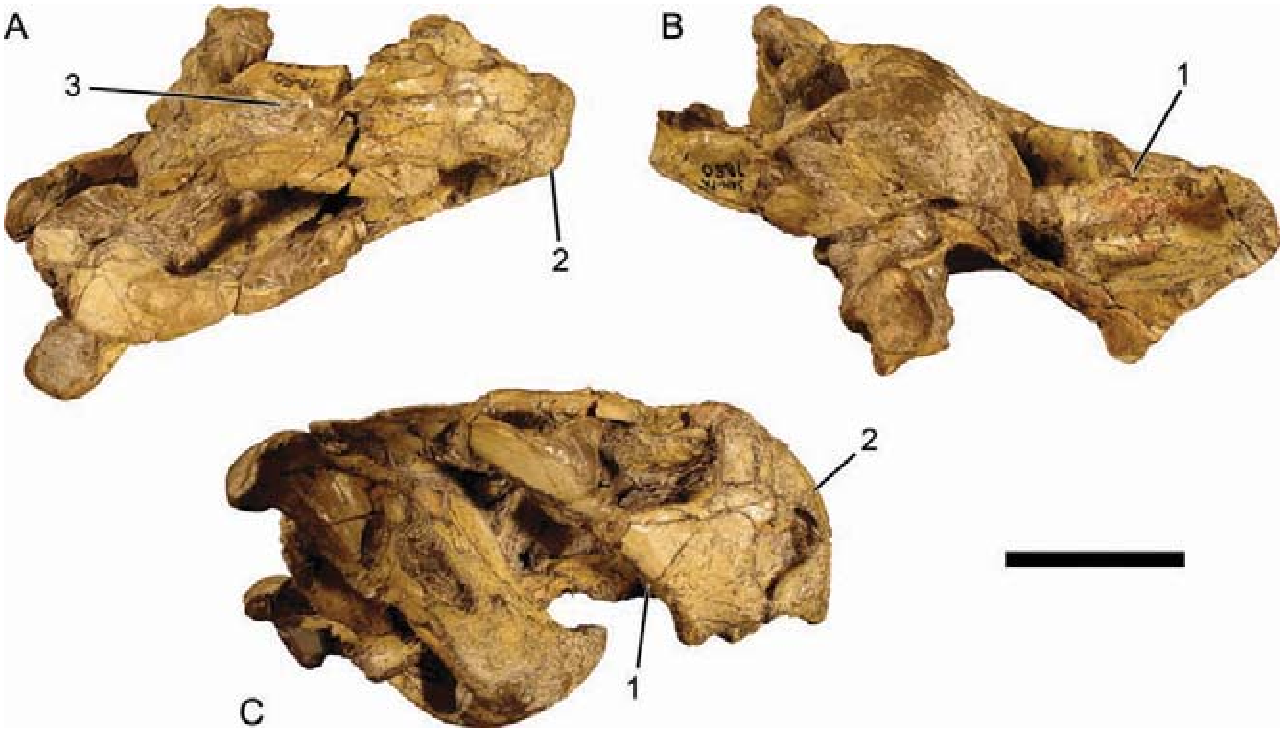

FIGURE 30. SAM-PK-7850, the holotype of *Dicynodon curtus* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

Tropidostoma in the new combination *Tropidostoma dubium*. The spelling of the specific epithet necessarily changes to *dubium* to agree in gender with the neuter generic name *Tropidostoma*, in accordance with Article 34.2 of the International Code of Zoological Nomenclature (ICZN, 1999).

Dicynodon duffianus (Newton, 1893)

Holotype—ELGNM 1978.559, a slab containing the natural mold of a partial skull and postcranium (vertebral column, ribs, and partial pelvis).

Locus Typicus—Cutties Hillock Quarry, Elgin, Scotland.

Horizon—Cutties Hillock Sandstone Formation (Upper Permian).

Status—Junior subjective synonym of *Gordonia traquairi* Newton, 1893.

Remarks—Newton (1893) distinguished *Gordonia duffiana* from *Gordonia traquairi* and *Gordonia huxleyana* by its proportionally broader skull. Von Huene (1940) transferred *G. duffiana* and its congeners to *Dicynodon*. The proportional differences between the skulls of *G. duffiana* and *G. huxleyana* are minor and probably attributable to individual variation. The type skull of *G. traquairi* is markedly narrower but appears to have suffered lateral crushing (based on the orientation of the sagittal crest and zygomatic arch), and is otherwise similar to *G. duffiana*. Refer to the entry on *Dicynodon traquairi* for further information.

Dicynodon dunnii Seeley, 1889

Holotype—NHMUK R866, a laterally compressed occiput and associated cervical vertebrae (Fig. 37).

Locus Typicus—Tafelberg, Beaufort West, South Africa.

Horizon—?*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Tropidostoma dubium* (Owen, 1876).

Remarks—Seeley (1889) described *Dicynodon dunnii* and *Dicynodon microtrema* based on isolated occipital material from a single locality, and referred additional cranial material to these taxa. In the body of this paper he established *Tropidostoma* as a subgenus of *Dicynodon* for *D. dunnii*, but in the figure captions (Seeley, 1889:294) lists *Tropidostoma* as "a new Anomodont genus allied to *Dicynodon*." Broom (1915b) reviewed the Tafelberg anomodont material and concluded that only a single species was present, which he called *Tropidostoma microtrema* (separating it from *Dicynodon* because of the presence of postcanines), combining *Tropidostoma* with *D. microtrema* by reason of page priority. Subsequent workers (e.g., Haughton and Brink, 1954; Keyser, 1973; Brink, 1986; King, 1988) have accepted this synonymy, although Botha and Angielczyk (2007) noted that the incompleteness of NHMUK R866 (as well as NHMUK R868, the holotype of *D. microtrema*) complicates identification of this material as what is usually considered '*Tropidostoma microtrema*.' To maintain current usage of the biostratigraphically important genus *Tropidostoma*, here we take Seeley's collective Tafelberg material (all of which is consistent with identification as *Tropidostoma*, even though not all specimens exhibit autapomorphies of *Tropidostoma*) as hypodigmatic of *T. dunnii*. Unfortunately, some nomenclatural alteration of this taxon is inescapable, given our determination that *Dicynodon dubius* Owen, 1876 (see above), also represents *Tropidostoma*, necessitating the new combination *T. dubium*.

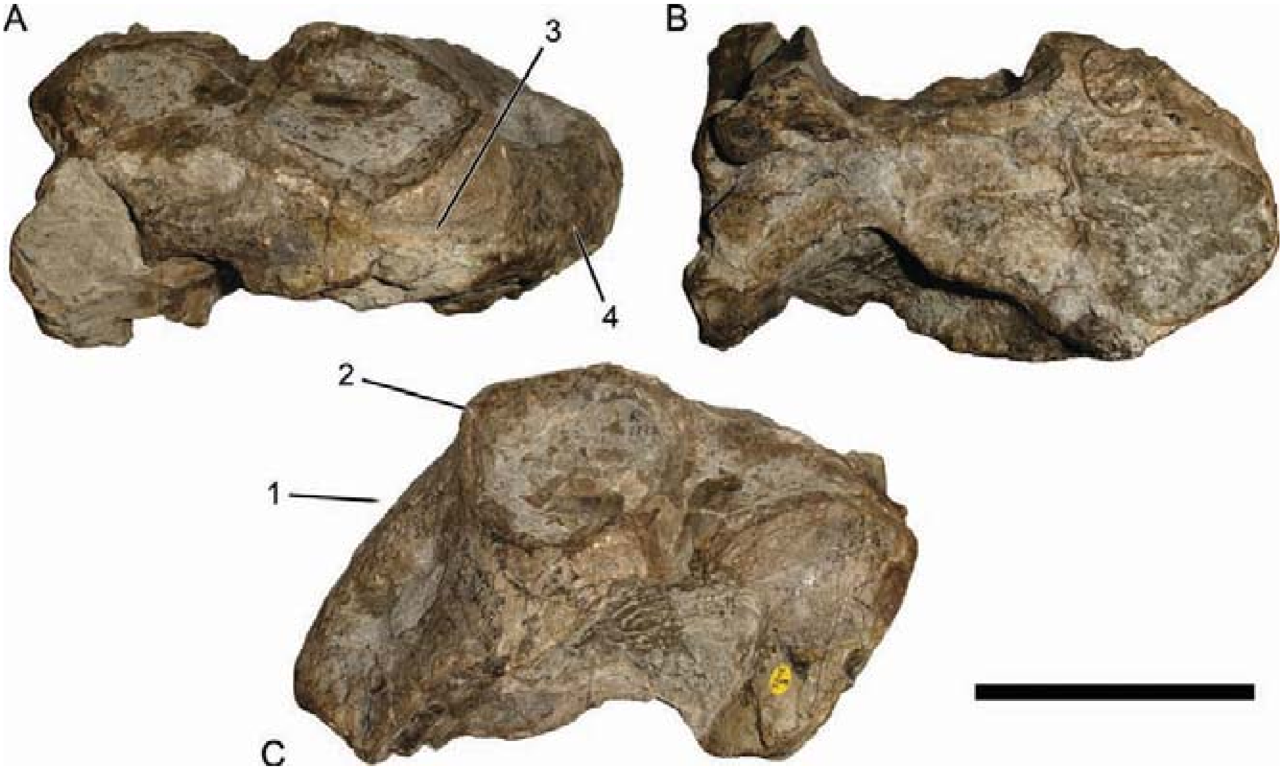

FIGURE 31. NHMUK R3792, the holotype of *Dicynodon curvatus* (= *Lystrosaurus curvatus*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a lystrosaurid on the basis of the (1) tall, strongly deflected snout and (2) well-developed prefrontal bosses. *Lystrosaurus curvatus* is diagnosed by the (3) curvature of the snout profile, with an indistinct transition between frontal and premaxillary planes and (4) absence of a median ridge on the dorsal surface of the premaxilla. Scale bar equals 10 cm.

Dicynodon dutoiti Broom and Schepers, 1937

Holotype—BP/1/3710, a nearly complete but anteroposteriorly crushed skull (Fig. 38).

Locus Typicus—Seymour, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodon lacerticeps* (Owen, 1845).

Remarks—Broom and Schepers (1937) described *Dicynodon dutoiti* based on a highly distorted skull from the Seymour-Fairbairn area. Haughton and Brink (1954) and King (1988) listed *D. dutoiti* as a valid species of *Dicynodon*, whereas Kitching (1977) considered it to be synonymous with *Daptocephalus leoniceps* and Brink (1986) considered it (and *D. leoniceps*) synonymous with *Dicynodon lacerticeps*. King (1988) lists the holotype for this species as a lost specimen from the Transvaal Museum, but in fact this specimen is housed in the Bernard Price Institute, as BP/1/3710. Although incomplete and poorly preserved, this specimen exhibits several diagnostic features of *Dicynodon lacerticeps*: short, narrow intertemporal region with overlap of parietals by postorbitals, premaxilla squared-off in palatal view, gradually sloping snout profile, caniniform process and tusk angled forwards, and squamosal rami acutely angled in lateral view.

Dicynodon duvenhagei Broom, 1948

Holotype—RC 64, a crushed partial skull missing the tip of the snout and the temporal arches (Fig. 39).

Locus Typicus—Doornkloof, Graaff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodontoides recurvidens* (Owen, 1876).

Remarks—Broom (1948) described *Dicynodon duvenhagei* as a new species most similar to tuskless forms such as *Dicynodon latirostris*, *Dicynodon lutriceps*, and *Dicynodon platyceps* (all considered synonyms of *Oudenodon bainii* herein), but distinguished by a narrow parietal region and an unusually elongate pineal foramen. Cluver and Hotton (1981) transferred this species to *Kingoria* (see also King, 1988), and more recently Angielczyk et al. (2009) have demonstrated that it is conspecific with *Dicynodontoides recurvidens*.

Dicynodon euryceps Boonstra, 1938

Holotype—SAM-PK-11316, a complete, somewhat dorsoventrally crushed skull (Fig. 40).

Locus Typicus—Luangwa Valley, Zambia.

Horizon—Upper Madumabisa Mudstone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Boonstra (1938) named *Dicynodon euryceps* for an exceptionally broad skull exhibiting the typical 'heart-shaped' morphology of Zambian *Oudenodon* specimens. Broom (1948) considered *D. euryceps* to be synonymous with another Zambian species, *Dicynodon helenae*, and Keyser (1975) argued that both of these species were synonymous with *Oudenodon luangwanensis*. Refer to the entry on *Dicynodon luangwanensis* for our rationale in referring the Zambian *Oudenodon* species to *O. bainii*.

Dicynodon feliceps Owen, 1876

Holotype—NHMUK 47052, a nearly complete skull (missing the right zygomatic arch) and lower jaws (Fig. 41).

Locus Typicus—Fort Beaufort, South Africa.

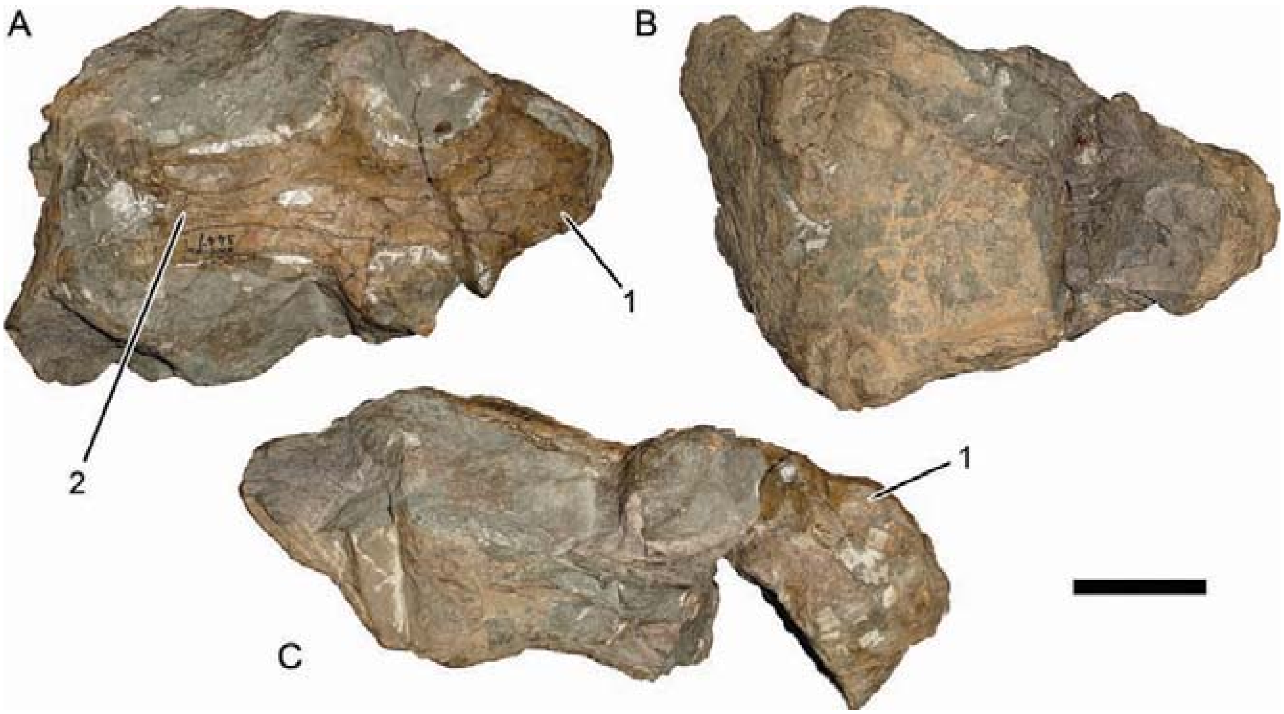

FIGURE 32. SAM-PK-3447, the holotype of *Dicynodon cyclops* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Valid as *Diictodon feliceps* (Owen, 1876).

Remarks—Owen (1876) described *Dicynodon feliceps* based on a complete skull from the vicinity of Fort Beaufort (a stratigraphically uncertain locality including both *Cistecephalus* and *Dicynodon* AZ exposures [Kitching, 1977]). Cluver and Hotton (1981) recognized that *D. feliceps* was highly distinct from *Dicynodon lacerticeps* and should instead be referred to *Diictodon* Broom, 1913c. Brink (1986), Sullivan and Reisz (2005), and Angielczyk and Sullivan (2008) considered *D. feliceps* to be the only valid species of *Diictodon*. NHMUK 47052 is a well-preserved, undistorted skull and lower jaws. Although overprepared, this specimen still clearly illustrates the diagnostic features of *Diictodon*: precaniniform notch, ventral edge of caniniform process at level of anterior edge of the orbit, dentary table present as an elongate grooved surface on the dorsal surface of the dentary bounded laterally by a low ridge and medially by a tall, thin, dorsally convex blade, postcanines absent, and postorbitals broadly exposed dorsally on the intertemporal bar, nearly meeting at midline. At 10.6 cm dorsal skull length, NHMUK 47052 is one of the larger known specimens of *Diictodon*. Given the ubiquity of *Diictodon* in Karoo collections and its significantly greater abundance than *Dicynodon* or *Aulacephalodon*, it is remarkable that a specimen of this taxon was not described until 1876, rather than being among the species of *Dicynodon* initially described by Owen.

Dicynodon galecephalus Broom and Robinson, 1948

Holotype—RC 77, a dorsoventrally crushed, poorly preserved skull (missing the zygomatic arches and portions of the snout) and lower jaws (Fig. 42).

Locus Typicus—Ferndale, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dinanomodon gilli* (Broom, 1932).

Remarks—Broom and Robinson (1948:406) described *Dicynodon galecephalus* as a “remarkably aberrant” new species of *Dicynodon*, with no close relatives among the nominal species of the genus. In particular, they noted that the presence of a well-developed lateral dentary shelf in this taxon made it more similar to dicynodonts “which have retained small molar teeth” (e.g., *Emydops*, *Pristerodon*) than to other species of *Dicynodon*. The lack of any postcanine teeth and general skull shape led Broom and Robinson to ultimately assign this species to *Dicynodon* rather than one of the ‘endothiodonts’ or a new genus, however. Cox (1959) referred this species to his new genus *Kingoria* and retained it as valid, a position followed by Cluver and Hotton (1981) and King (1988). Brink (1986) synonymized *D. galecephalus* (or *K. galecephala*) with *Dicynodontoides parringtoni*, but Angielczyk et al. (2009) disagreed with the association of this specimen with *Kingoria*/*Dicynodontoides*, noting that RC 77 lacks the diagnostic features of *Dicynodontoides*. Instead, they suggested that this specimen is referable to *Dicynodon* sensu lato, most probably *D. lacerticeps*. The poor preservation of RC 77 makes identification to species difficult, but the presence of a narrow intertemporal bar even at small size and a boss at the top of the naris, giving it a ‘saddle-shape,’ suggests that this represents a small juvenile of *Dinanomodon*.

Dicynodon gamkaensis Broom, 1937b

Holotype—TM 1465, a poorly preserved skull missing the left temporal arch, now lost.

Locus Typicus—Klipbank, Beaufort West, South Africa.

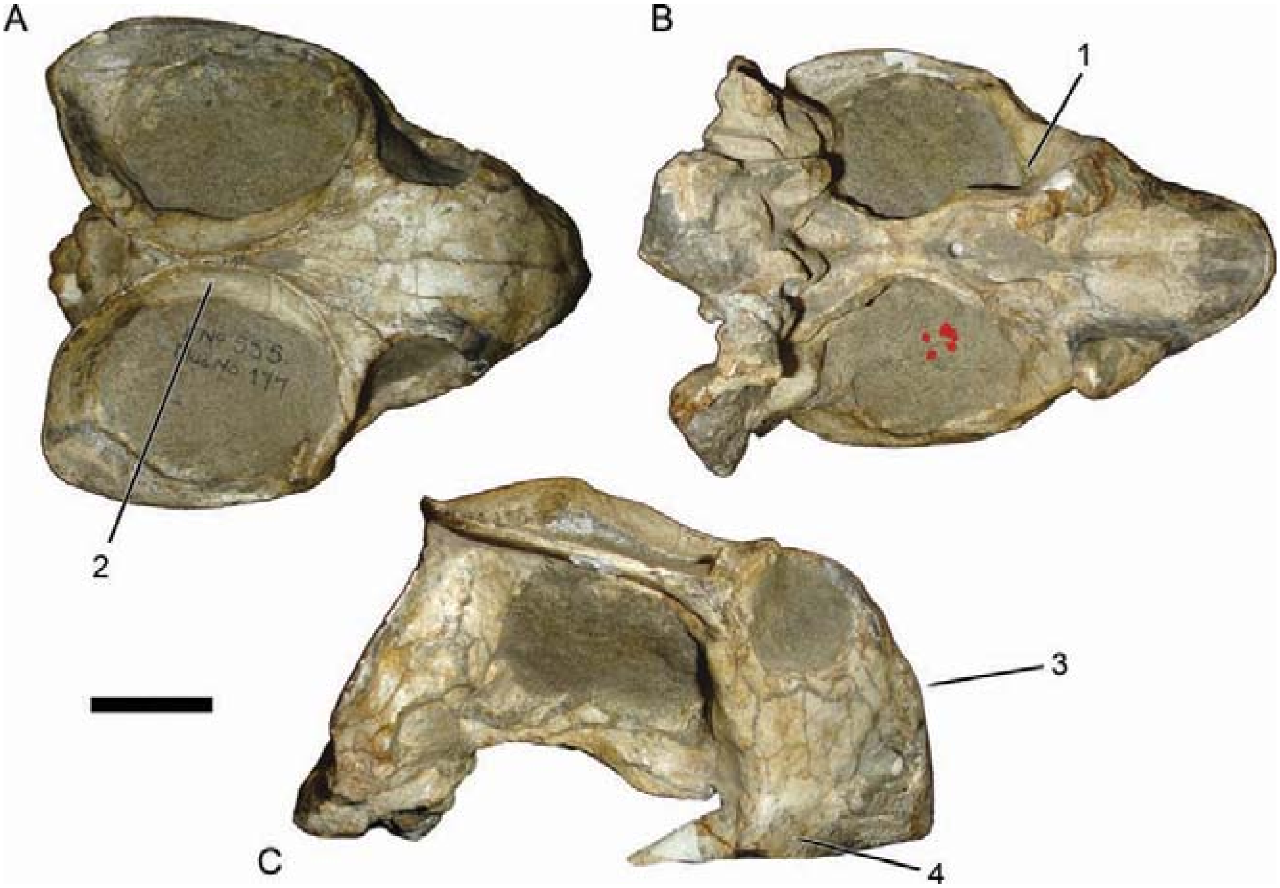

FIGURE 33. BP/1/555, the holotype of *Dicynodon daptocephaloides* (= *Daptocephalus leoniceps*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *D. leoniceps* on the basis of the (2) narrow intertemporal bar with nearly complete postorbital-parietal overlap, with a vertical orientation of the postorbitals, (3) steeply sloping snout profile, and (4) ventrally directed caniniform process. Scale bar equals 5 cm.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom (1937b) described *Dicynodon gamkaensis* as being most similar to the other *Tapinocephalus* AZ species *Dicynodon jouberti* and *Dicynodon microrhynchus*. Additional study of this species has been rendered difficult by the loss of the holotype. Haughton and Brink (1954) and King (1988) listed *D. gamkaensis* as a valid species of *Dicynodon*, but Brink (1986) considered it a synonym of *Diictodon feliceps*. Broom's (1937b) original description indicates that TM 1465 was almost certainly a specimen of *Diictodon*. Although he did not figure the specimen in lateral view (so the presence of a precaniniform notch is uncertain), the median nasal boss, large preparietal, and short intertemporal region with extensive postorbital-parietal overlap is typical for *Diictodon*.

Dicynodon gilli Broom, 1932

Holotype—SAM-PK-4008, a very poorly preserved skull missing the temporal arches and large portions of the snout and palate (Fig. 43).

Locus Typicus—Watervlei, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Valid as *Dinanomodon gilli* (Broom, 1932), comb. nov.

Remarks—Broom (1932) described *Dicynodon gilli* based on a very poor skull, with only the dorsal skull roof satisfactorily preserved. Van Hoepen (1934) included *D. gilli* with *Dicynodon alticeps* in his new genus *Sintocephalus*, and Haughton and Brink (1954), Kitching (1977), Cluver and Hotton (1981), and King (1988) considered it to be a valid species of *Dicynodon*. Brink (1986) considered it a valid species as *Sintocephalus gilli*, a nomenclaturally problematic referral given that he considered the type species of *Sintocephalus* (*S. alticeps*) to be synonymous with *Dicynodon lacerticeps*. The presence of a well-preserved labial fossa allows SAM-PK-4008 to be identified as a dicynodontoid. The most remarkable feature of this specimen is a clear contact between an anterior process of the frontals and an elongate ascending process of the premaxilla. Among Karoo dicynodontoids, this character is otherwise only observed in *Dinanomodon*. Although SAM-PK-4008 has a significantly shorter intertemporal bar than most specimens referred to *Dinanomodon*, this feature is known to be ontogenetically variable within dicynodontoids and the condition in SAM-PK-4008 is consistent with that of other juvenile *Dinanomodon* specimens (e.g., RC 22, the holotype of *Dicynodon macrodon*). Although SAM-PK-4008 is generally very poorly preserved, it can clearly be distinguished from extrabasinal dicynodontoids with a premaxillary-frontal contact

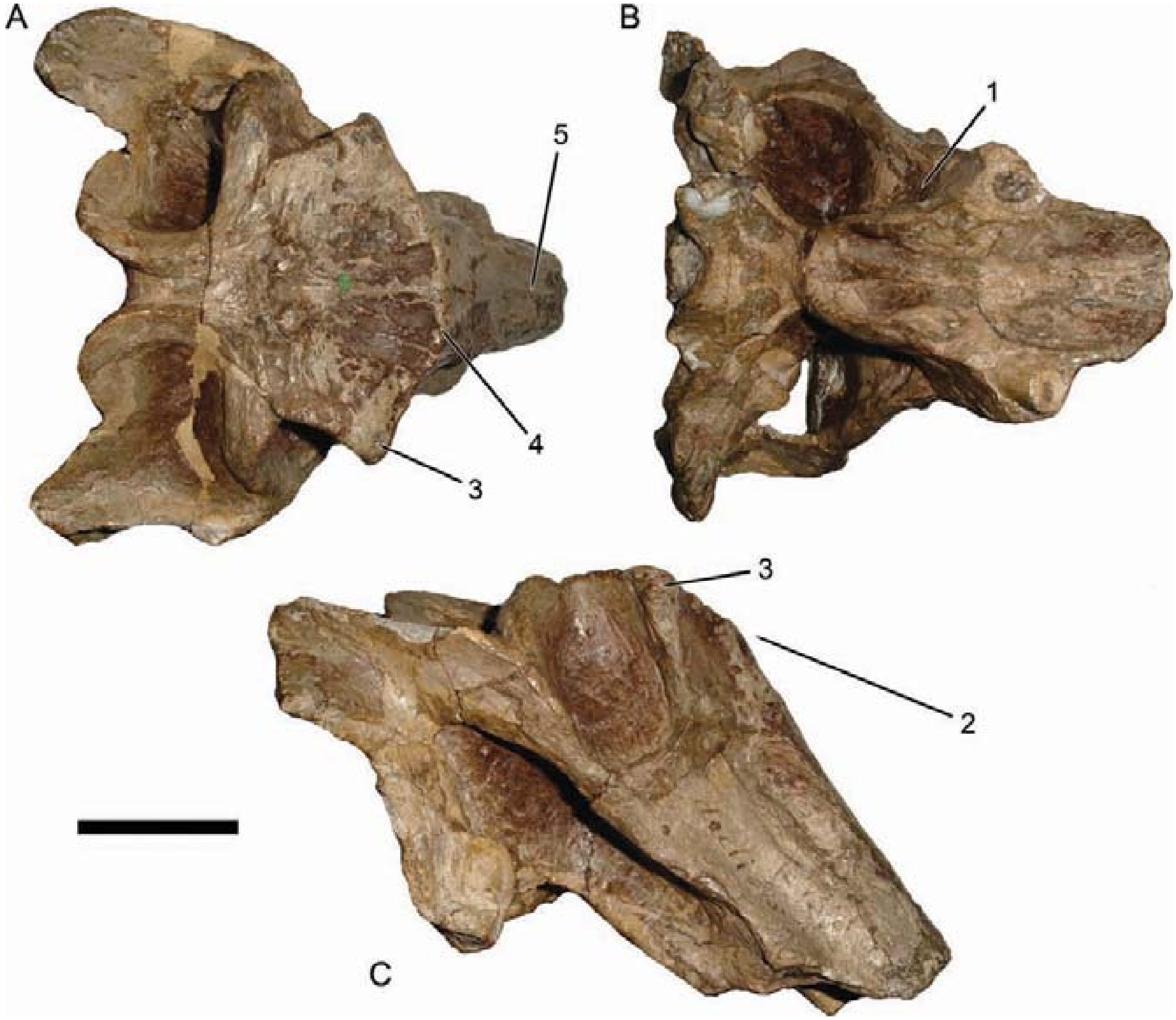

FIGURE 34. NHMUK 36221, the holotype of *Dicynodon declivis* (= *Lystrosaurus declivis*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as a lystrosaurid on the basis of the (2) tall, strongly deflected snout and (3) well-developed prefrontal bosses. *Lystrosaurus declivis* can be distinguished from other species of the genus by the combination of a (2) biplanar snout profile, with a distinct break between the frontal and nasal-premaxillary planes of the skull, (4) a transverse ridge running between the prefrontals, (5) a median ridge on the dorsal surface of the premaxilla, and the absence of postorbital bosses. Scale bar equals 5 cm.

("*Dicynodon*" *trautscholdi* and *Turfanodon bogdaensis*) by the absence of a depressed preparietal. As *D. gilli* predates Broom's (1938) description of *Dinanomodon rubidgei*, it takes priority as the valid specific name for this taxon in the new combination *Dinanomodon gilli*.

Dicynodon glaucops Broom, 1948

Holotype—RC 84, a sheared skull missing the left temporal arch and part of the snout (Fig. 44).

Locus Typicus—Doornplaats, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1948) described *Dicynodon glaucops* as a new member of a group of tuskless *Dicynodon* species including *D. platyceps* and *D. wellwoodensis*, but distinguished by its longer, narrower skull, broader parietal region, larger preparietal, and larger pineal foramen. Toerien (1953) resurrected use of *Oudenodon* for these 'tuskless *Dicynodon*,' and Keyser (1975) synonymized the majority of these species (including *D. glaucops*) with *Oudenodon bainii* (see also Brink, 1986; King, 1988). RC 84 is a typical *O. bainii* skull, with the proportional peculiarities described by Broom (1948) being attributable entirely to deformation.

Dicynodon graaffi Broom, 1940b

Holotype—A skull missing portions of the intertemporal bar and temporal arches, now lost.

Locus Typicus—20 miles northwest of Graaff-Reinet, South Africa.

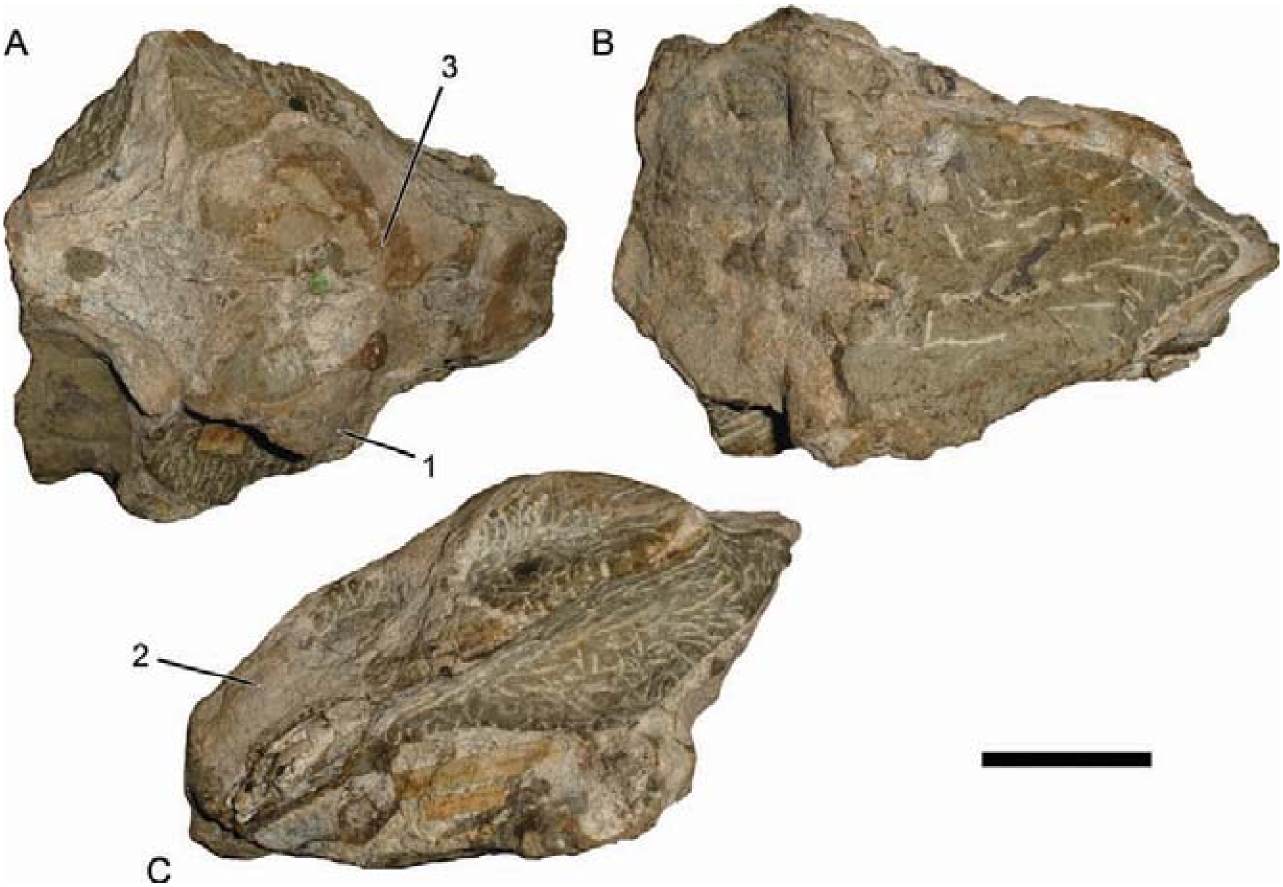

FIGURE 35. NHMUK 47064, the holotype of *Dicynodon depressus* (= *Lystrosaurus declivis*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a lystrosaurid by the (1) well-developed prefrontal bosses and (2) tall, strongly deflected snout and as *L. declivis* by the combination of the biplanar snout profile, with a distinct break between the frontal and nasal-premaxillary planes of the skull, the (3) transverse ridge running between the prefrontals, and the absence of postorbital bosses. Scale bar equals 5 cm.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—In his description of *Dicynodon graaffi*, Broom (1940b) did not specifically list differences that allowed it be distinguished from other *Dicynodon* species, but did note that the region of postorbital overlap of the parietals was more weakly developed than in most other species of *Dicynodon* and that no tusks were present. The loss of the holotype has made additional study of *D. graaffi* difficult, and Brink (1986) considered it a nomen dubium. However, Broom's (1940b) original description provides strong evidence that this was a specimen of *Oudenodon bainii*. The absence of tusks, short snout, width of the intertemporal bar, and position and shape of the nasal bosses (small, ovoid, and overhanging the external nares) in Broom's figure of *D. graaffi* closely match the morphology of *Oudenodon*.

Dicynodon gracilis (Broom, 1901)

Holotype—SAM-PK-590, a dorsoventrally crushed skull missing the right temporal arch (Fig. 45).

Locus Typicus—Pearston, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodontoides recurvidens* (Owen, 1876).

Remarks—Broom (1901) described *Udenodon* [sic] *gracilis* on the basis of a nearly complete (missing only the right zygomatic arch) but somewhat crushed skull from near Pearston. He distinguished it from other species of *Oudenodon* by its more elongate skull and much wider interorbital than intertemporal region. At the time of this taxon's description, dicynodonts were, with few exceptions, split between the genera *Dicynodon* and *Oudenodon* (or '*Udenodon*') based on the presence or absence of tusks (respectively). Following his recognition of *Oudenodon* as the female of *Dicynodon*, Broom (1913a) transferred *O. gracilis* and other species to *Dicynodon*. Cluver and Hotton (1981) transferred this species to *Kingoria*, and most recently Angielczyk et al. (2009) argued that it represents a junior synonym of *Dicynodontoides recurvidens.*

Dicynodon grahami Broom, 1940b

Holotype—RC 40, a dorsoventrally crushed skull (missing the left postorbital bar) and symphysis of the lower jaw (Fig. 46).

Locus Typicus—St. Olives, Graff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontoidea indet.).

Remarks—Broom (1940b) described *Dicynodon grahami* as a new species most similar to *Dicynodon taylori*, but distinguished from it by the longer, narrower snout. Cluver and

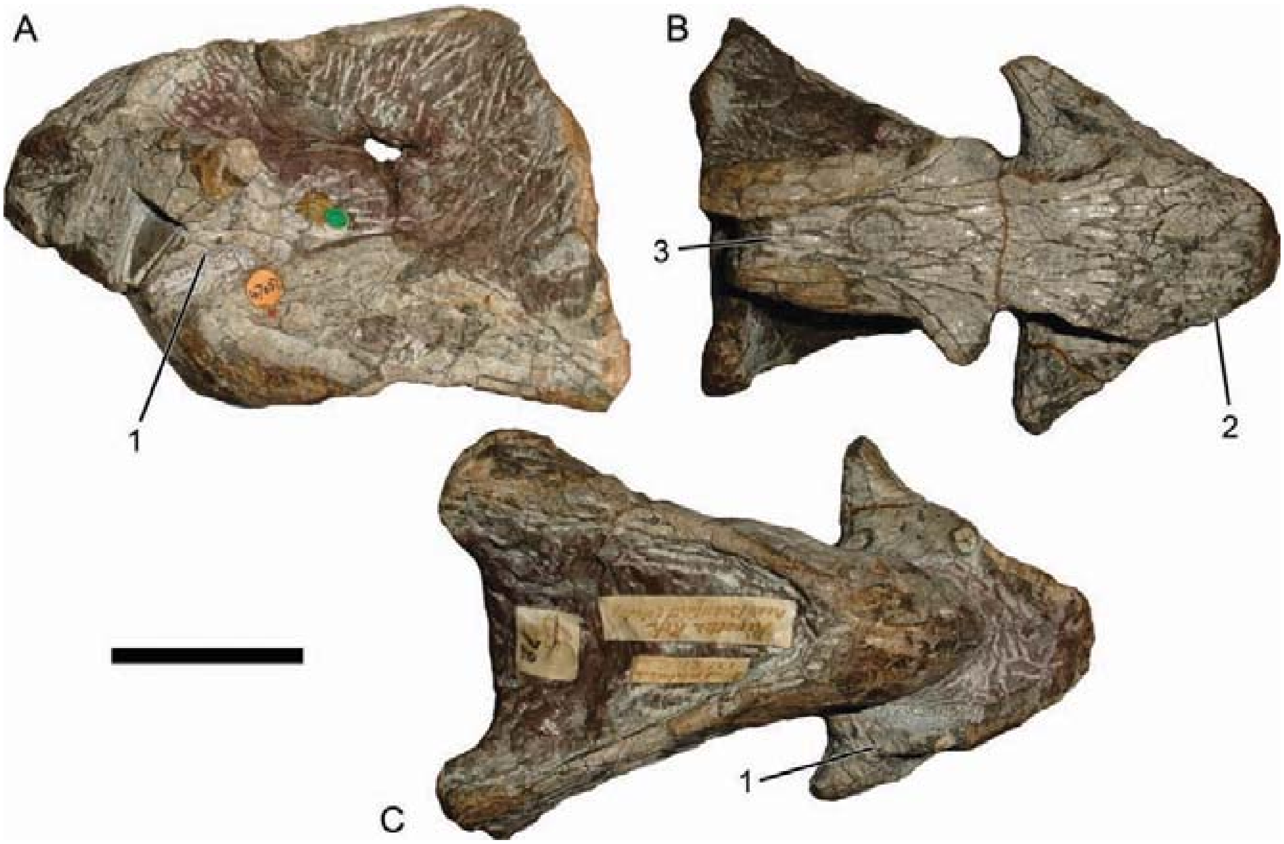

FIGURE 36. NHMUK 47051, the holotype of *Dicynodon dubius* (= *Tropidostoma dubium*), in left lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a cryptodont by the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal, and as *Tropidostoma* on the basis of the tusks and snout proportions. Scale bar equals 5 cm.

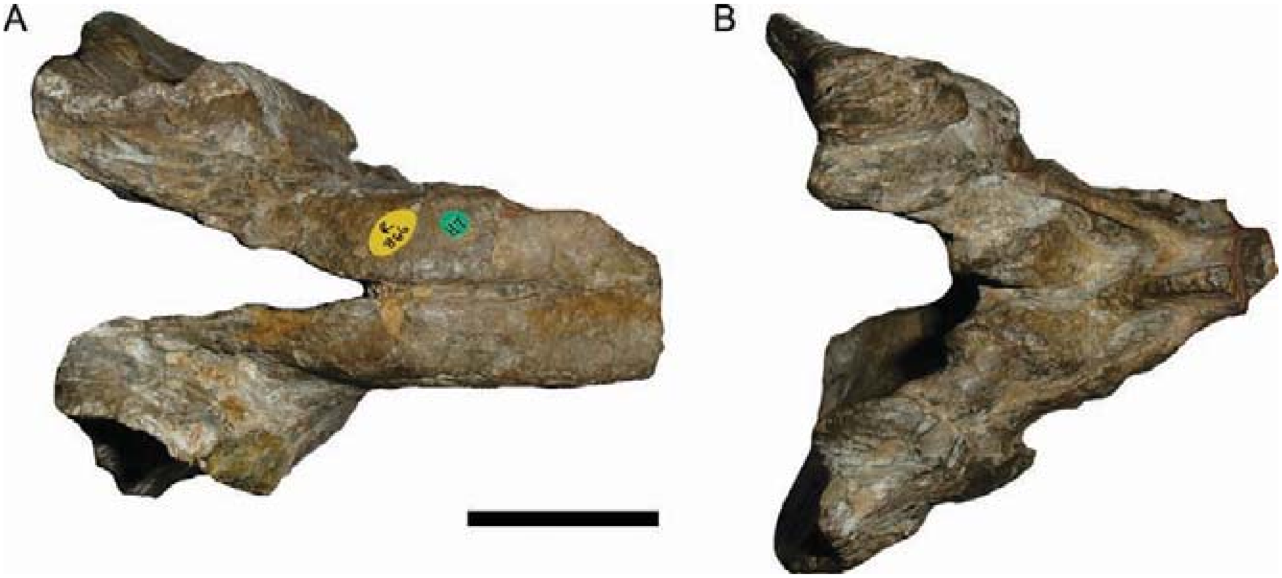

FIGURE 37. NHMUK R866, the holotype of *Dicynodon dunnii* (= *Tropidostoma dubium*), in dorsal (**A**) and ventral (**B**) views. This specimen and NHMUK R868 (the holotype of *Dicynodon microtrema*) are consistent with but not diagnostic for *Tropidostoma*. Together with the initially referred material from Tafelberg, however, they form a diagnosable hypodigm for the genus. Scale bar equals 5 cm.

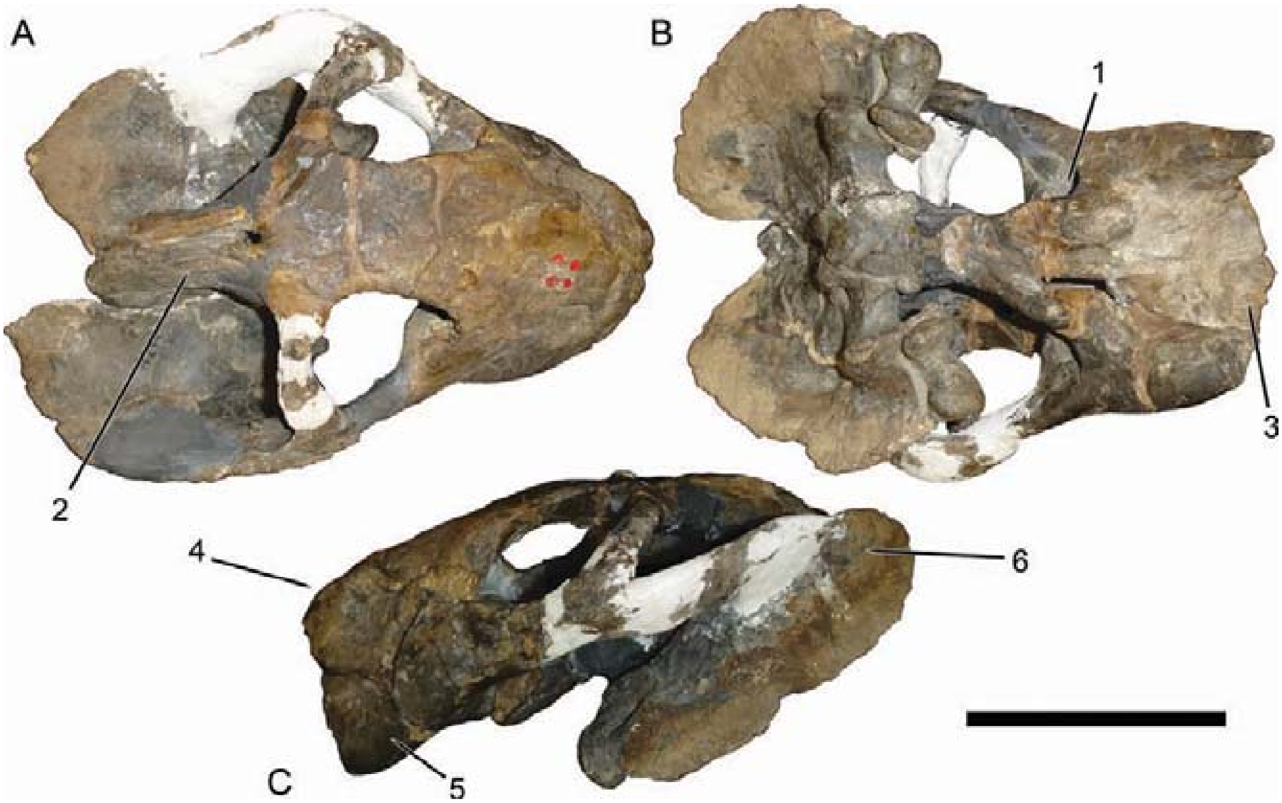

FIGURE 38. BP/1/3710, the holotype of *Dicynodon dutoiti* (= *Dicynodon lacerticeps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *D. lacerticeps* on the basis of the (2) short, narrow intertemporal bar with nearly complete postorbital-parietal overlap, (3) squared-off premaxillary tip, (4) gradually sloping snout profile, (5) anteriorly directed caniniform process, and (6) acutely angled rami of the squamosal in lateral view. Scale bar equals 10 cm.

Hotton (1981) transferred this species to *Kingoria*, a position followed by King (1988), although Brink (1986) listed *D. grahami* as a junior synonym of *Dicynodon lacerticeps*. Angielczyk et al. (2009) disagreed with previous referrals of this species to *Kingoria*/*Dicynodontoides* and argued that it did represent *Dicynodon* sensu lato (i.e., basal dicynodontoid), but was probably best considered a nomen dubium based on the poor condition of the holotype. RC 40 is a small, highly distorted, and poorly preserved skull, but some salient features of its anatomy are evident. The intertemporal bar is extremely narrow, with complete postorbital-parietal overlap posteriorly, and very short (shorter than the snout in dorsal view, although this may be partially due to distortion). The intertemporal bar curves upwards in lateral view, forming a sagittal crest. The absence of an anterior process of the frontals indicates that RC 40 is not a juvenile specimen of *Dinanomodon*, but the extreme dorsoventral compression of this specimen confounds interpretation of the characters used to separate small juvenile *Dicynodon lacerticeps* and *Daptocephalus leoniceps* (e.g., although RC 40 exhibits strongly anteriorly directed caniniforms, this could be the result of deformation). We concur with Angielczyk et al. (2009) that *D. grahami* should be considered a nomen dubium.

Dicynodon grandis Haughton, 1917

Holotype—SAM-PK-2679, a complete, somewhat laterally sheared skull and lower jaws (Fig. 47).

Locus Typicus—Dunedin, Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Uncertain (see below).

Remarks—Haughton (1917) described *Dicynodon grandis* as one of the largest known Permian dicynodonts, placing this species in *Dicynodon* rather than *Eocyclops* (= *Rhachiocephalus*) because of the absence of a pineal boss. Van Hoepen (1934) transferred this species to *Oudenodon*, within the subgenus *Mastocephalus*. Keyser (1975) also recognized the similarity between *D. grandis* and *Oudenodon*, but retained it as a valid species of that genus based on its exceptional size and the presence of a depressed pineal region (as opposed to the low boss observed in large specimens of *O. bainii*). Brink (1986) and King (1988) both recognized *Oudenodon grandis* as a valid species. Despite being known from a complete, well-preserved skull, "*Dicynodon*" *grandis* is one of the most problematic dicynodont species. If SAM-PK-2679 had a pineal boss, it would probably have been considered a specimen of *Rhachiocephalus magnus*, as it is otherwise similar to skulls of that taxon. The absence of this boss is a real feature of the skull, not a taphonomic artifact: the pineal foramen in SAM-PK-2679 is well preserved and exhibits only a slightly raised edge. The pineal boss is frequently eroded or broken off in *Rhachiocephalus* skulls, but in these cases the base of the boss remains evident (see, for example, the holotype of *Dicynodon tealei*, Fig. 129). Furthermore, even small skulls of *Rhachiocephalus* have a well-developed pineal boss (indeed, in small, presumably subadult rhachiocephalid skulls such as CGP WB102, the boss is proportionally even more prominent) so this cannot be explained as an ontogenetically variable

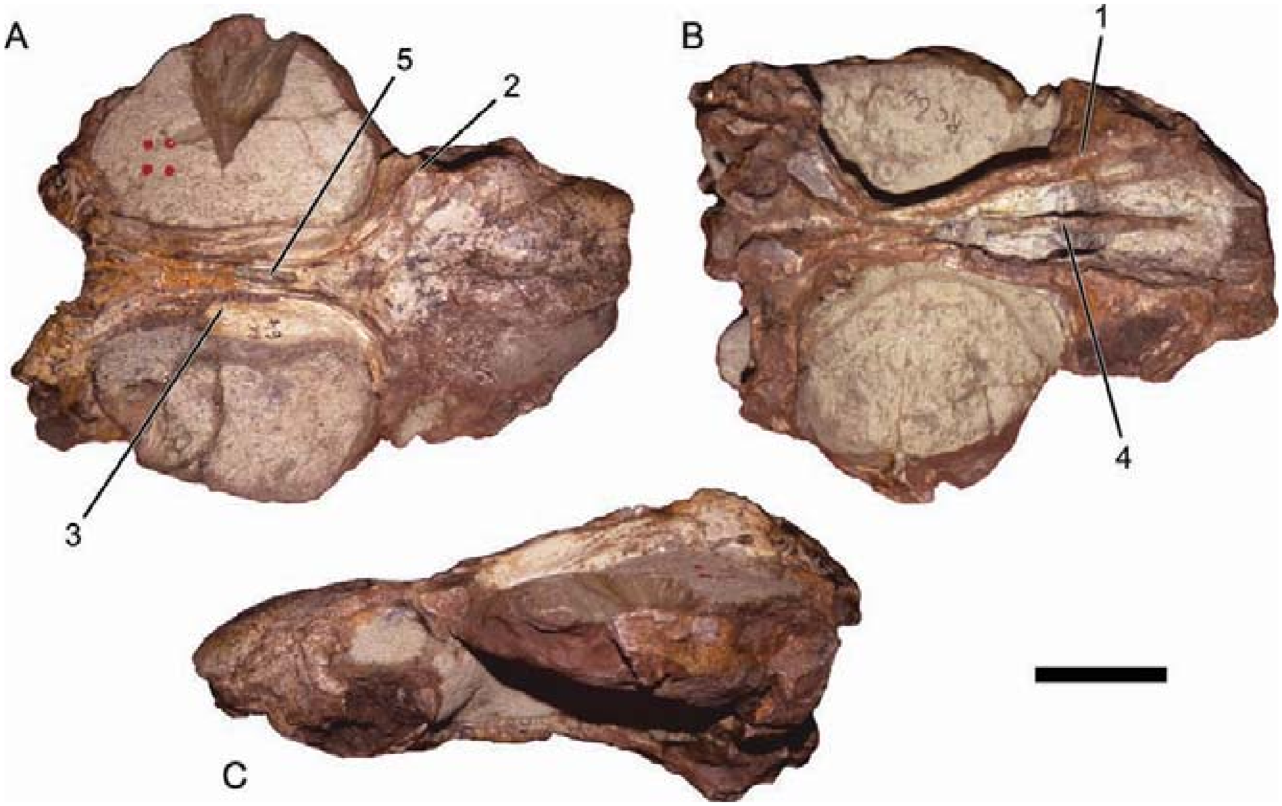

FIGURE 39. RC 64, the holotype of *Dicynodon duvenhagei* (= *Dicynodontoides recurvidens*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) postcaniniform keel, as a kistecephalian on the basis of the (2) absence of the postfrontal, and as a kingoriid on the basis of the (3) postorbitals sloping slightly ventrolaterally, overlapping the parietals except for a narrow exposure of the latter as a sagittal crest and the (4) relatively wide mid-ventral plate of the vomer. This specimen can be identified as *Dicynodontoides* rather than *Kombuisia* based on the (5) elongate, well-developed pineal foramen. Scale bar equals 5 cm.

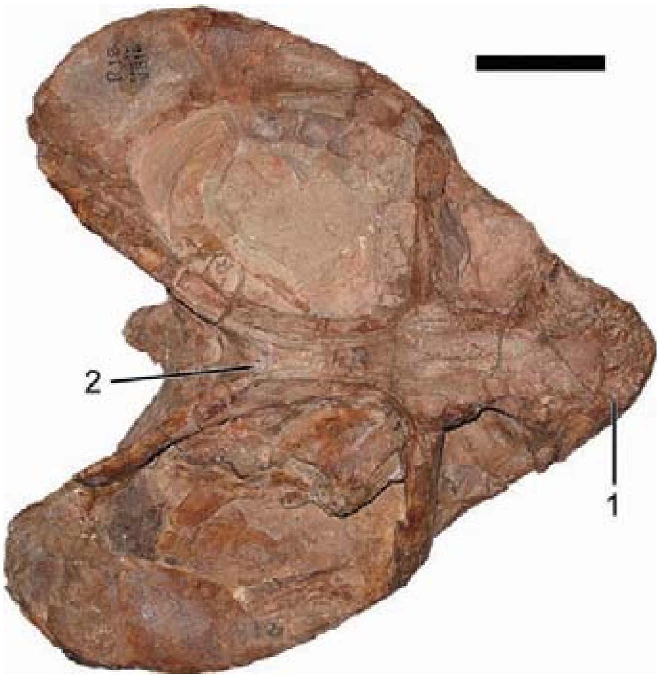

FIGURE 40. SAM-PK-11316, the holotype of *Dicynodon euryceps* (= *Oudenodon bainii*), in dorsal view. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontoid on the basis of the (2) postparietal contribution to the dorsal skull roof, and as *O. bainii* based on the lack of tusks and snout proportions. Scale bar equals 5 cm.

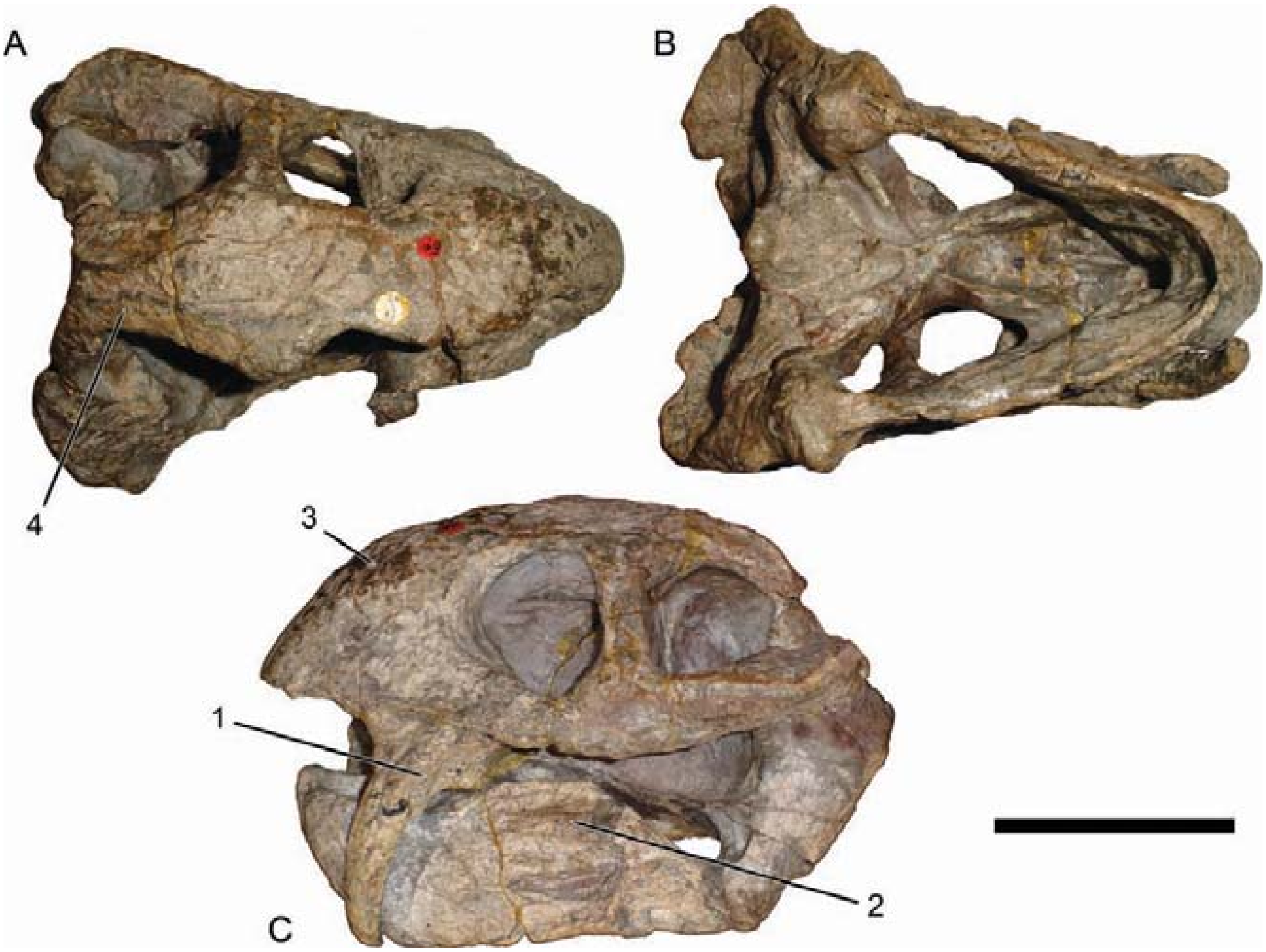

FIGURE 41. NHMUK 47052, the holotype of *Dicynodon feliceps* (= *Diictodon feliceps*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) ventral edge of the caniniform process at same level of anterior margin of orbits (the precaniniform notch has been prepared off on this side of the skull, but is visible on the right side), (2) sharp lateral dentary shelf, and (3) median snout boss. *Diictodon feliceps* can be distinguished from other pylaecephalids by the absence of postcanine teeth and the (4) relatively narrow intertemporal bar, with extensive but incomplete overlap of the parietals by the postorbitals. Scale bar equals 5 cm.

feature (which would be difficult in any case, considering that at 55.3 cm dorsal length, SAM-PK-2679 is as large as most *Rhachiocephalus* skulls). The possibility that SAM-PK-2679 represents a very large specimen of *Oudenodon bainii* cannot at present be discounted. Although the differences in pineal foramen morphology between the two species may be real, the absence of small skulls of "*D*." *grandis* or comparably large skulls of *O. bainii* makes it difficult to gauge variation in this feature. An enormous dicynodont skeleton, SAM-PK-K6445, with skull morphology more similar to typical *O. bainii* than SAM-PK-2679, may help to resolve this quandary, but the former specimen has yet to be properly described. We tentatively consider "*D*." *grandis* to be a distinct species of giant cryptodont, but refrain from any generic assignment pending further study. Whether SAM-PK-2679 represents a gigantic individual of *Oudenodon bainii*, an aberrant rhachiocephalid, or the sole known representative of a separate cryptodont taxon remains to be determined.

Dicynodon greyii (Owen, 1860b)

Holotype—NHMUK 36231, a poorly preserved but nearly complete skull (missing the right zygomatic arch), lower jaws, and associated postcranial elements (Fig. 48).

Locus Typicus—Rhenosterberg, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Owen (1860b) described *Oudenodon greyii* on the basis of a weathered, strongly dorsoventrally compressed, laterally sheared skull that nevertheless preserves the pattern of dorsal cranial sutures well. Broom (1913a) transferred this species (and all species of *Oudenodon*) to *Dicynodon* (although misspelling it as '*D. grayi*'). Keyser (1975) synonymized this species with *Oudenodon bainii*, a position maintained by Brink (1986) and King (1988). NHMUK 36231 clearly exhibits contribution of the postparietals to the skull roof typical of oudenodontids, and the lack of tusks and snout profile is characteristic of *O. bainii*.

Dicynodon grimbeeki Broom, 1935

Holotype—TM 253, a complete, well-preserved, slightly dorsoventrally crushed skull (Fig. 49).

Locus Typicus—Leeukloof, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

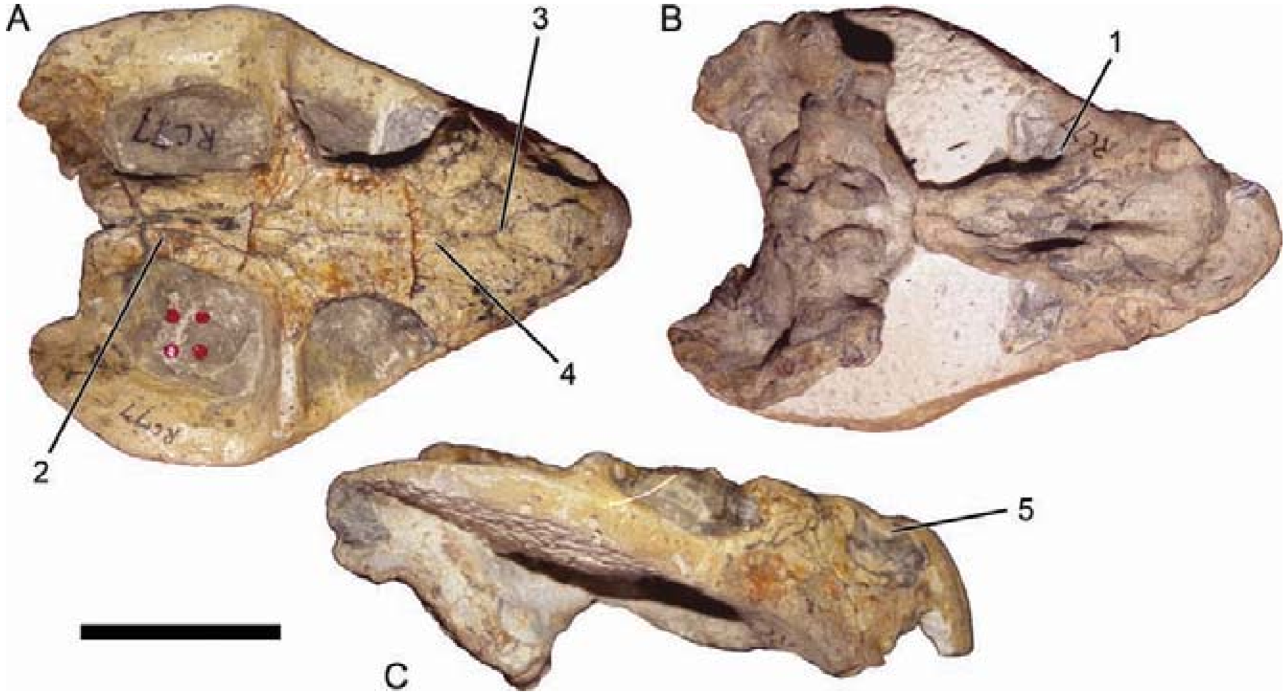

FIGURE 42. RC 77, the holotype of *Dicynodon galecephalus* (= *Dinanomodon gilli*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *Dinanomodon* on the basis of the (2) narrow intertemporal bar (even at small size, because this specimen is probably a juvenile, showing complete overlap of the parietals by the postorbitals posteriorly), (3) ascending process of the premaxilla nearing an (4) anterior process of the frontals (not developed to the extent usually seen in adult *Dinanomodon*, so this may be ontogenetically variable), and (5) nasal boss giving the external nares a 'saddle-shaped' appearance. Scale bar equals 5 cm.

Remarks—Broom (1935) described *Dicynodon grimbeeki* on the basis of a large collection of small dicynodont skulls from Leeukloof, with nearly equal representation by tusked and tuskless specimens. Cluver and Hotton (1981) transferred this species to *Diictodon*, and it was listed as a valid species of *Diictodon* by King (1988), but synonymized with *Diictodon feliceps* by Brink (1986) and Sullivan and Reisz (2005). The precaniniform region of TM 253 is worn but a notch appears to be present, and in palatal and intertemporal morphology this specimen is typical of *D. feliceps*.

Dicynodon grossarthi Broili and Schröder, 1937

Holotype—BSP 1934 VIII 48, a complete skull (Fig. 50).

Locus Typicus—La-de-da, Beaufort West, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—*Dicynodon grossarthi* was one of several *Tapinocephalus* AZ *Dicynodon* species named by Broili and Schröder (1937) from collections at La-de-da, others including *D. broomi* and *D. huenei*. Cluver and Hotton (1981; see also King, 1988) transferred these species to *Diictodon* but retained them as valid, whereas Brink (1986) and Sullivan and Reisz (2005) considered them synonymous with *Diictodon feliceps*, which is the position taken here.

Dicynodon halli Watson, 1914a

Holotype—NHMUK R4067, a complete, well-preserved, slightly laterally sheared skull (Fig. 51), lower jaws, and most of the postcranium.

Locus Typicus—Kuilspoort, Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Watson (1914a) described *Dicynodon halli* based on a well-preserved, nearly complete skeleton, missing only portions of the axial column and extremities. He distinguished *D. halli* from its presumed closest relative, *Dicynodon kolbei*, by the relatively shorter snout and non-tripartite occipital condyle. Van Hoepen (1934) transferred this species to *Oudenodon*, and Keyser (1975) synonymized it with *Oudenodon bainii*, arguing that the differences between it and '*D. kolbei*' are within the normal range of variation for the species and in part preservational. NHMUK R4067 is a typical specimen of *O. bainii*, exhibiting the tuskless caniniform process, postcaniniform crest, postparietal contribution to the skull roof, lengthy interpterygoid vacuity, and snout morphology characteristic of the species.

Dicynodon hartzenbergi Broom, 1940b

Holotype—TM 1480, a complete, somewhat weathered skull and lower jaws (Fig. 52).

Locus Typicus—Petersburg, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Uncertain (see below).

Remarks—Broom (1940b) considered *Dicynodon hartzenbergi* most similar to *Dicynodon andrewsi* (= *Oudenodon bainii*), but distinguished it by its narrower parietals and different-shaped postfrontals. *Dicynodon hartzenbergi* has received little study since its description. Haughton and Brink (1954) and King (1988) listed it as a valid species of *Dicynodon*, but Brink (1986) listed it as a synonym of *Aulacephalodon bainii*. Both of these identifications are confounded by the absence of tusks in TM 1480. The well-developed postcaniniform crest indicates that this

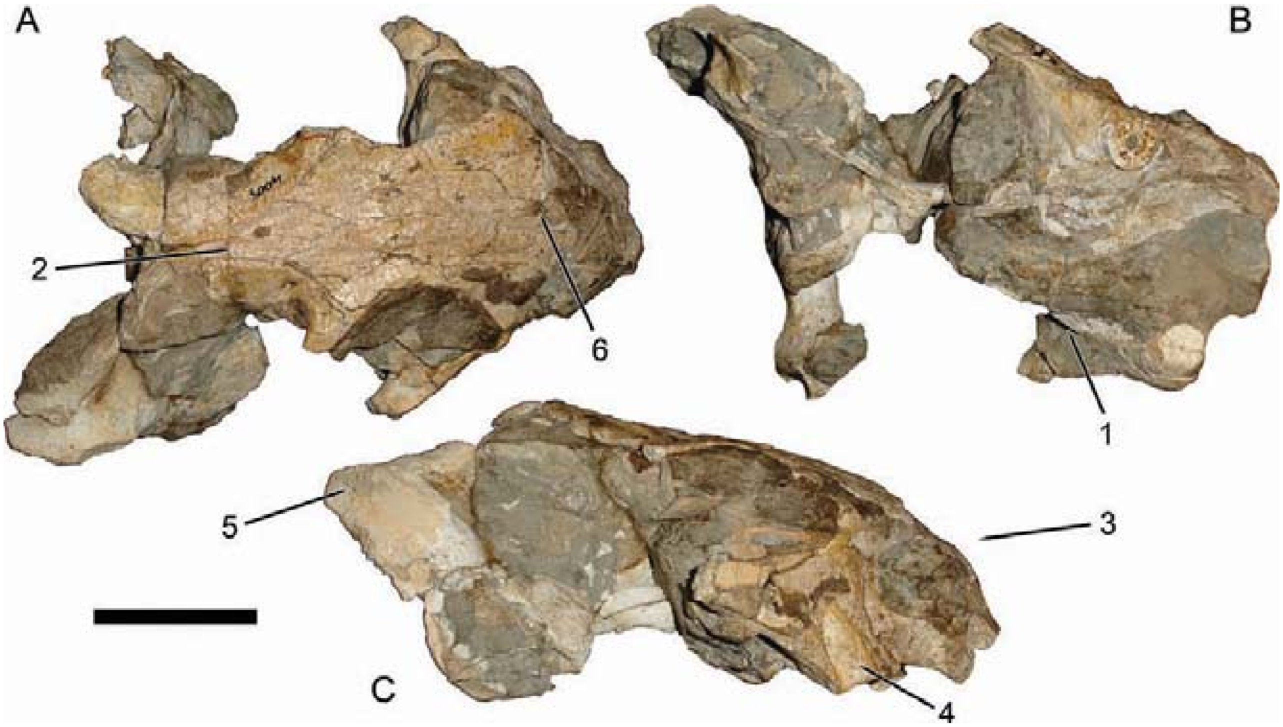

FIGURE 43. SAM-PK-4008, the holotype of *Dicynodon gilli* (= *Dinanomodon gilli*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *Dinanomodon* on the basis of the combination of a (2) narrow intertemporal bar with extensive postorbital-parietal overlap, (3) shallowly sloping snout profile, (4) massive canine, and (5) squamosal rami without broadly rounded dorsal margin (as in *Daptocephalus*). The most important diagnostic feature of *Dinanomodon* visible in this specimen is the (6) contact between an anterior process of the frontals and the elongate ascending process of the premaxilla. Scale bar equals 5 cm.

specimen is a cryptodont. Additionally, "*D*." *hartzenbergi* has a very short, broad skull, large pineal foramen with a raised edge, and broad intertemporal bar, as in geikiine cryptodonts. Unlike typical geikiines (*Aulacephalodon*, *Geikia*, and *Pelanomodon*), TM 1480 has negligible nasal and prefrontal bosses, and no trace of a transverse crest between the prefrontals. This could be an ontogenetic feature, as TM 1480 is a relatively small skull. The lack of tusks is problematic, however, as they are usually well developed even in small, presumably juvenile specimens of *Aulacephalodon*. TM 1480 is likely to represent a juvenile geikiid of some kind, but whether it is a pathological tuskless *Aulacephalodon*, an early range extension of *Pelanomodon*, or a distinct taxon remains to be determined. A further complication is the existence of small, *Pelanomodon*-like skulls with extremely narrow intertemporal bars (e.g., RC 44, the holotype of *Dicynodon sidneyi*) that suggest intertemporal bar width may increase with size in the group. Further research on geikiine ontogeny is required to resolve the identification of these specimens.

Dicynodon haughtonianus von Huene, 1931

Holotype—GPIT unnumbered, a well-preserved partial skull (missing the right side of the skull posterior to the snout) and anterior portion of the lower jaws (Fig. 53).

Locus Typicus—Bloukrans, Prince Albert, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Von Huene (1931) described *Dicynodon haughtonianus* based on a tuskless specimen representing one of the first records of *Dicynodon* from the *Tapinocephalus* AZ. Cluver and Hotton (1981) transferred this species to *Diictodon* (see also King, 1988), although Brink (1986) tentatively retained it as a valid species of *Dicynodon*. Sullivan and Reisz (2005) synonymized this species with *Diictodon feliceps*, and we concur—a clear precaniniform notch is present and the short intertemporal region has extensive postorbital-parietal overlap.

Dicynodon helenae Boonstra, 1938

Holotype—SAM-PK-11312, a complete, poorly preserved, dorsoventrally crushed skull (Fig. 54).

Locus Typicus—Luangwa Valley, Zambia.

Horizon—Upper Madumabisa Mudstone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Boonstra (1938) described *Dicynodon helenae* based on a large, dorsoventrally compressed, 'heart'-shaped skull. Broom (1948) argued that this species and the similar Zambian taxon *Dicynodon euryceps* were synonymous, and Keyser (1975) synonymized all tuskless Zambian species of *Dicynodon* with *Dicynodon luangwanensis*, as *Oudenodon luangwanensis*. For rationale of our referral of these species to *Oudenodon bainii*, see entry on *D*. *luangwanensis*.

Dicynodon howardi Broom, 1948

Holotype—RC 83, a complete, well-preserved skull (Fig. 55).

Locus Typicus—Riverdale, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

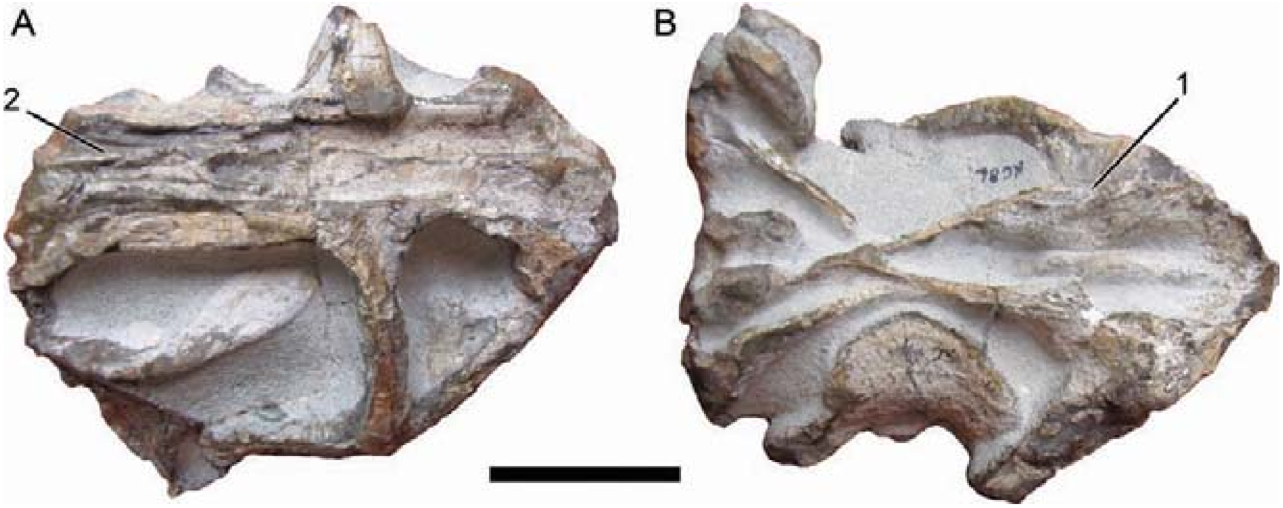

FIGURE 44. RC 84, the holotype of *Dicynodon glaucops* (= *Oudenodon bainii*), in dorsal (**A**) and palatal (**B**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest, as an oudenodontid on the basis of a (2) postparietal contribution to the dorsal skull roof, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

Status—Junior subjective synonym of *Dicynodontoides recurvidens* (Owen, 1876).

Remarks—Broom (1948) considered *Dicynodon howardi*, with its extremely narrow skull, to be greatly dissimilar from all previously described species of *Dicynodon*. He suggested that its nearest relative could be *Dicynodon gracilis*, but stated that the two species were clearly differentiated by squamosal structure. Cluver and Hotton (1981) agreed with the comparison to *D. gracilis*, and transferred both of these species to *Kingoria*. Angielczyk et al. (2009) argued that all South African

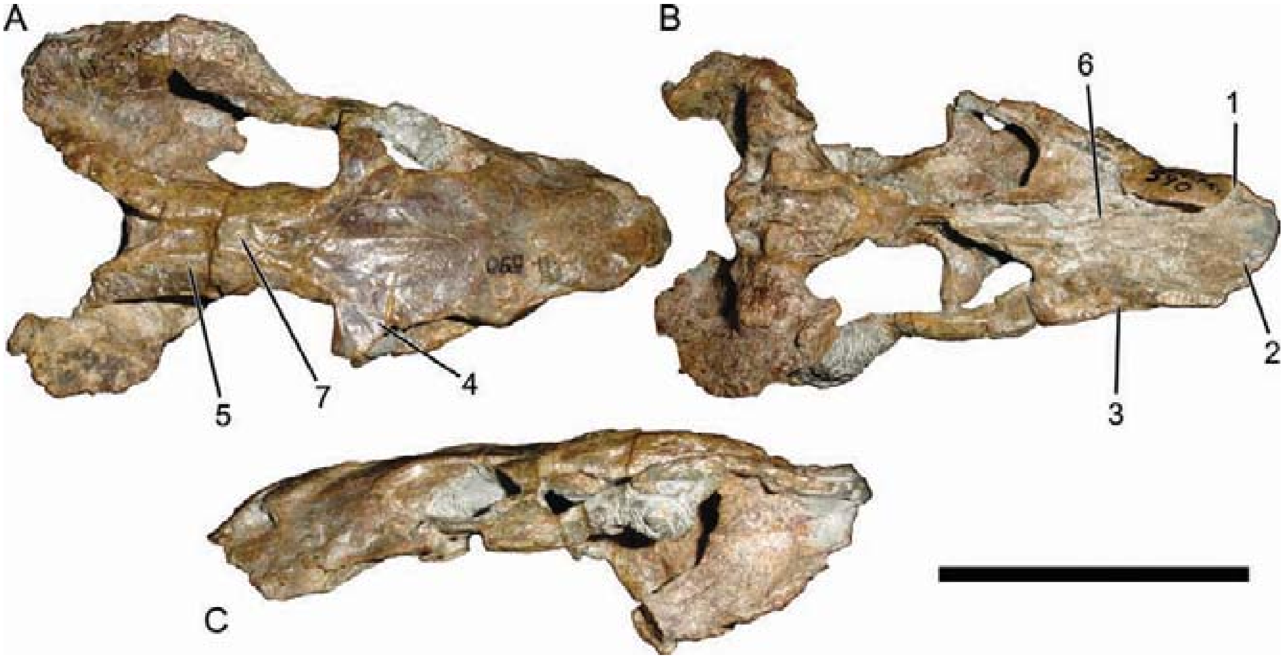

FIGURE 45. SAM-PK-590, the holotype of *Dicynodon gracilis* (= *Dicynodontoides recurvidens*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) embayment of the palatal rim anterior to the caniniform process, (2) palatal surface of premaxilla with groove-like depression with rounded anterior end, and (3) keel-like extension of the palatal rim posterior to the caniniform process, as a kistecephalian on the basis of the (4) absence of the postfrontal, and as a kingoriid on the basis of the (5) postorbitals sloping slightly ventrolaterally, overlapping the parietals except for a narrow exposure of the latter as a sagittal crest and the (6) relatively wide mid-ventral plate of the vomer. This specimen can be identified as *Dicynodontoides* rather than *Kombuisia* based on the (7) elongate, well-developed pineal foramen. Scale bar equals 5 cm.

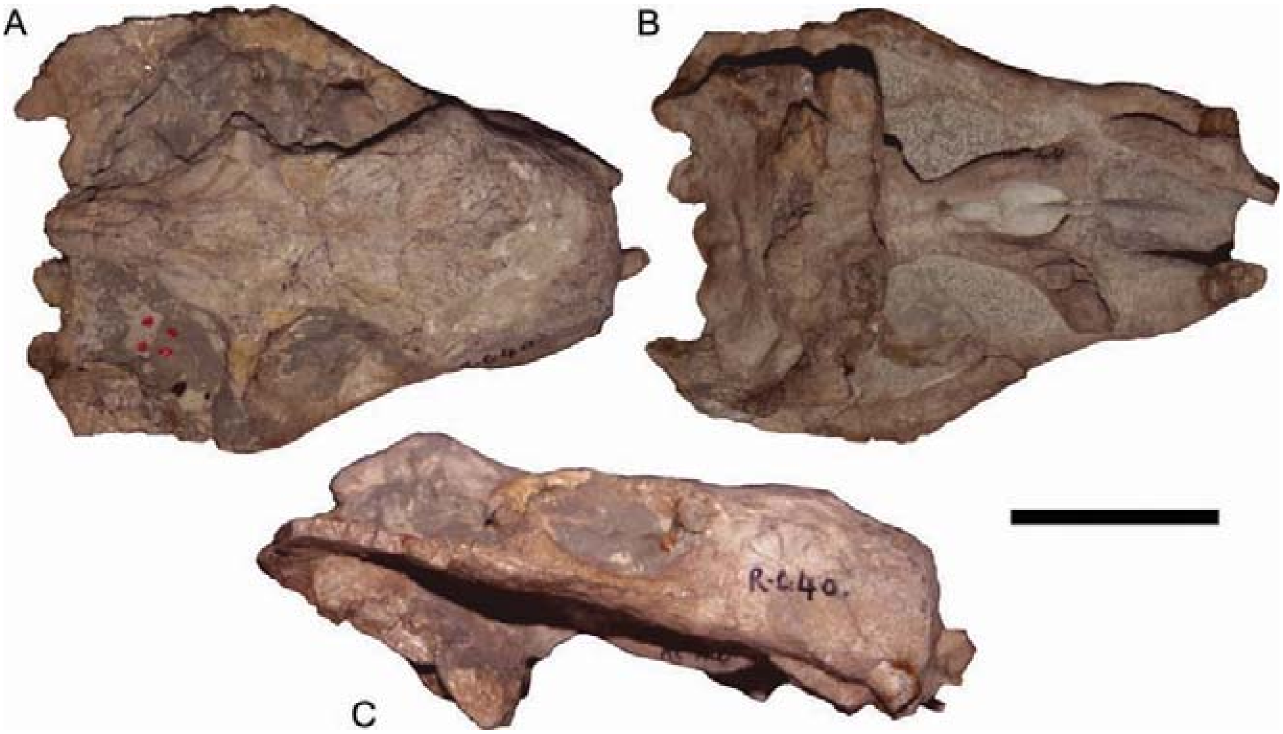

FIGURE 46. RC 40, the holotype of *Dicynodon grahami*, in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. Although clearly not a specimen of *Dicynodontoides* as previously argued (Cluver and Hotton, 1981), this specimen is difficult to identify beyond Dicynodontoidea because of its poor preservation and strong deformation, and is here considered a nomen dubium. Scale bar equals 5 cm.

specimens of '*Kingoria*' (including RC 83) are referable to a single species, *Dicynodontoides recurvidens*, a position maintained here.

Dicynodon huenei Haughton, 1932

Holotype—SAM-PK-10630, a fragmentary skull (preserving much of the left side) and postcranial elements (Fig. 56).

Locus Typicus—Locality B2, Kingori, Ruhuhu Basin, Tanzania.

Horizon—Upper Usili Formation (Upper Permian).

Status—Valid.

Remarks—Haughton (1932) described *Dicynodon huenei*, the first representative of the genus *Dicynodon* from the Ruhuhu Basin of Tanzania, on the basis of a largely complete but fragmented skull missing the right temporal arch and the tip of the snout. Haughton (1932:641) did not specify any characters separating *D. huenei* from its South African congeners, noting only that it "differs in form" from other *Dicynodon* species. Von Huene (1942) described several additional specimens of *D. huenei* from the Ruhuhu Basin, transferring this species to *Platypodosaurus* (a taxon previously known only from postcranial material in South Africa) as *P. huenei*. Subsequent studies have retained this species as valid, albeit retaining the original referral to *Dicynodon* (Haughton and Brink, 1954; King, 1988). With the exception of the holotype of *Dicynodon bathyrhynchus*, all Permian dicynodontoid material from the Ruhuhu Basin is very similar and exhibits the same suite of characters. These specimens are most similar to the *Dicynodon lacerticeps* morphotype among South African Permian dicynodontoids, sharing the acutely angled rami of the squamosal in lateral view, short intertemporal bar with extensive overlap of the parietals by the postorbitals, and gradually sloping snout. However, the Tanzanian specimens differ from *D. lacerticeps* in possessing a thickened ventral portion of the postorbital bar, flattened anteriorly and forming a plate at the posteroventral edge of the orbit. Based on this character, we retain *D. huenei* as a valid species; for referral of this species to the newly restricted genus *Dicynodon*, refer to the Phylogenetic Analysis.

Dicynodon huenei Broili and Schröder, 1937

Holotype—BSP 1934 VIII 46, a complete, well-preserved skull (Fig. 57).

Locus Typicus—La-de-da, Beaufort West, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broili and Schröder (1937) used the name *Dicynodon huenei* for a new species of small *Tapinocephalus* AZ dicynodont, unaware that this name had already been used by Haughton (1932) for a species from *Cistecephalus* AZ-equivalent rocks in Tanzania. As such, Boonstra (1948) renamed this species *D. broilii*, which remained in use until Toerien (1953) transferred this species to *Oudenodon*, making the specific name revert to *Oudenodon huenei*. Keyser (1975) made *D. huenei* the type species of his new genus *Anomodon* (itself preoccupied by a fossil mole), but Cluver and Hotton (1981) recognized tht BSP 1934 VIII 46 represented a specimen of *Diictodon*, creating the new combination *Diictodon huenei* (see also King, 1988). Brink (1986) and Sullivan and Reisz (2005) synonymized *D. huenei* with *Diictodon feliceps*, and this approach is followed here.

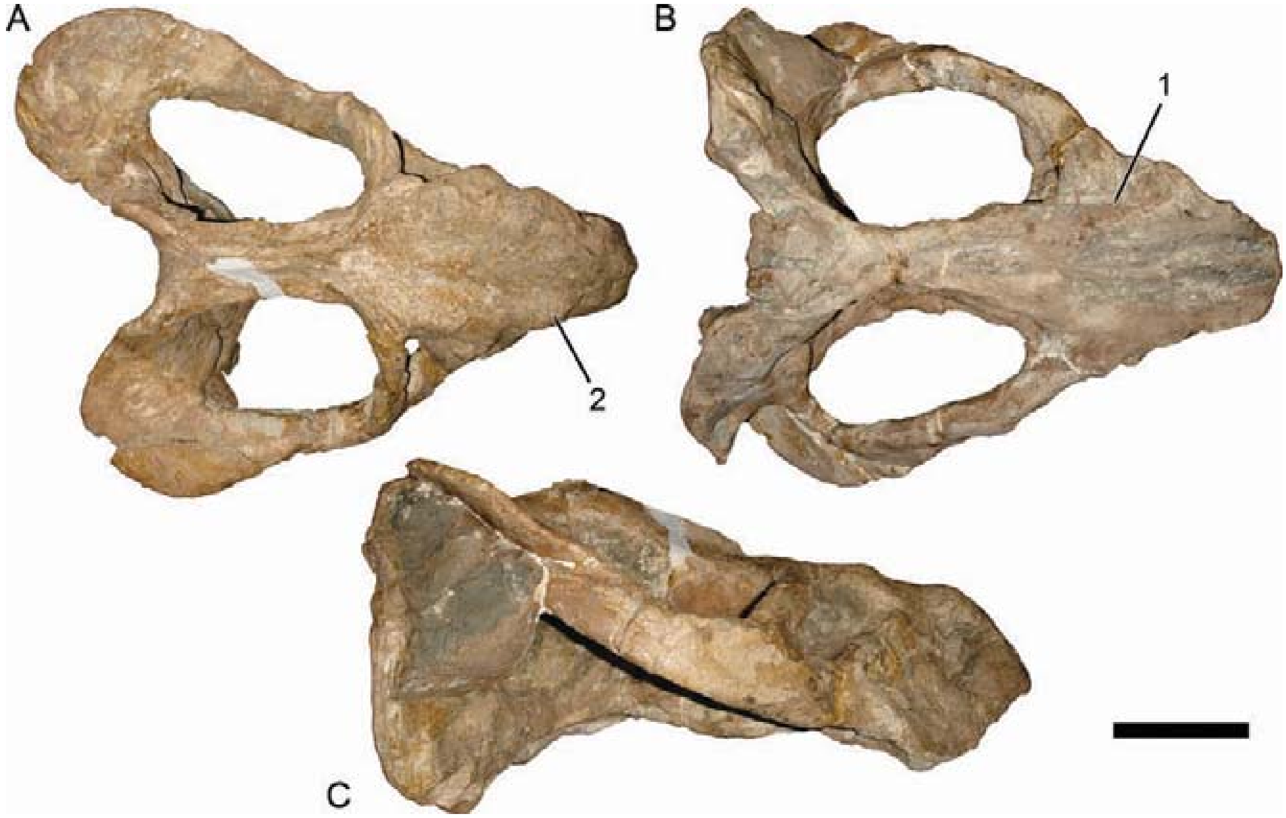

FIGURE 47. SAM-PK-2679, the holotype of *Dicynodon grandis*, in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, but its lower-level relationships are obscure. It may be an aberrant rhachiocephalid or very large *Oudenodon*. Scale bar equals 10 cm.

Dicynodon huxleyanus (Newton, 1893)

Holotype—BGS GSE11704, a slab containing the natural mold of a skull, partial lower jaw, and postcranial elements (clavicle, left scapula, shaft of right humerus, and left ilium). NHMUK R2109 (Fig. 58) is a cast of the left side of the skull made from this mold.

Locus Typicus—Cutties Hillock Quarry, Elgin, Scotland.

Horizon—Cutties Hillock Sandstone Formation (Upper Permian).

Status—Junior subjective synonym of *Gordonia traquairi* Newton, 1893.

Remarks—Newton (1893) distinguished *Gordonia huxleyana* from the type species *G. traquairi* by its proportionally wider and more depressed skull and absence of an interorbital concavity. Von Huene (1940) transferred *G. huxleyana* and its congeners to *Dicynodon*. The proportional distinctions between *G. huxleyana* and *G. traquairi* can be attributed to opposite modes of deformation in these two skulls. Otherwise, they are quite similar, particularly in the shared possession of a slender, rod-like lateral dentary shelf angled anterodorsally immediately above the mandibular fenestra. Refer to the entry on *Dicynodon traquairi* for further information.

Dicynodon ictidops Broom, 1913c

Holotype—AMNH FARB 5510, a poorly prepared, laterally crushed complete skull (Fig. 59).

Locus Typicus—Beaufort West Commonage, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom (1913c) described *Dicynodon ictidops* on the basis of a complete, somewhat laterally crushed skull and mandible (the holotype) and several additional skulls, all from Beaufort West Commonage. He did not explicitly distinguish *D. ictidops* from any other *Dicynodon* species, and listed in the diagnosis a set of characters present in various other dicynodont taxa (skull narrow, orbits directed laterally, external naris large, zygoma deep at level of postorbital bar). In particular, no comparison was made with the previously described *Dicynodon psittacops* (= *Diictodon feliceps*), whose own species distinction was based entirely on being the only small "*Dicynodon*" from Beaufort West Commonage. Cluver and Hotton (1981) transferred this species to *Diictodon* (see also King, 1988). Brink (1986) and Sullivan and Reisz (2005) regarded this species as a junior synonym of *Diictodon feliceps*, and this approach is followed here.

Dicynodon ictinops Broom, 1921

Holotype—MMK 4165, a nearly complete skull (missing the right temporal arch) and postcranium (Fig. 60).

Locus Typicus—Sekretariskraal, Murraysburg, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Emydops arctatus* (Owen, 1876).

Remarks—Broom (1921) diagnosed *Dicynodon ictinops* based on its broad postorbitals and intertemporal region. Haughton and

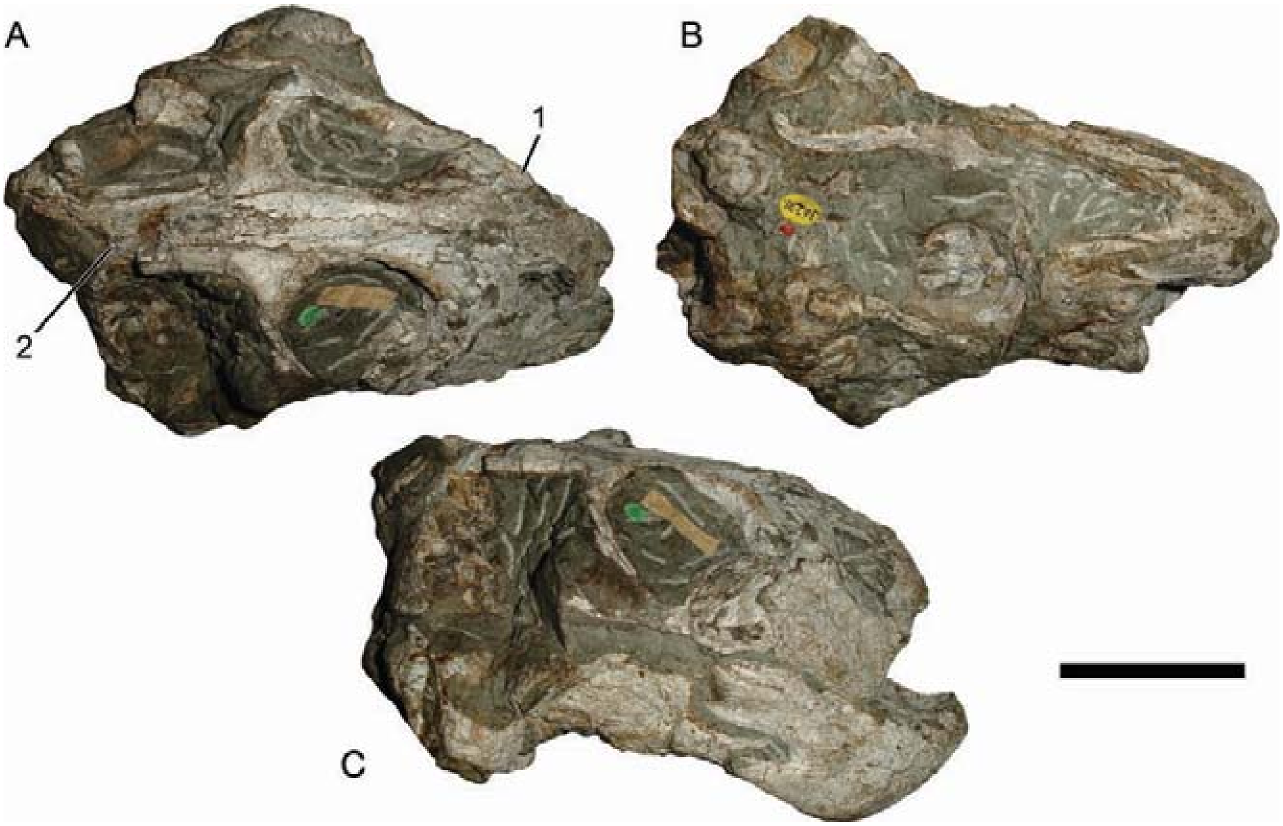

FIGURE 48. NHMUK 36231, the holotype of *Dicynodon greyii* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of a (2) postparietal contribution to the dorsal skull roof, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

Brink (1954) and King (1988) listed *D. ictinops* as a valid species of *Dicynodon*, but Brink (1986) considered it to be a synonym of *Diictodon feliceps*. However, MMK 4165 lacks a precaniniform notch, has a relatively long, extremely broad intertemporal bar, and lacks a median ridge on the anterior surface of the snout, indicating that it is not *Diictodon*. Rather, the broadly exposed parietals, embayment on the medial surface of the palatal rim, jaw symphysis drawn into a sharp, cutting edge, and prominent, angled, triangular lateral dentary shelf indicates that this is a specimen of *Emydops arctatus*. MMK 4165 represents the most complete skeleton of *Emydops* currently known.

Dicynodon incisivum Repelin, 1923

Holotype—A fragmentary, dorsoventrally crushed snout, now lost.

Locus Typicus—North of Luang Prabang, Laos.

Horizon—'Purple beds' (Upper Permian).

Status—Nomen dubium (Dicynodontoidea indet.).

Remarks—Repelin (1923) described *Dicynodon incisivum* as a new species of Southeast Asian *Dicynodon* similar to *D. orientalis* (= *Lystrosaurus murrayi*) from India. The history of *D. incisivum* has recently been reviewed by Battail (2009), who notes that although the loss of the holotype renders interpretation of this record difficult, available information suggests that this specimen represented a Permian *Dicynodon*-grade dicynodont rather than *Lystrosaurus* (as listed by Woodward [1932] and Yuan and Young [1934]). We agree with this interpretation and with the dubious status of this species, given that poor drawings are the only remaining evidence of the holotype.

Dicynodon ingens Broom, 1907

Holotype—A poorly preserved palatal portion of the skull housed in the Natal Museum, now lost. Haughton and Brink (1954) designated a second poorly preserved skull from the type locality housed in the Durban Museum as the neotype of *D. ingens*, but recent efforts to locate this specimen have failed and it must also be considered lost.

Locus Typicus—Ennersdale, Natal, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontoidea indet.).

Remarks—Broom (1907) named *Dicynodon ingens* based on two large, fragmentary skulls from Natal. Van Hoepen (1934) included this species in his genus *Daptocephalus* and King (1988) listed it as a valid species of *Dicynodon*. Little information is currently available about this species, and Broom's (1907) description provides few characters of taxonomic merit. The holotype appears to represent a large dicynodontoid and the blunt morphology of the premaxilla suggests that it is not *Dinanomodon*, but whether this was a specimen of *Daptocephalus leoniceps* (as is likely, given that this species is common at the type locality [Kitching, 1977], but not demonstrable) or a large *Dicynodon lacerticeps* is uncertain. Broom (1932) figured the topotypic specimen later designated as the neotype (Haughton and Brink, 1954). The lateral view of this specimen (Broom,

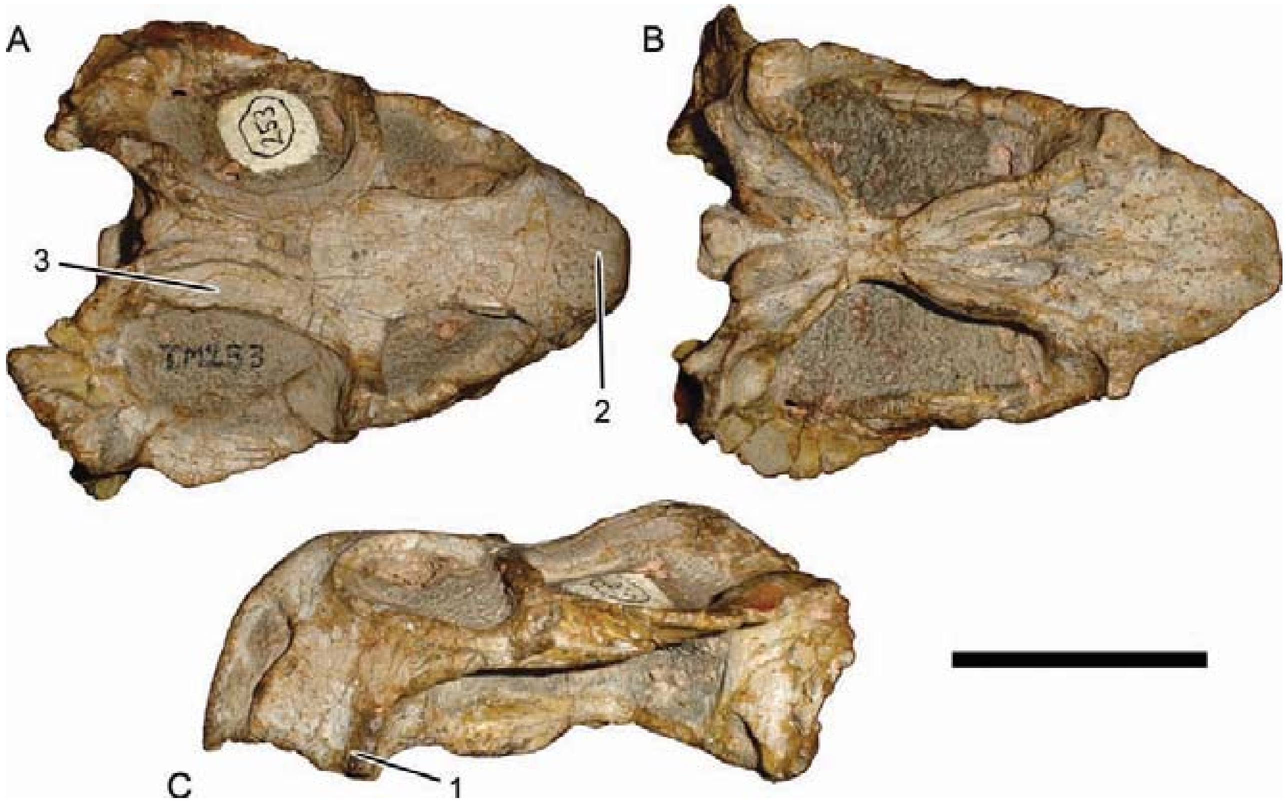

FIGURE 49. TM 253, the holotype of *Dicynodon grimbeeki* (= *Diictodon feliceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) ventral margin of the caniniform process at the level of the anterior margin of the orbit and (2) the presence of a median snout boss and as *D. feliceps* on the basis of the (3) relatively thin intertemporal bar with broad postorbital-parietal overlap and the lack of teeth. Scale bar equals 5 cm.

1932:fig. 61D) shows a long, sharply 'hooked' premaxilla suggesting that this was a specimen of *Dinanomodon*. Unless the holotype and neotype are rediscovered, however, their conspecificity and identification as *Daptocephalus* or *Dinanomodon* will remain unclear, and *D. ingens* must be considered a nomen dubium.

Dicynodon jouberti Broom, 1905b

Holotype—SAM-PK-695, a complete but poorly preserved skull and lower jaws still mostly encased in matrix (Fig. 61).

Locus Typicus—Gouph Tract, South Africa.

Horizon—*Tapinocephalus* or *Pristerognathus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom (1905b) described *Dicynodon jouberti* as the geologically earliest species of *Dicynodon*, the first known from the *Tapinocephalus* AZ (at the time known as the '*Pareiasaurus* Zone'). 'Gouph Tract' is a vague locality covering spans of outcrop making up the current *Tapinocephalus* and *Pristerognathus* AZs (Angielczyk et al., 2005a), making the precise stratigraphic origin of *D. jouberti* uncertain. Van Hoepen (1934) included *D. jouberti* in *Sintocephalus* (with *Dicynodon alticeps* and *Dicynodon gracilis*). Cluver and Hotton (1981) transferred this species to *Diictodon* (see also King, 1988), and Brink (1986) and Sullivan and Reisz (2005) specifically synonymized it with *Diictodon feliceps*.

Dicynodon juddianus (Newton, 1893)

Holotype—ELGNM 1890.3, a slab containing the natural mold of a skull. NHMUK R2108 (Fig. 62) is a cast made from this mold.

Locus Typicus—Cutties Hillock Quarry, Elgin, Scotland.

Horizon—Cutties Hillock Sandstone Formation (Upper Permian).

Status—Junior subjective synonym of *Gordonia traquairi* Newton, 1893.

Remarks—Newton (1893) distinguished *Gordonia juddiana* from the type species *G. traquairi* on the basis of its weaker sagittal crest, thickened nasals overhanging the nares, and more ventrally directed caniniform process. Von Huene (1940) transferred *G. juddiana* and its congeners to *Dicynodon*. The difference in sagittal crest size between *G. juddiana* and *G. traquairi* is probably a combination of individual variation (*G. traquairi* represents a larger individual) and taphonomic deformation (the type skull of *G. traquairi* has suffered some lateral crushing, exaggerating the height of the crest). Regarding the thickened nasals, *G. juddiana* does not have discrete, cryptodont-like bosses overhanging the nares. Although there is a thickened ridge on the lateral surface of the nasal in *G. juddiana*, a similar ridge is present in *G. traquairi*, and these skulls agree in most other

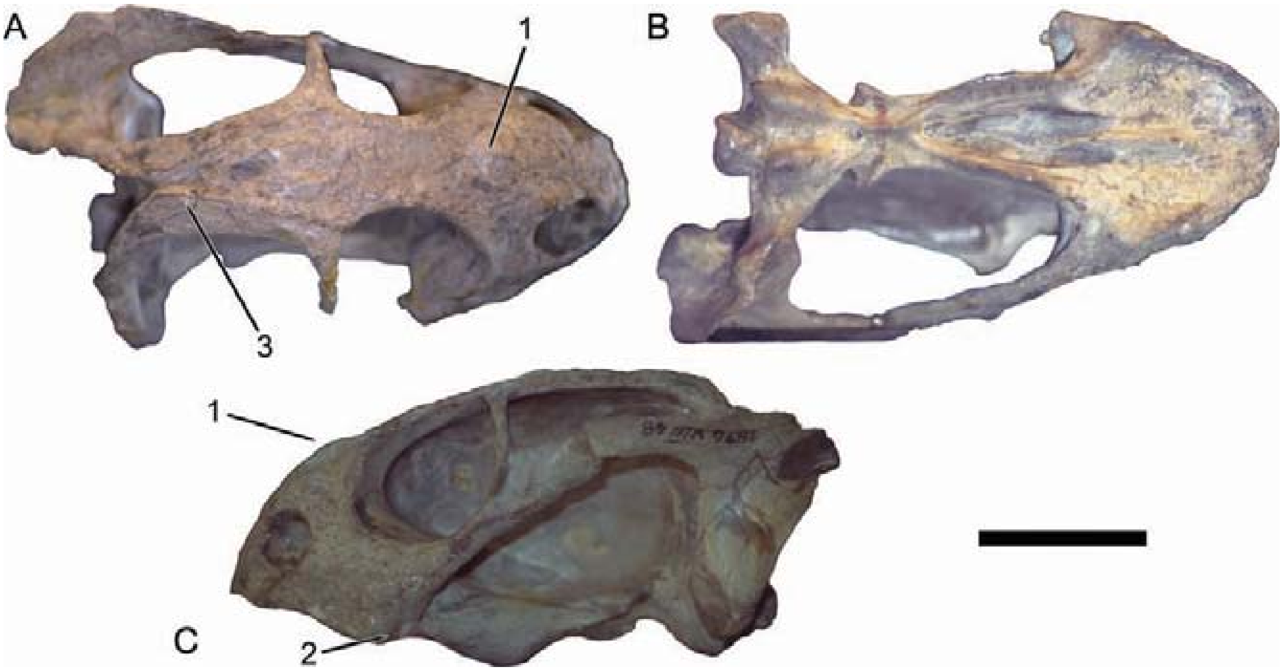

FIGURE 50. BSP 1934 VIII 48, the holotype of *Dicynodon grossarthi* (= *Diictodon feliceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) median snout boss and (2) ventral edge of the caniniform process at same level of anterior margin of orbits. *Diictodon feliceps* can be distinguished from other pylaecephalids by the absence of postcanine teeth and the (3) relatively narrow intertemporal bar, with extensive but incomplete overlap of the parietals by the postorbitals. Scale bar equals 5 cm.

regards. Refer to the entry on *Dicynodon traquairi* for further information.

Dicynodon kitchingi Broom, 1937a

Holotype—TM 345, a poorly preserved, strongly dorsoventrally crushed skull (Fig. 63).

Locus Typicus—Bluegum House, 4 miles east of Bethesda Road Station, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodon lacerticeps* Owen, 1845.

Remarks—Broom (1937a) considered *Dicynodon kitchingi* to be most similar to *Dicynodon woodwardi* in the shared possesion of a relatively broad parietal, but differing in having a much smaller pineal foramen. He additionally distinguished *D. kitchingi* from *Dicynodon gilli* by the wider frontal and apparent absence of a dorsal exposure of the postfrontals. He also characterized *D. kitchingi* by the marked anterior angulation of the tusks. Haughton and Brink (1954) and King (1988) listed *D. kitchingi* as a valid species; Cluver and Hotton (1981) did not address this species. TM 345 has a short intertemporal bar that is very narrow posteriorly, with complete postorbital-parietal overlap. The caniniform processes are strongly angled anteriorly, although this may be an artifact of dorsoventral compression. However, the combination of these characters and the short, squared-off premaxillary tip of the palate indicate that this specimen is referable to *Dicynodon lacerticeps*.

Dicynodon kolbei (Broom, 1912a)

Holotype—SAM-PK-1886, a well-preserved skull (missing part of the occiput and right temporal arch) (Fig. 64) and distal humerus.

Locus Typicus—Rhenosterfontein, Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1912a) described *Oudendon kolbei* on the basis of a nearly complete, well-preserved skull missing only the right temporal bar from Rhenosterfontein. Broom considered *O. kolbei* to be most similar to *Oudenodon bainii*, *Oudenodon brevirostris*, and *Oudenodon prognathus* (here considered to all represent a single species, *O. bainii*), but distinguished it on the basis of minor proportional differences in intertemporal width, nasal boss size, and fronto-parietal contour. These tenuous specific distinctions aside, this description is a valuable and unusually thorough account of *Oudenodon* cranial morphology, and laid to rest several problematic issues raised by earlier descriptions (e.g., Broom recognized that the supposed 'palatine teeth' of *Oudenodon* were actually irregular sculpturing of the bone surface and that the large bone making up most of the postorbital bar and medial edge of the temporal fenestra was the postorbital, not the postfrontal as had been described by Seeley [1889]). Unfortunately, in an act that was to greatly magnify the problems of *Dicynodon* taxonomy, Broom (1912a:351) included an addendum to the *O. kolbei* description mentioning the discovery of variable presence or absence of tusks in *Diaelurodon whaitsi* (= *Pristerodon mackayi*), and because of this, "there is no longer any question that *Oudenodon* is the female of *Dicynodon*." Following this logic, Broom then noted that *O. kolbei* must called *Dicynodon kolbei*, and the other nominal species of *Oudenodon* were eventually to follow suit (see Broom, 1913a, 1932). Van Hoepen (1934) placed *D. kolbei* in *Oudenodon* (in the new subgenus *Mastocephalus*). Keyser (1975) considered SAM-PK-1886 to fall within the range of variation of *Oudenodon bainii*, and synonymized *O. kolbei* with that

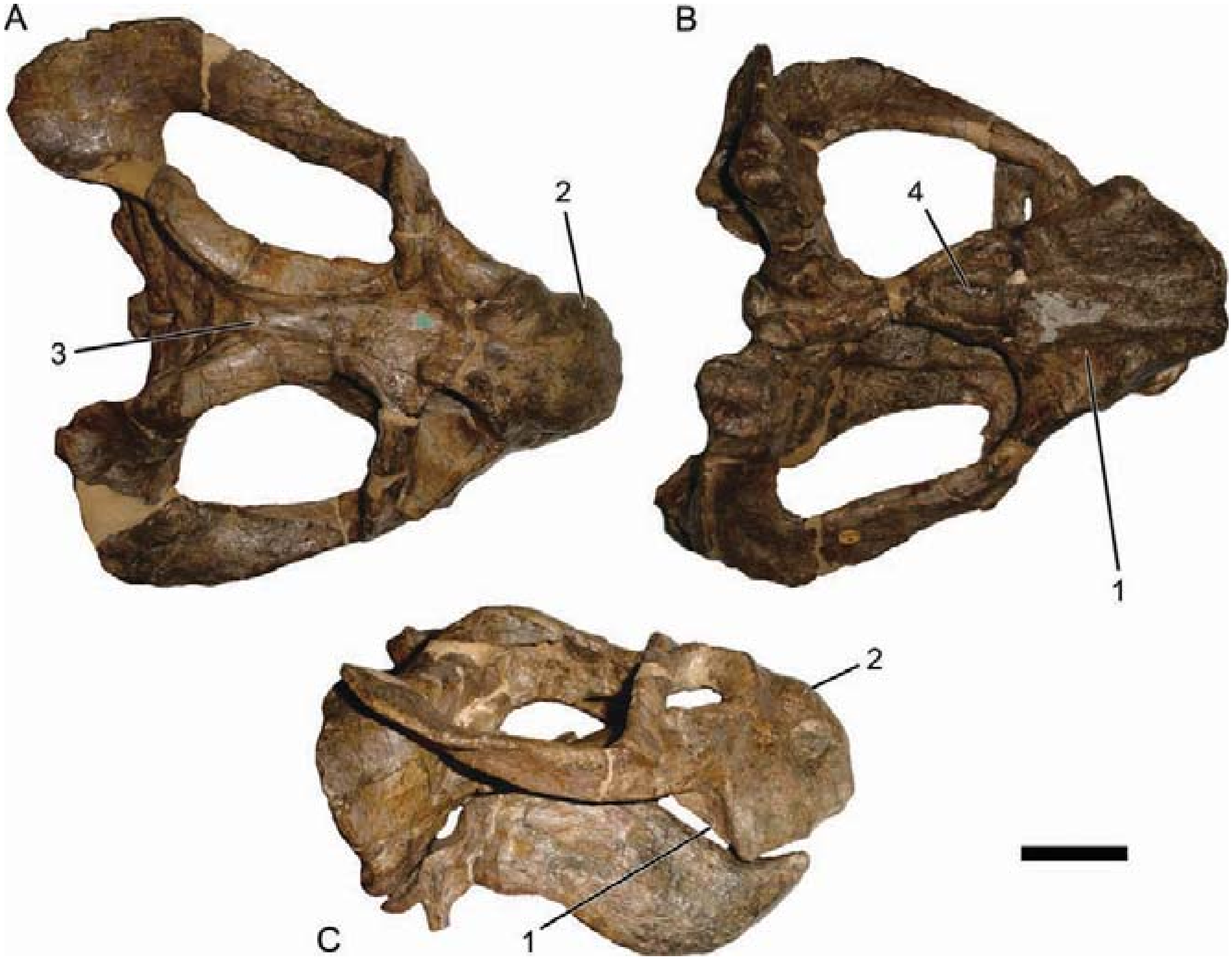

FIGURE 51. NHMUK R4067, the holotype of *Dicynodon halli* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

taxon, an approach followed by Brink (1986), King (1988), and the current study.

Dicynodon lacerticeps Owen, 1845

Holotype—NHMUK 36233, a complete but weathered and poorly prepared skull and lower jaws (Fig. 65).

Locus Typicus—Tarka prolongation of the Winterberg Range, South Africa.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Valid.

Remarks—*Dicynodon lacerticeps* was described by Owen (1845) as the first known dicynodont. As the type species of *Dicynodon*, *D. lacerticeps* has been recognized as valid by all subsequent workers, despite the highly inadequate state of the holotype. NHMUK 36233, the type of *Dicynodon lacerticeps*, is maddeningly poorly preserved, an unfortunate but perhaps inevitable side effect of its great historical antiquity. NHMUK 36233 is a complete skull and mandible that has, over 168 years of study, been subject to a variety of preparatory techniques of varying efficacy and destructiveness. As a result, the only undamaged bone surfaces still exposed on this specimen are the left frontal and preparietal. Because nearly all the skull elements have been chiseled or ground down below the surface of the bone, most of the cranial sutures are readily evident. As poor as it is, several characters are present in this specimen that confirm its placement in the '*Dicynodon lacerticeps* morphotype,' thereby validating usage of that name for the morphospecies. Despite the poor preparation, the skull as a whole is nearly undistorted and the remaining bone surfaces are well preserved. The caniniform process and tusk are strongly angled forwards. Although the ascending process of the premaxilla and the nasals are broken dorsal to the nares, based on the position of the relatively intact prefrontals, frontals, and premaxillary tip, this specimen could not have had the very steeply curved snout profile typical of *Daptocephalus leoniceps*. The area of postorbital overlap on the intertemporal bar is short, making up less than half of the length of the intertemporal bar (2.0 cm compared to 4.5 cm bar length). The large (2.4 cm long) preparietal suggest that this is a juvenile individual, which would explain the short intertemporal bar. Presumed *Daptocephalus* juveniles of similar or smaller skull size (e.g., USNM 23337) already

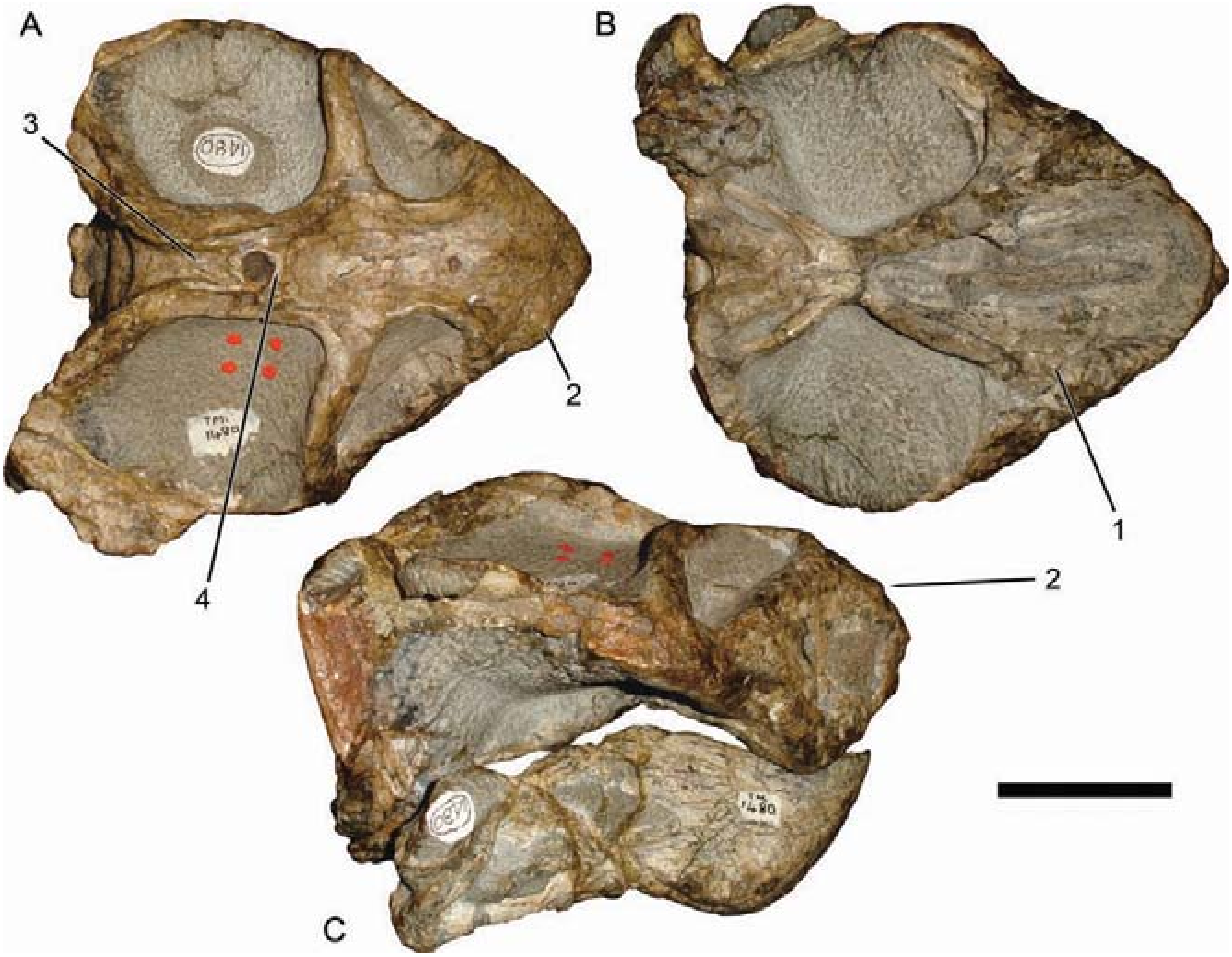

FIGURE 52. TM 1480, the holotype of *Dicynodon hartzenbergi*, in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses and as a geikiine on the basis of the (3) wide intertemporal bar with broad exposure of the parietals and (4) raised rim around the pineal foramen. The species-level identification of this specimen is uncertain, contingent on further study of ontogeny in geikiids. Scale bar equals 5 cm.

display proportionally longer overlapping postorbitals on the temporal bar. The mandible is massive in the symphysial region. The lateral dentary shelf has been prepared off on both sides of the mandible, but on the better-preserved right side its presence is indicated by an exposed area of broken bone at the same level as intact dentary surface bone. This broken region extends to a broad region anterodorsal to the mandibular fenestra, suggesting that a rounded boss was present. Locality data for this specimen is vague; it was found in a region with both *Cistecephalus* and *Dicynodon* AZ exposures. Referred specimens of *D. lacerticeps* occur in both assemblage zones.

Dicynodon laticeps Broom, 1912b

Holotype—AMNH FARB 5564, a nearly complete, strongly dorsoventrally crushed skull (Fig. 66).

Locus Typicus—Nieuwveld, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian)

Status—Junior subjective synonym of *Aulacephalodon bainii* (Owen, 1845).

Remarks—Broom (1912b) described *Dicynodon laticeps* on the basis of a complete, highly dorsoventrally crushed skull from the Nieuwveld. Broom considered *D. laticeps* to be most similar to *Dicynodon tigriceps* (= *Aulacephalodon bainii*), but distinguished it on the basis of its relatively larger tusks. Subsequent revisions of *Aulacephalodon* (Keyser, 1972; Tollman et al., 1981) have recognized only a single species (*A. bainii*), including *D. laticeps* as a junior synonym.

Dicynodon latifrons Broom, 1899

Holotype—AMG 4799 (formerly PEM/1199P), an anteroposteriorly crushed skull missing the premaxillary region, both temporal arches, and the right edge of the occiput (Fig. 67).

Locus Typicus—Burgersdorp, South Africa.

Horizon—*Cynognathus* Assemblage Zone (Middle Triassic).

Status—Junior subjective synonym of *Kannemeyeria simocephala* (Weithofer, 1888).

Remarks—Broom (1899) described *Dicynodon latifrons* on the basis of a distorted partial skull missing the temporal arches and the tip of the snout (the missing snout fragment

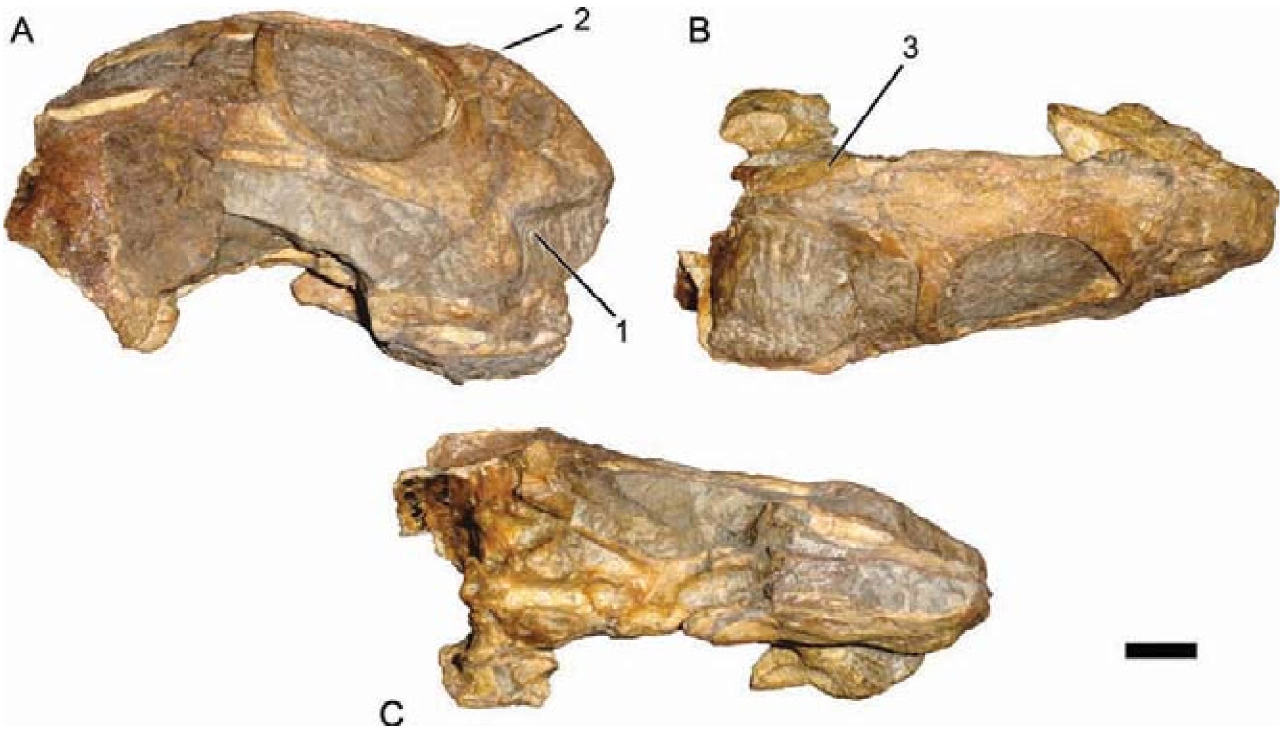

FIGURE 53. GPIT unnumbered, the holotype of *Dicynodon haughtonianus* (= *Diictodon feliceps*), in right lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch and (2) median snout boss and as *D. feliceps* on the basis of the (3) relatively narrow intertemporal bar with extensive postorbital-parietal overlap. Scale bar equals 5 cm.

was originally found with the specimen, but had been lost by the time of Broom's description) from Burgersdorp. He noted its similarity to *Dicynodon simocephalus* (= *Kannemeyeria*), but distinguished his new species on the basis of its comparatively narrower palate and more laterally directed orbits. Broom (1932) transferred this species to *Kannemeyeria* but retained it as valid. Cruickshank (1965) considered *K. latifrons* to be valid, and referred a specimen from the Manda beds of Tanzania to this species, but later (Cruickshank, 1970) synonymized it with *K. simocephala* (see also King, 1988).

Dicynodon latirostris Owen, 1860b

Holotype—NHMUK 36222, a nearly complete, weathered skull missing part of the right temporal arch (Fig. 68).

Locus Typicus—Rhenosterberg, South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Junior subjective synonym of *Lystrosaurus declivis* (Owen, 1859).

Remarks—As noted in the section on *Dicynodon declivis*, early in the history of dicynodont research, Owen (1860b) included *Ptychognathus* (= *Lystrosaurus*) as a subgenus of *Dicynodon*. For the sake of completeness, we include the three species assigned to "*Dicynodon*: Subgenus *Ptychognathus*" by Owen (1860b:49) (*D. declivis*, *D. latirostris*, and *D. verticalis*) in the listing of nominal *Dicynodon* species here. Brink (1951) and Cluver (1971) considered *D. latirostris* to be synonymous with *Lystrosaurus declivis*, a result subsequently borne out by morphometric analysis (Grine et al., 2006) and supported here.

Dicynodon latirostris Broom, 1932

Holotype—SAM-PK-5141, a poorly preserved, dorsoventrally crushed skull (missing the right temporal arch) and lower jaws (Fig. 69).

Locus Typicus—Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—In his description of *Dicynodon latirostris*, Broom (1932) did not specify any characters uniquely diagnosing the species. Van Hoepen (1934) included *D. latirostris* within *Oudenodon* in the subgenus *Mastocephalus*. Keyser (1975) synonymized *D. latirostris* with *Oudenodon bainii*, a referral upheld in subsequent studies (Brink, 1986; King, 1988).

Dicynodon leoniceps Owen, 1876

Holotype—NHMUK 47047, a complete, well-preserved, somewhat laterally crushed skull (Fig. 70).

Locus Typicus—Gats River, Graaff-Reinet, South Africa.

Horizon—?*Dicynodon* Assemblage Zone (Upper Permian).

Status—Valid as *Daptocephalus leoniceps* (Owen, 1876).

Remarks—Owen (1876) described *Dicynodon leoniceps* as the largest known *Dicynodon* species based on a skull rivaling the holotype of *Oudenodon magnus* (= *Rhachiocephalus*) in size. Seeley (1898) included *D. leoniceps* in the 'narrow-headed' *Dicynodon* subgenus *Rhachicephalodon*, which also included *D. lacerticeps*, *D. pardiceps*, and *D. feliceps*. Van Hoepen (1934) made *D. leoniceps* the type species of a new genus, *Daptocephalus*, which included other large *Dicynodon* species (e.g., *D. ingens*, *D. pardiceps*). Haughton and Brink (1954) treated

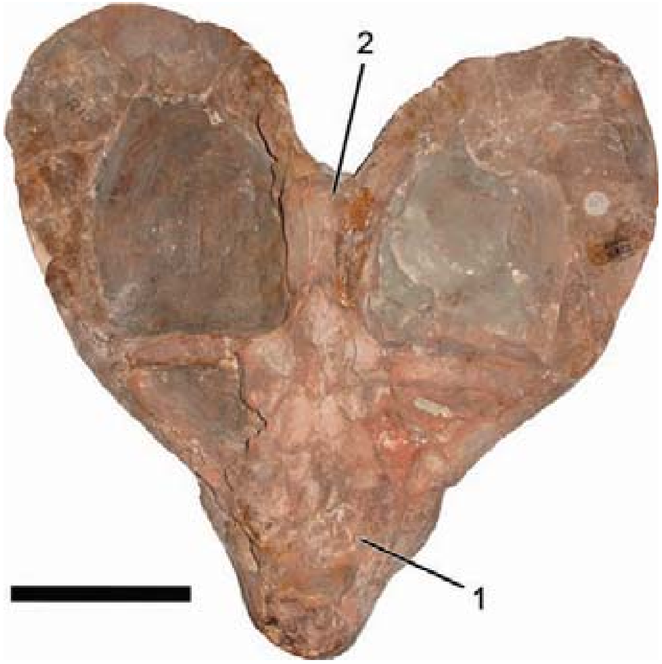

FIGURE 54. SAM-PK-11312, the holotype of *Dicynodon helenae* (= *Oudenodon bainii*), in dorsal view. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 10 cm.

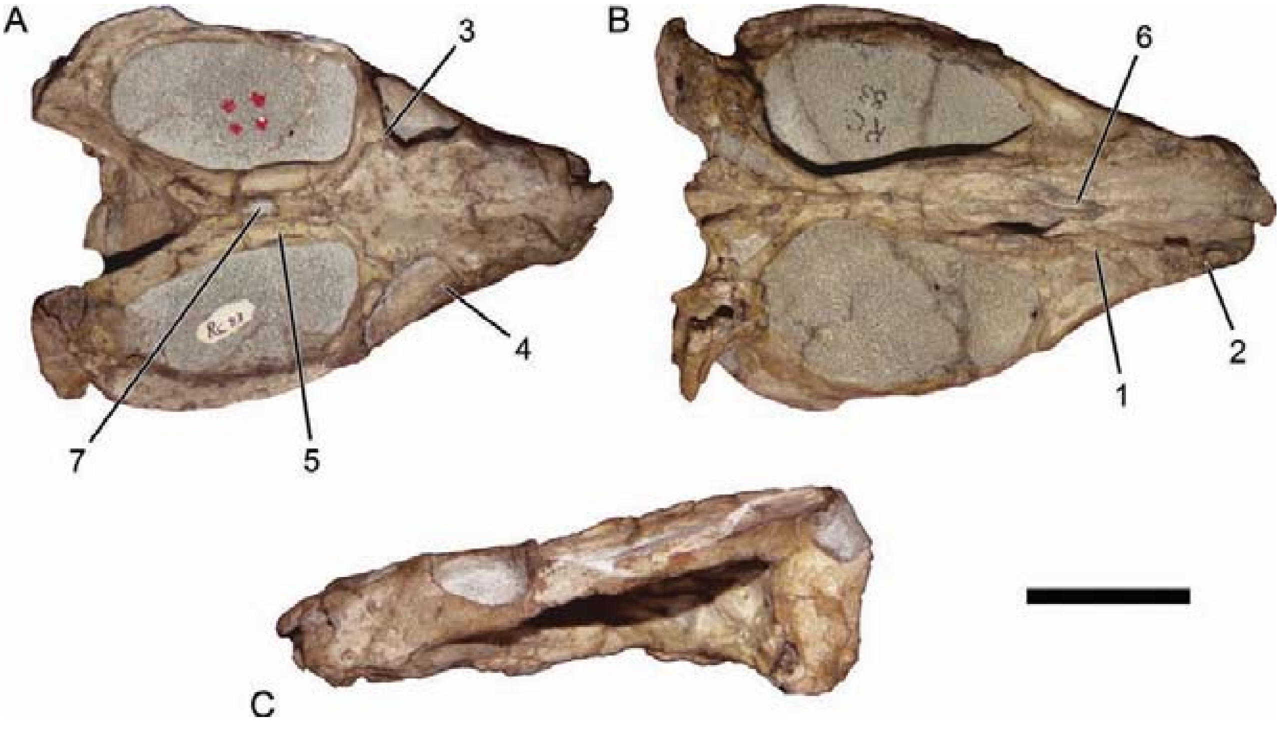

FIGURE 55. RC 83, the holotype of *Dicynodon howardi* (= *Dicynodontoides recurvidens*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) postcaniniform keel and (2) embayment of the palatal rim anterior to the caniniform process, as a kistecephalian on the basis of the (3) absence of the postfrontal and (4) posteromedial extension of the anterior margin of the orbit, partially closing off the snout, and as a kingoriid on the basis of the (5) postorbitals sloping slightly ventrolaterally, overlapping the parietals except for a narrow exposure of the latter as a sagittal crest and the (6) relatively wide mid-ventral plate of the vomer. This specimen can be identified as *Dicynodontoides* rather than *Kombuisia* based on the (7) elongate, well-developed pineal foramen. Scale bar equals 5 cm.

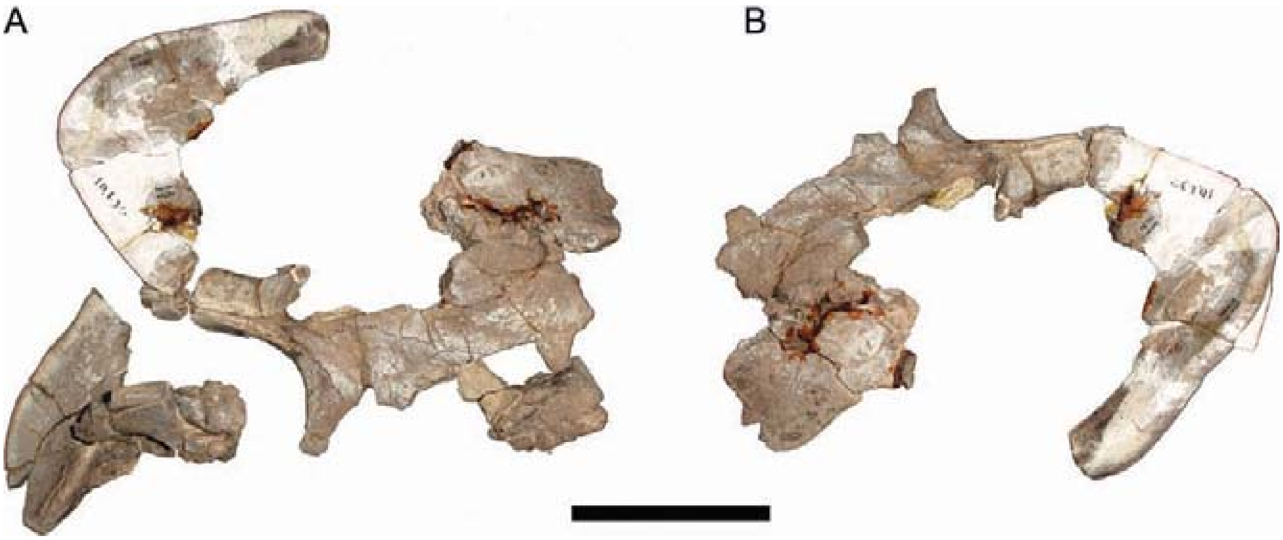

FIGURE 56. SAM-PK-10630, the holotype of *Dicynodon huenei* Haughton, in dorsal (**A**) and left lateral (**B**) views. Unfortunately this specimen is highly fragmentary, and the validation of this species is based largely on referred specimens. Additional fragments of this specimen (not figured) exhibit the thickened anterior plate of the lower portion of the postorbital bar, which distinguishes this species from *Dicynodon lacerticeps*. Scale bar equals 10 cm.

Daptocephalus as a valid genus, with only *D. leoniceps* included, but noted that many nominal *Dicynodon* species may be referrable to it with further study. Kitching (1977) also treated *Daptocephalus* as valid and monotypic (but considered a number of large *Dicynodon* species to be junior synonyms), using it to characterize the terminal Permian *Daptocephalus* Zone. Cluver and Hotton (1981) considered *Daptocephalus* to be synonymous with *Dicynodon*, but retained *D. leoniceps* as a valid species. Subsequent studies have either considered *D. leoniceps* a valid species of *Dicynodon* (e.g., King, 1988) or a synonym of *D. lacerticeps* (e.g., Brink, 1986), and Kitching's '*Daptocephalus* Zone' is currently known as the *Dicynodon* AZ (Rubidge, 1995). *Dicynodon leoniceps* can be distinguished from *D. lacerticeps* specimens of similar size by the proportionally much longer, narrower

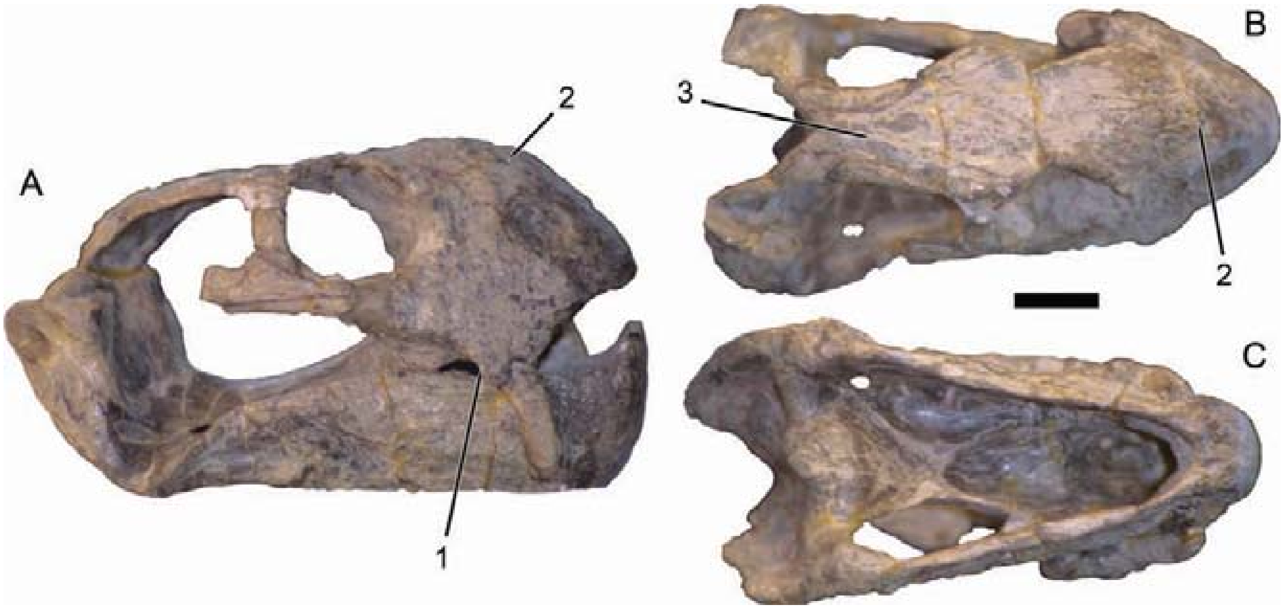

FIGURE 57. BSP 1934 VIII 46, the holotype of *Dicynodon huenei* Broili and Schröder (renamed *Dicynodon broilii*) (= *Diictodon feliceps*), in right lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) ventral edge of the caniniform process at same level of anterior margin of orbits and (2) median snout boss. *Diictodon feliceps* can be distinguished from other pylaecephalids by the absence of postcanine teeth and the (3) relatively narrow intertemporal bar, with extensive but incomplete overlap of the parietals by the postorbitals. Scale bar equals 1 cm.

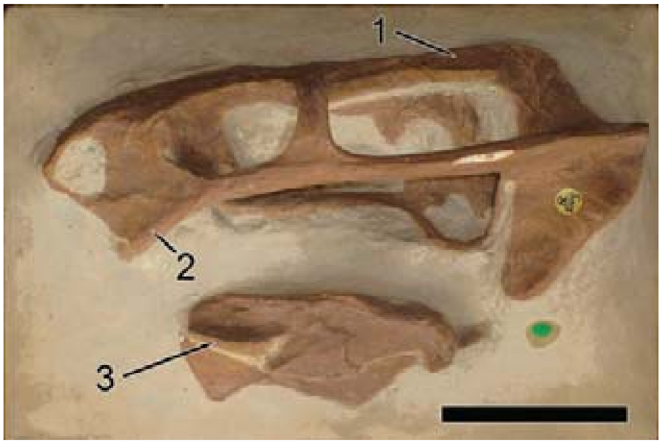

FIGURE 58. NHMUK R2109, a cast made from the holotype of *Dicynodon huxleyanus* (= *Gordonia traquairi*) (a natural sandstone mold), in left lateral view. This specimen can be identified as an individual of *D. traquairi* by the (1) elongate, narrow intertemporal region with a raised sagittal crest, (2) anteriorly directed caniniform process, and (3) narrow, rod-like lateral dentary shelf. Scale bar equals 5 cm.

intertemporal bar, with almost complete overlap of the parietals by the postorbitals. Because length and breadth of the postorbital bar is an ontogenetically variable feature in dicynodonts, this character is less reliable in small and juvenile individuals, but there remains a suite of consistent features that differentiate *D. leoniceps* from *D. lacerticeps*. *Dicynodon leoniceps* has a steeply sloping snout profile, ventrally directed caniniform process and tusk (this is anteriorly directed in *D. lacerticeps*), broadly rounded dorsal edge to the squamosal in lateral view (as opposed to the sharp angle in *D. lacerticeps*), and very thin, strap-like exposure of the postfrontals in the dorsal skull roof. For resurrection of the genus *Daptocephalus* to refer to *D. leoniceps*, refer to the Phylogenetic Analysis.

Dicynodon leontocephalus Broom, 1950

Holotype—RC 96, a complete, well-preserved but dorsoventrally crushed skull (Fig. 71).

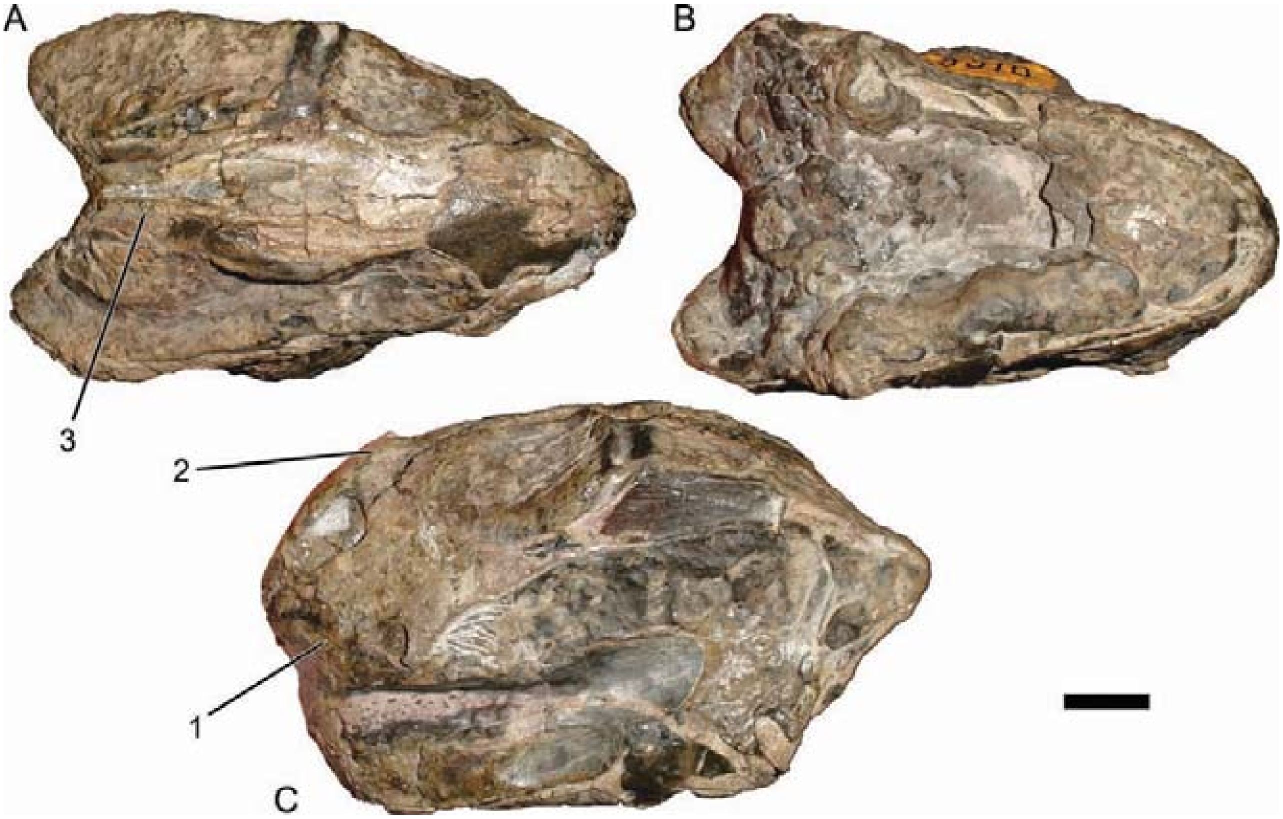

FIGURE 59. AMNH FARB 5510, the holotype of *Dicynodon ictidops* (= *Diictodon feliceps*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch and (2) median snout boss and as *D. feliceps* on the (3) basis of the relatively narrow intertemporal bar, with extensive postorbital-parietal overlap, and the lack of teeth. Scale bar equals 1 cm.

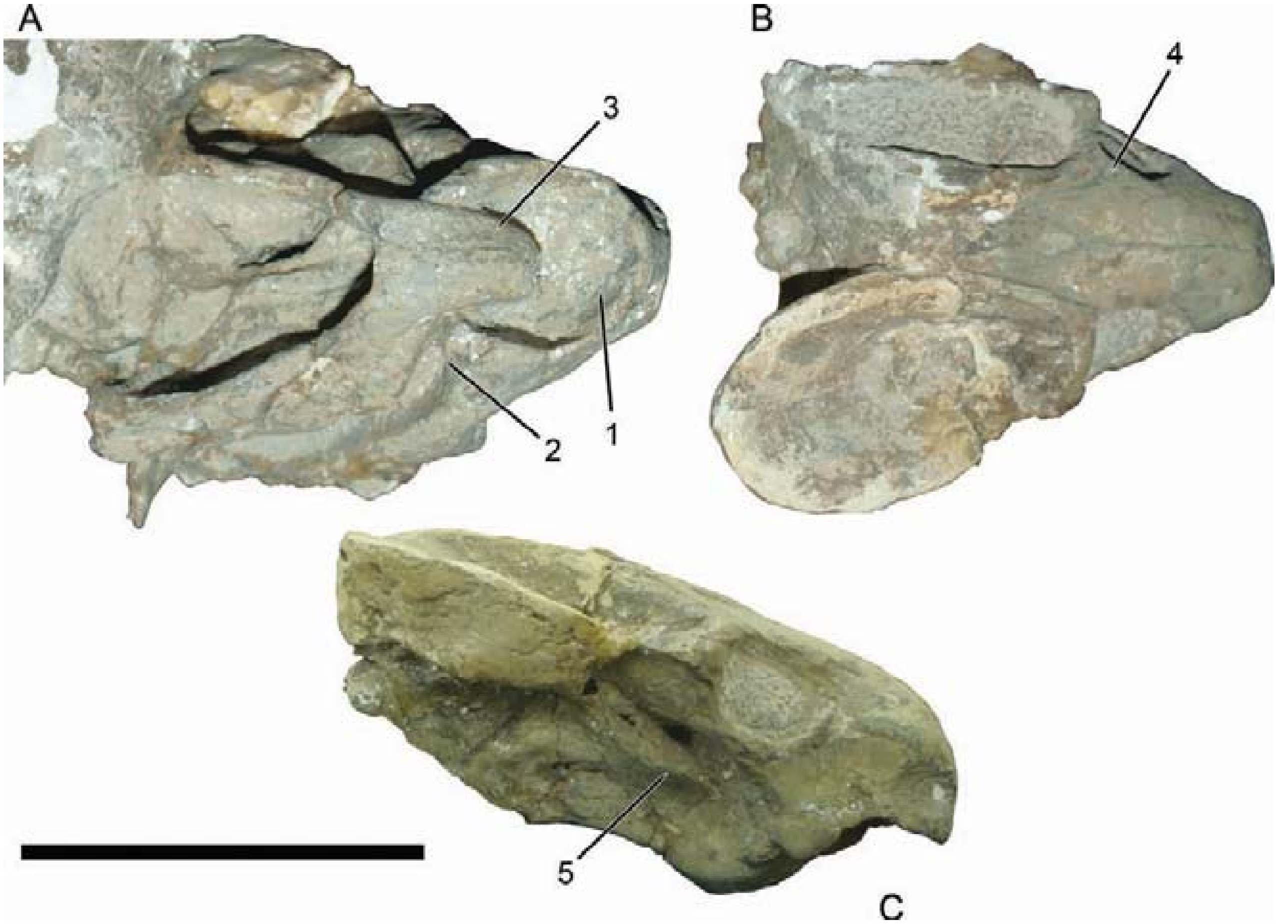

FIGURE 60. MMK 4165, the holotype of *Dicynodon ictinops* (= *Emydops arctatus*), in ventral (**A**), dorsal (**B**), and right lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) palatal surface of the premaxilla with a groove-like depression with a rounded anterior end, (2) postcaniniform keel, and (3) 'shovel-shaped' dentary symphysis and as *Emydops* on the basis of the (3) elongate dentary symphysis, (4) presence of a postfrontal, and (5) large, triangular lateral dentary shelf. The strong angulation of the lateral dentary shelf allows this specimen to be identified as *E. arctatus* rather than *E. oweni*. Scale bar equals 5 cm.

Locus Typicus—Springfontein, Middelburg, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Daptocephalus leoniceps* (Owen, 1876).

Remarks—Broom (1950) described *Dicynodon leontocephalus* based on a large skull with massive tusk roots. Haughton and Brink (1954), Cluver and Hotton (1981), and King (1988) listed *D. leontocephalus* as a valid species of *Dicynodon*. RC 96 is clearly a *Dicynodon*-grade dicynodontoid, as indicated by the large labial fossa and extensive overlap of the parietals by postorbitals, although it displays a problematic mixture of characteristics of *Dicynodon lacerticeps* and *Daptocephalus leoniceps*. RC 96 has ventrally directed caniniform processes, broad lateral exposure of the squamosal, and a very long intertemporal bar (as in *D. leoniceps*), but a gradually sloping snout and lack of a broadly rounded dorsal margin of the squamosal in lateral view (as in *D. lacerticeps*). However, this skull has been dorsoventrally compressed, and we interpret the '*lacerticeps*-like' features of RC 96 to be artifacts of deformation. *Dicynodon leontocephalus* is best regarded as a junior synonym of *Daptocephalus leoniceps*.

Dicynodon leontops Broom, 1913c

Holotype—AMNH FARB 5582, a nearly complete, strongly laterally crushed skull (missing part of the right temporal arch) (Fig. 72), lower jaws, and cervical vertebrae.

Locus Typicus—Bethulie, Free State, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Daptocephalus leoniceps* (Owen, 1876).

Remarks—Broom (1913c) described *Dicynodon leontops* on the basis of a complete but laterally crushed skull, mandible, and cervical series. He distinguished *D. leontops* from the similar species *Dicynodon leoniceps* and *Dicynodon pardiceps* based on its narrower skull in general and smaller, narrower preparietal in particular. Van Hoepen (1934) included *D. leontops* in *Daptocephalus*, but Haughton and Brink (1954), Kitching (1977), and King (1988) placed this species in *Dicynodon*. Although highly laterally compressed, AMNH FARB 5582 is typical of the *Daptocephalus leoniceps* morphotype, with a long, narrow intertemporal bar with complete overlap of the parietals by the postorbitals, narrow exposure of the postfrontals in the skull roof as thin, strap-like elements bordering the postorbitals, a steeply angled

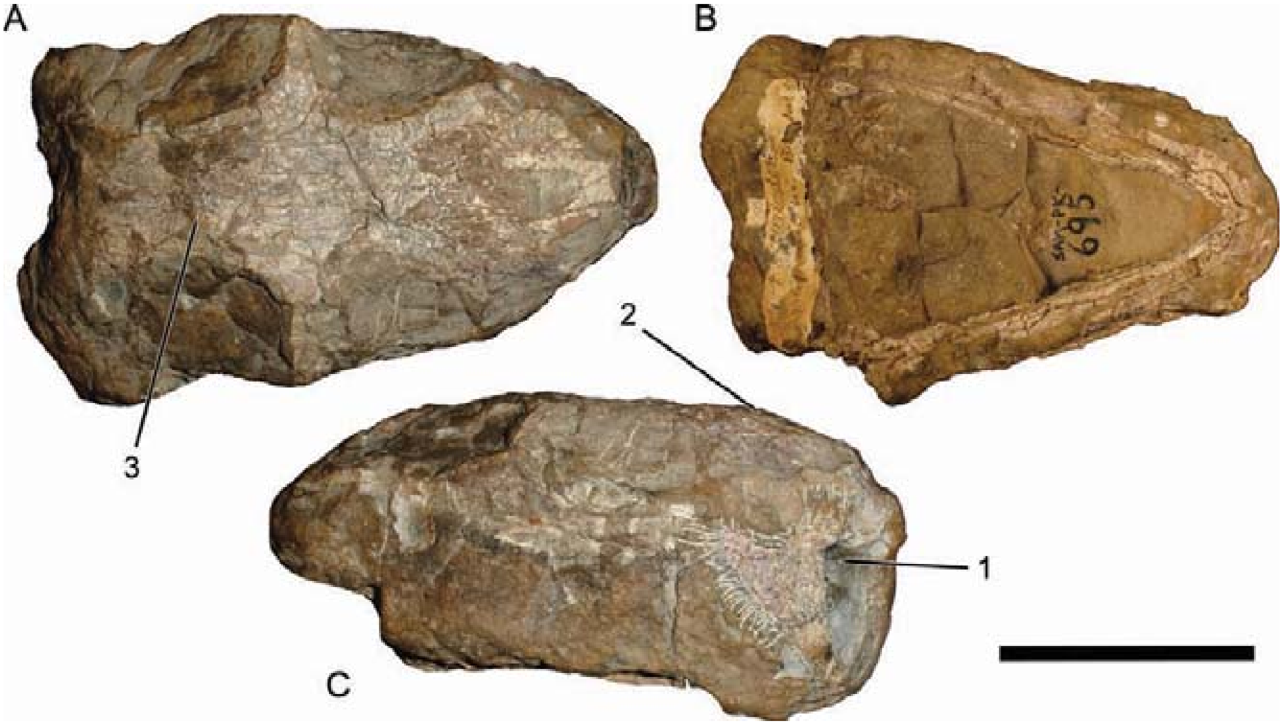

FIGURE 61. SAM-PK-695, the holotype of *Dicynodon jouberti* (= *Diictodon feliceps*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch and (2) median ridge on the snout and as *D. feliceps* on the basis of the (3) relatively narrow intertemporal bar with extensive but incomplete postorbital-parietal overlap. Scale bar equals 5 cm.

snout profile, ventrally directed caniniform process, and broadly rounded dorsal edge of the squamosals in lateral view.

Dicynodon leptorhinus (Owen, 1876)

Holotype—NHMUK 47067, an extremely poorly preserved anterior half of a skull (Fig. 73).

Locus Typicus—Steilkrans, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian)

Status—Nomen dubium (Dicynodontia indet.).

Remarks—Owen (1876) originally described *D. leptorhinus* as a species of *Kistecephalus* (= *Cistecephalus*). Broom (1932) recognized that this species was not referable to *Cistecephalus* and transferred it to *Dicynodon*. Van Hoepen (1934) made *D. leptorhinus* the type species of the new genus *Baiopsis*, but most subsequent authors (e.g., Haughton and Brink, 1954; Kitching, 1977; King, 1988) retained this species in *Dicynodon*. NHMUK 47067 is very poorly preserved, with no original bone surface dorsally and no preservation of the palate save for rough outlines of the pterygoids and maxillae. Tusk roots are present. The most informative part of this skull is the interorbital region. A large preparietal is present and the parietals are broadly exposed in the intertemporal bar behind the pineal foramen. The presence of tusks, moderately broad intertemporal region, and relatively narrow

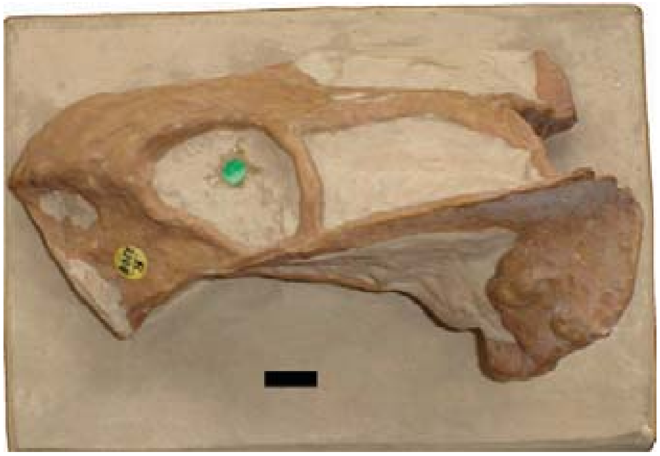

FIGURE 62. NHMUK R2108, a cast made from the holotype of *Dicynodon juddianus* (= *Gordonia traquairi*) (a natural sandstone mold), in left lateral view. Scale bar equals 1 cm.

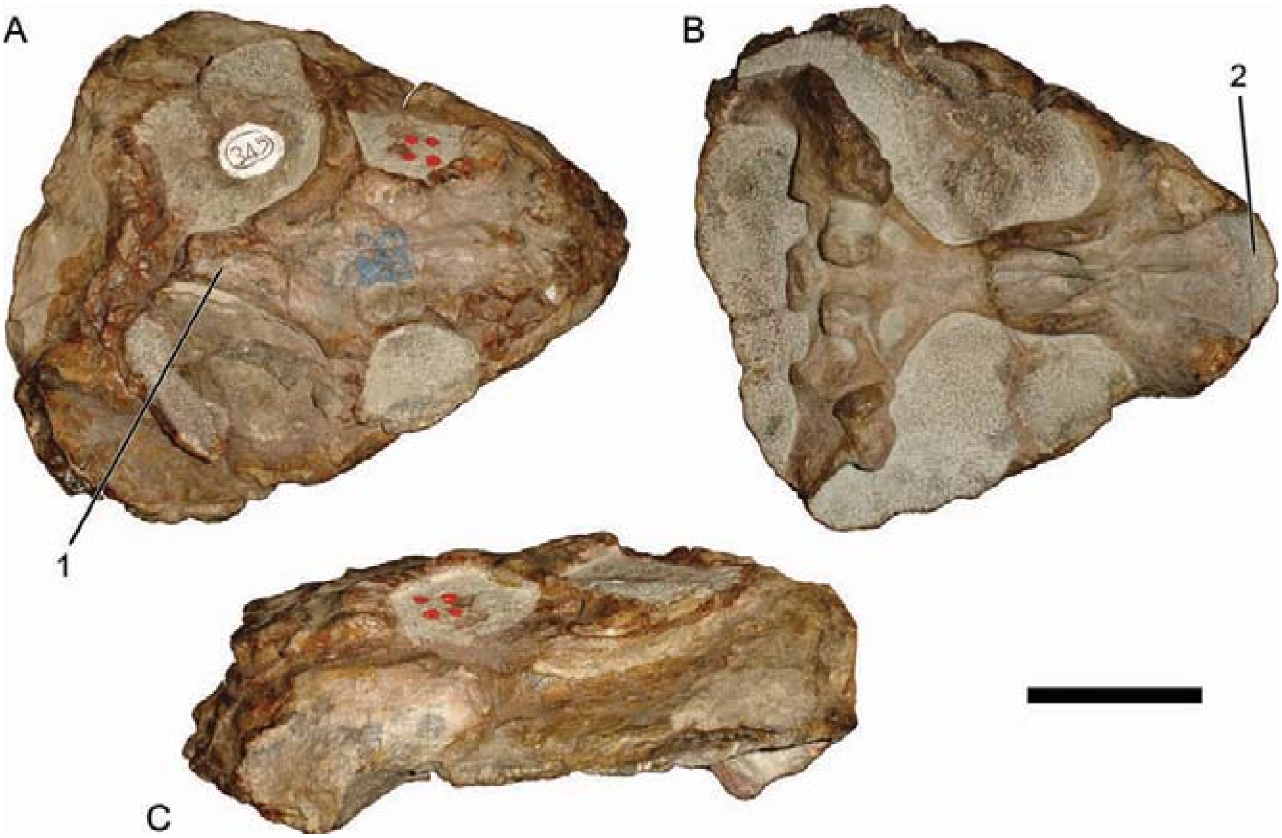

FIGURE 63. TM 345, the holotype of *Dicynodon kitchingi* (= *Dicynodon lacerticeps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as *D. lacerticeps* on the basis of the (1) narrow, short intertemporal bar with complete postorbital-parietal overlap and a (2) squared-off premaxillary tip. Scale bar equals 5 cm.

interorbital region suggests that, among South African *Cistecephalus* AZ dicynodonts, NHMUK 47067 is a specimen of *Diictodon feliceps*. *Diictodon* retains a relatively large preparietal at large skull size (unlike dicynodontoids), and NHMUK 47067 would be at the larger end of known *Diictodon* skulls (it is similar in size to the holotype of *D. feliceps*, NHMUK 47052). Alternatively, this skull could represent a juvenile *Aulacephalodon*. However, no uniquely identifying features of any dicynodont species (or even higher clades) are preserved in this specimen, and *D. leptorhinus* should be considered a nomen dubium, Dicynodontia indet.

Dicynodon leptoscelus (Seeley, 1900)

Holotype—AMG 407, a slab containing the natural mold of most of a dicynodont skeleton (occipital region of skull, axial column excluding caudal vertebrae, scapulae, left humerus, pelvis, left femur, tibia, and fibula) (Fig. 74).

Locus Typicus—Eilodon, Bedford, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontia indet.).

Remarks—Seeley (1900) described *Dicranozygoma leptoscelus* based on the mold of a nearly complete, articulated skeleton, but unfortunately preserving only a portion of the occiput and temporal arch of the skull. Broom (1932) transferred this species to *Dicynodon* (the approach followed by most subsequent workers, e.g., King, 1988) and van Hoepen (1934) transferred it to *Oudenodon*. The incomplete skull of *D. leptoscelus* makes comparison with other dicynodonts difficult, although the breadth of the temporal arch preserved is suggestive of a geikiine cryptodont, such as *Aulacephalodon*. In the absence of identifiable diagnostic features, however, *D. leptoscelus* must be considered a nomen dubium. Additional comparative studies of dicynodont postcrania will be required if this specimen is to be identified beyond Dicynodontia indet.

Dicynodon limbus (Zhu, 1989)

Holotype—IVPP V7940, a nearly complete, well-preserved skull (missing part of the left postorbital bar) and lower jaws (Fig. 75).

Locus Typicus—Shiguai, Nei Monggol, China.

Horizon—Naobaogou Formation (Upper Permian).

Status—Valid as *Daqingshanodon limbus* Zhu, 1989.

Remarks—Zhu (1989) described *Daqingshanodon limbus* as the first Permian dicynodont recovered from Inner Mongolia. Lucas (1998a, 2001) synonymized *Daqingshanodon* with *Dicynodon*, but retained it as a valid species in the new combination *Dicynodon limbus*. We agree with the validity of this species, but it is not referable to *Dicynodon*. For rationale in resurrecting the name *Daqingshanodon* for this species, refer to the Phylogenetic Analysis.

Dicynodon lissops Broom, 1913c

Holotype—AMNH FARB 5508, a strongly laterally compressed skull missing most of the temporal arches (Fig. 76).

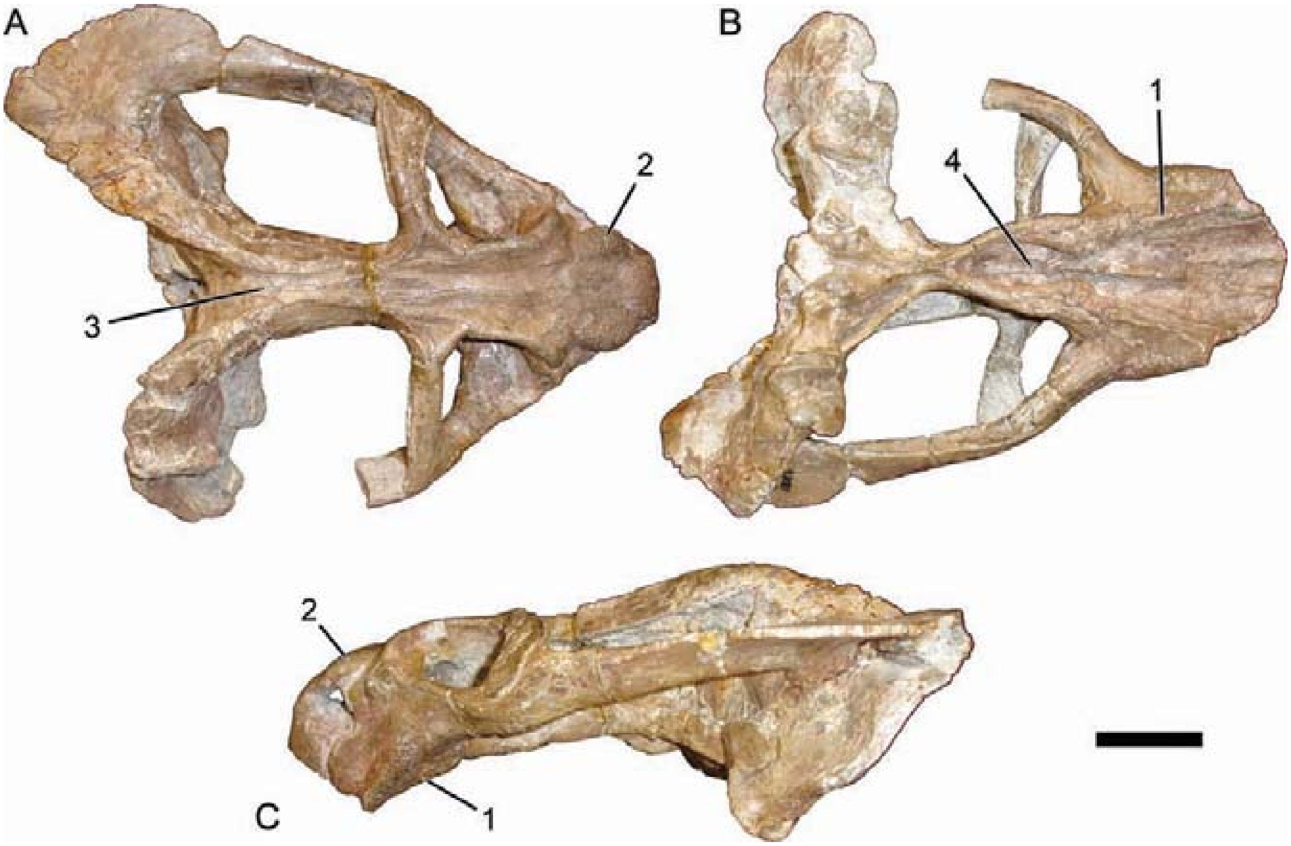

FIGURE 64. SAM-PK-1886, the holotype of *Dicynodon kolbei* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

Locus Typicus—Wilgerbosch, New Bethesda (Nieu-Bethesda), South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Daptocephalus leoniceps* (Owen, 1876).

Remarks—Broom (1913c) described *Dicynodon lissops* on the basis of a nearly complete but laterally crushed skull from Wilgerbosch. Broom considered this taxon to be most similar to *Dicynodon lacerticeps*, but distinguished *D. lissops* based on the more anterior position of the orbit. Van Hoepen (1934) included *D. lissops* in *Daptocephalus*, but most other authors (e.g., Haughton and Brink, 1954; King, 1988) retained it in *Dicynodon* as a valid species. AMNH FARB 5508 is a poorly prepared, highly laterally crushed specimen that nevertheless exhibits several features diagnostic of the *Daptocephalus leoniceps* morphotype, notably the long, extremely narrow intertemporal bar, steeply sloping snout profile, and ventrally directed caniniform process.

Dicynodon locusticeps von Huene, 1942

Holotype—GPIT/RE/7186, a well-preserved skull missing the left temporal arch (Fig. 77).

Locus Typicus—Ca. 2 km west of the northern peak of Kingori, Ngaka area of the Ruhuhu Basin, Tanzania.

Horizon—Upper Usili Formation (Upper Permian).

Status—Valid as *Geikia locusticeps* (von Huene, 1942).

Remarks—Von Huene (1942) described *Dicynodon locusticeps* on the basis of a well-preserved skull from rocks of the Usili Formation west of Kingori Mountain in the Ruhuhu Basin (Nowack, 1937). Walker (1973) first recognized a close relationship between *D. locusticeps* and the aberrant Scottish dicynodont *Geikia elginensis*, which had previously been considered most closely related to *Lystrosaurus*. Rowe (1980) formalized this relationship, transferring *D. locusticeps* to the genus *Geikia* based on shared possession of a squared-off premaxilla, a single large preorbital boss composed of fused nasal and prefrontal bones, and septomaxilla with exposure on the lateral surface of the snout behind the external nares (although the latter two characters are also present in *Pelanomodon*). Maisch and Gebauer (2005) redescribed *D. locusticeps*, reaffirming its placement in *Geikia* and establishing synonymy with another Usili Formation dicynodont, *Pelanomodon tuberosus* von Huene, 1942. Maisch and Gebauer (2005) listed a number of autapomorphies of *Geikia* that allow *G. elginensis* and *G. locusticeps* to be distinguished from the related geikiids *Pelanomodon* and *Aulacephalodon*, including a squared-off premaxilla, anterior surface of snout without median ridge, and reduced occipital exposure of the squamosal.

Dicynodon luangwanensis Boonstra, 1938

Holotype—SAM-PK-11310, a fragmentary skull still mostly encased in matrix (Fig. 78).

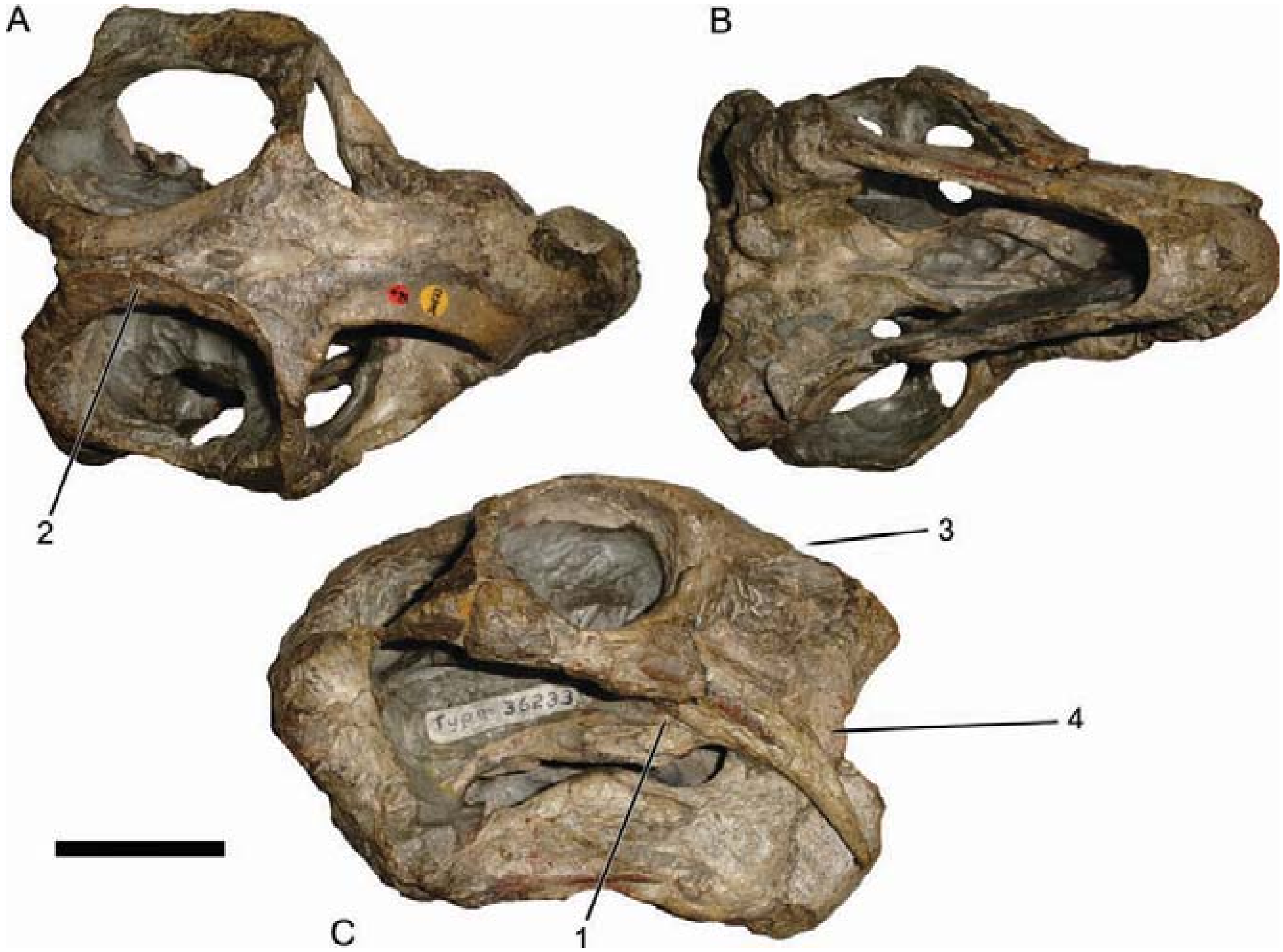

FIGURE 65. NHMUK 36233, the holotype of *Dicynodon lacerticeps*, in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen is unfortunately poorly preserved but is recognizably dicynodontoid by the presence of the (1) labial fossa. The combination of the (2) short, narrow intertemporal bar, (3) gradually sloping snout, and (4) anteriorly directed caniniform process allow the referral of better-preserved specimens to *D. lacerticeps* and suffice to validate this species and thus the genus *Dicynodon*. Scale bar equals 5 cm.

Locus Typicus—Three miles from Chikonda on the M'pundu Road, Luangwa Valley, Zambia.

Horizon—Upper Madumabisa Mudstone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Boonstra (1938) described *Dicynodon luangwanensis* as one of a series of tuskless *Dicynodon* species from the Luangwa Valley (the others being *D. euryceps*, *D. helenae*, and *D. parabreviceps*). Keyser (1975) recognized that these specimens represent specimens of *Oudenodon*, but although he synonymized the four Zambian species, he retained this cluster (using *O. luangwanensis* as the senior name) as distinct from the South African species *O. bainii*, based on the characteristically 'heart-shaped' dorsal profile of these skulls. *Oudenodon luangwanensis* has been recognized as a valid species in most subsequent treatments of *Oudenodon* (e.g., King, 1988). Botha and Angielczyk (2007) expressed doubt as to the validity of *O. luangwanensis*, but noted that further research was necessary. On a discrete character basis, the Zambian *Oudenodon* specimens are indistinguishable from South African *O. bainii*, a fact recognized by Keyser (1975). Regarding the 'heart-shaped' dorsal profile, this shape is frequently observed in South African specimens of *Oudenodon* (and *Tropidostoma*), usually in dorsoventrally compressed specimens in which the temporal arches have been splayed outwards. The most complete Zambian specimens, the holotypes of *D. euryceps* and *D. helenae*, have both suffered dorsoventral compression, and we regard the shape of these specimens as deformational. In the absence of any characters to separate these specimens from their South African counterparts, we consider the Zambian material to represent a single species, *O. bainii*.

Dicynodon luckhoffi Broom, 1937b

Holotype—SAM-PK-K1219, a small, complete skull, now lost.

Locus Typicus—Zuurplaats, Graaff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontoidea indet.).

Remarks—Broom (1937b) described *Dicynodon luckhoffi* based on a very small skull. Although he recognized the juvenile nature of this specimen, he argued that, "No species has been described of which this might be either a young specimen or a female, and I therefore think it ought to be named" (Broom, 1937b:307). Subsequent studies (Haughton and Brink, 1954;

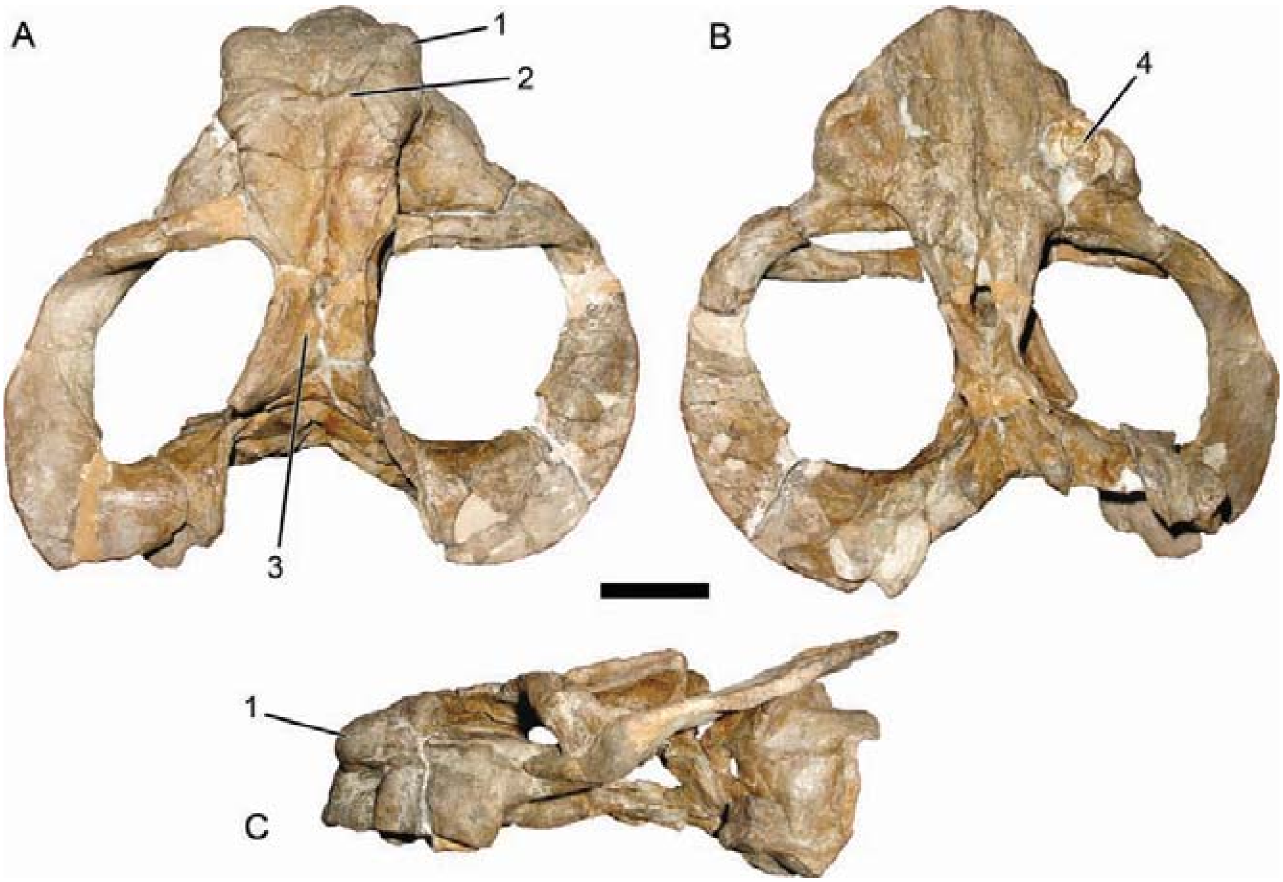

FIGURE 66. AMNH FARB 5564, the holotype of *Dicynodon laticeps* (= *Aulacephalodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views (anterior is up in **A** and **B**). This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as a geikiine on the basis of the (1) massive nasal bosses, (2) transverse ridge running between the prefrontals, (3) broad exposure of the parietal in the intertemporal bar, and as *Aulacephalodon* on the basis of the (4) massive tusks. Scale bar equals 5 cm.

Cluver and Hotton, 1981; King, 1988) have retained *D. luckhoffi* as a valid species, but Brink (1986) listed it as a nomen dubium. The loss of the holotype makes further study difficult, but Broom's (1937b) figure of the specimen offers some clues as to its identity. The proportionally large orbits, small temporal fenestrae, and large preparietal are in keeping with a juvenile identification (also, Broom mentions that this specimen has small, still-erupting tusks). Broom depicts a wide intertemporal exposure of the parietals with no complete overlap by the postorbitals, but does show constriction of the bar and greater postorbital overlap posteriorly as is typical in Permian dicynodontoids. Although small skulls of *Dicynodon lacerticeps* generally have a greater degree of postorbital-parietal overlap than is depicted for *D. luckhoffi*, without the specimen for reference it is uncertain whether this morphology has been influenced by postmortem deformation or weathering. As such, we cannot refer this specimen to *Dicynodon lacerticeps*, *Basilodon woodwardi*, or *Sintocephalus alticeps* with any confidence, and must consider it a nomen dubium unless the holotype is rediscovered.

Dicynodon lutriceps Broom, 1912b

Holotype—AMNH FARB 5501, a poorly preserved, dorsoventrally crushed skull missing the temporal arches (Fig. 79).

Locus Typicus—Kuilspoort, Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1912b) described *Dicynodon lutriceps* on the basis of a poorly preserved skull missing the temporal arches and the tip of the snout from Kuilspoort. Without making any explicit comparisons to other species, he distinguished *D. lutriceps* on the basis of its relatively short snout, broad and concave frontal region, and flattened intertemporal region, with the parietals mostly covered by the postorbitals. Broom (1912b) also referred an isolated maxilla from the same locality to this species. Keyser (1975) synonymized this species with *Oudenodon bainii*, a referral followed by subsequent authors (e.g., King, 1988) and supported here. Given that the anterior region of the snout is missing in the holotype, it is difficult to justify Broom's proportional distinction from other dicynodonts, and in all other regards this is a typical specimen of *O. bainii*.

Dicynodon maccabei Broom, 1940b

Holotype—RC 52, a laterally compressed skull missing the left temporal arch and much of the premaxillary region (Fig. 80).

Locus Typicus—St. Olives, Graaff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

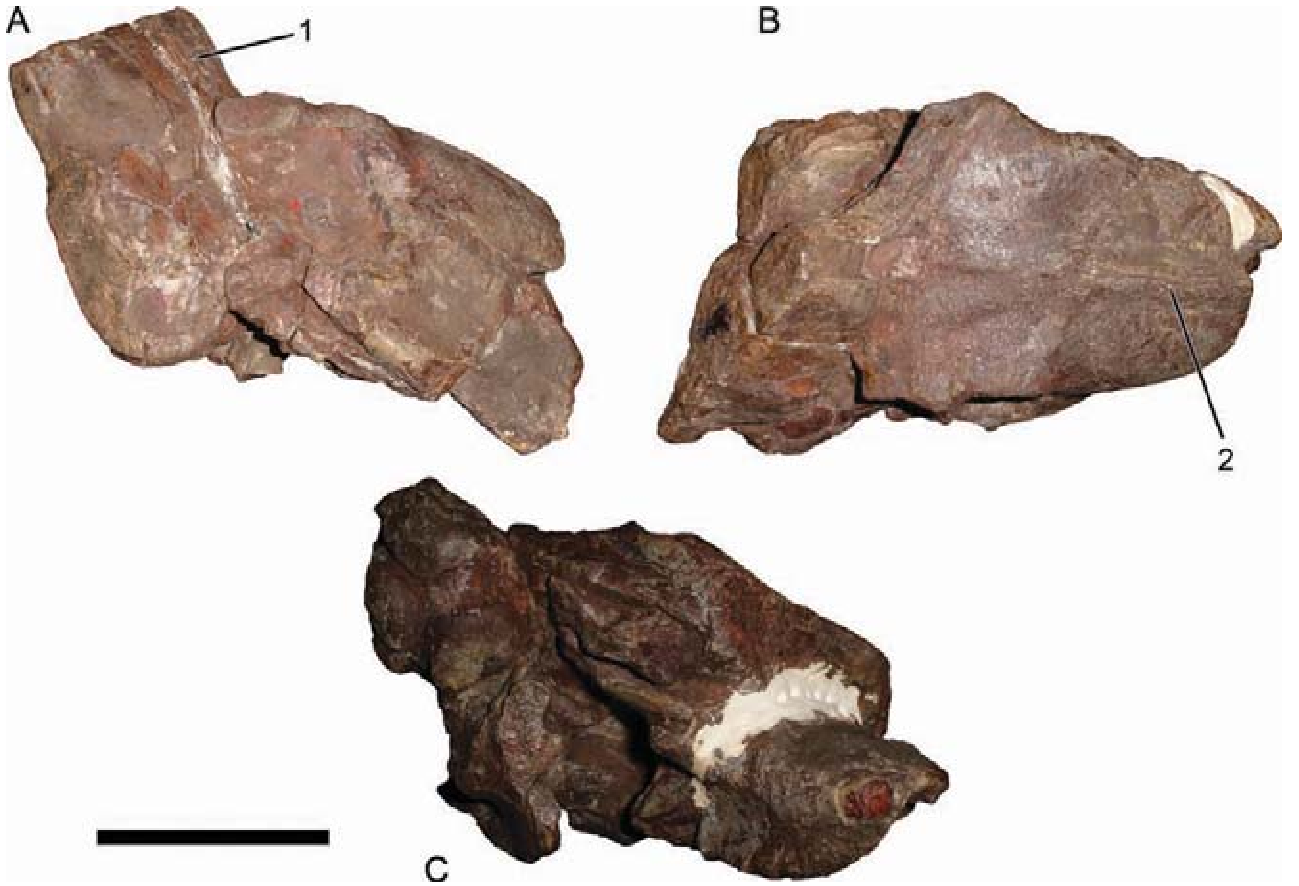

FIGURE 67. AMG 4799, the holotype of *Dicynodon latifrons* (= *Kannemeyeria simocephala*), in right lateral (**A**), dorsal (**B**), and palatal (**C**) views. This specimen can be identified as *Kannemeyeria* on the basis of its (1) steeply angled sagittal crest, at a plane above that of the snout (this has probably been exaggerated in this specimen due to anteroposterior compression), and (2) swollen nasals forming a median ridge. Scale bar equals 10 cm.

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1940b) distinguished *Dicynodon maccabei* by its remarkably small, narrow preparietal. No comparisons were made to other species of *Dicynodon*. Keyser (1975) synonymized this species with *Oudenodon bainii*, noting that the proportions described for this species were heavily influenced by taphonomic distortion. He did not address preparietal shape, but this character is highly variable within most dicynodont species (Toerien, 1953). Brink (1986) and King (1988) also list this species in the synonymy of *O. bainii*, and this synonymy is accepted here.

Dicynodon macrodon Broom, 1940a

Holotype—RC 22, a laterally crushed skull missing the temporal arches (Fig. 81).

Locus Typicus—Groot Driefontein, Murraysburg, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dinanomodon gilli* (Broom, 1932).

Remarks—As indicated by its name, Broom (1940a) considered the most distinctive feature of *Dicynodon macrodon* to be its elongate tusks. He distinguished this species from *Dicynodon mustoi* by the larger preparietal and less exposed parietals and from *Dicynodon lissops* by the narrower snout and presence of dorsal exposure of the postfrontal. Haughton and Brink (1954), Kitching (1977), Cluver and Hotton (1981), and King (1988) listed *D. macrodon* as a valid species, whereas Brink (1986) listed it as a synonym of *Dicynodon lacerticeps*. The intertemporal bar of RC 22 is similar to that of *D. lacerticeps* (short but with nearly complete postorbital-parietal overlap), but in very small specimens the intertemporal bar morphology of most Permian dicynodontoids is indistinguishable. RC 22 has several features that are dissimilar to the typical condition in *D. lacerticeps* but are consistent with *Dinanomodon*, such as an elongate, triangular snout with sharply hooked premaxilla and strongly ventrally directed caniniform process. The presence of an elongate dorsal process of the premaxilla nearing an anterior process of the frontals in RC 22 lends further support to this identification, and *D. macrodon* should be added to the synonymy of *Dinanomodon gilli*.

Dicynodon macrorhynchus Broom, 1921

Holotype—NHMUK R4954, a poorly preserved, strongly dorsoventrally crushed skull still mostly encased in matrix (Fig. 82).

Locus Typicus—New Bethesda, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

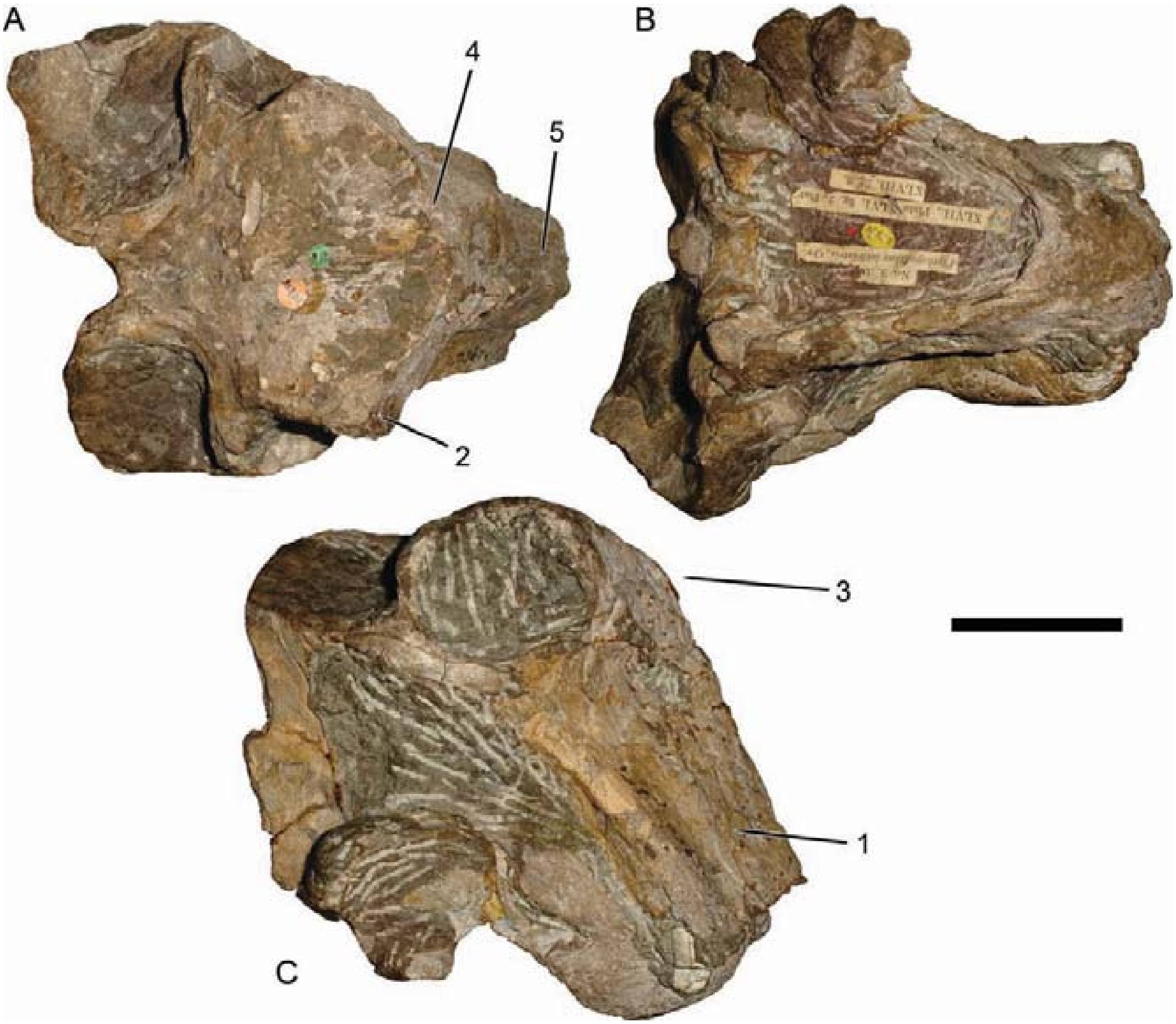

FIGURE 68. NHMUK 36222, the holotype of *Dicynodon latirostris* Owen (= *Lystrosaurus declivis*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a lystrosaurid by the (1) tall, strongly deflected snout and (2) well-developed prefrontal bosses and as *L. declivis* by the combination of the (3) biplanar snout profile, with a distinct break between the frontal and nasal-premaxillary planes of the skull, (4) transverse ridge running between the prefrontals, (5) median ridge on the dorsal surface of the premaxilla, and the absence of postorbital bosses. Scale bar equals 5 cm.

Remarks—Broom (1921) initially considered that NHMUK R4954 could represent a juvenile specimen of *Dicynodon platyceps* (= *Oudenodon bainii*), but named it as a new species based on its unusually long orbit and snout relative to the postorbital region. He noted that this specimen possesses a median snout boss, as in *Dicynodon sollasi* (= *Diictodon feliceps*). Cluver and Hotton (1981) transferred this species to *Diictodon* (see also King, 1988), and Brink (1986) and Sullivan and Reisz (2005) considered it synonymous with *Diictodon feliceps*. NHMUK R4954 is a small (5.7 cm dorsal length), badly distorted skull, with the dorsal surface sheared leftwards and much of the right side broken. The occiput and much of the left side of the skull are still embedded in matrix. No tusks are present. Based on the presence of a precaniniform notch, lack of postcanines, median nasal boss, and posterior overlap of the parietals by the postorbitals on the intertemporal bar, this specimen can indeed be identified as a specimen of *Diictodon feliceps*.

Dicynodon magnus (Owen, 1876)

Holotype—NHMUK 36252, a weathered skull missing the right zygomatic arch (Fig. 83).

Locus Typicus—Brakrivier, Fort Beaufort, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Valid as *Rhachiocephalus magnus* (Owen, 1876).

Remarks—Owen (1876) named *Oudenodon magnus* as the largest known tuskless dicynodont from South Africa. Seeley (1898) split *Oudenodon* into two subgenera, *Aulacocephalus* (with the type species of *Oudenodon*, *O. bainii*, as type) and *Rhachiocephalus* (with *O. magnus* as type). *Rhachiocephalus* was

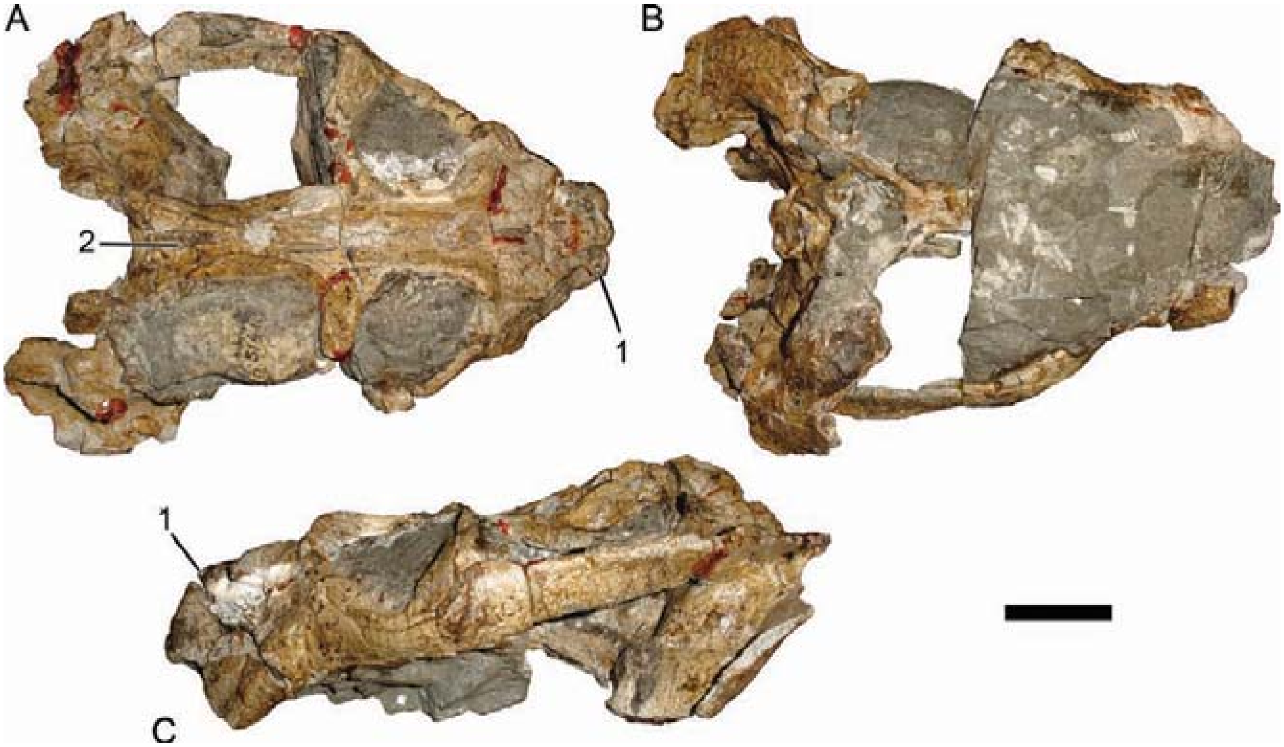

FIGURE 69. SAM-PK-5141, the holotype of *Dicynodon latirostris* Broom (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

established to accommodate the 'prognathous' species of *Oudenodon*: *O. magnus*, *O. greyii*, *O. prognathus*, and *O. brevirostris*. Seeley's subgeneric classification was largely ignored at the time, and the species he assigned to *Rhachiocephalus* were treated as 'standard' *Oudenodon* by subsequent authors (a legitimate approach in the case of *O. greyii*, *O. prognathus*, and *O. brevirostris*, all of which are currently [King, 1988] considered junior synonyms of *O. bainii*). Broom (1913c) recognized the similarity between his new taxon *Eocyclops longus* and *Oudenodon magnus*, but did not take any taxonomic action regarding the latter. Broom (1913a) transferred all nominal species of *Oudenodon* to *Dicynodon* (creating, among many others, the new combination *Dicynodon magnus*), as he thought the former genus was merely the female of the latter. Haughton (1917) described a new, well-preserved skull referred to *Eocyclops longus* (SAM-PK-3425, later made the holotype of *Megacyclops whaitsi* by Broom [1931]) and argued that this taxon was not generically separable from "*O*." *magnus*, creating the new combination *Eocyclops magnus*. Broom (1932) resurrected Seeley's (1898) subgenera *Aulacephalodon* (albeit misspelled '*Aulacocephalodon*') and *Rhachiocephalus* to refer to *Dicynodon bainii* and *D. magnus* (respectively), although he retained *Eocyclops* to refer to *E. longus*. Keyser (1975) recognized *Rhachiocephalus magnus* as a valid taxon, and argued that all giant, tuskless Late Permian dicynodont specimens are probably referable to this taxon, although Kitching (1977) argued for the distinction of *Platycyclops*. More recently, Maisch (2002b) considered the type species of *Platycyclops* (*P. haughtoni* Broom, 1932) to be synonymous with *Rhachiocephalus magnus*, but separated some of the nominal species of *Platycyclops* as the new genus *Kitchinganomodon*. NHMUK 36252, the holotype of *Rhachiocephalus magnus*, is weathered, poorly prepared, and somewhat dorsoventrally crushed, but exhibits many diagnostic features for the species: the massive, anteriorly directed pineal boss and strongly ossified braincase are characteristic of rhachiocephalids and the narrow, triangular snout, elongate, confluent nasal and prefrontal bosses, and narrow anterior pterygoid rami clearly differentiate it from *Kitchinganomodon*.

Dicynodon magnus (Sun, 1978)

Holotype—IVPP V4694, a dorsoventrally crushed partial skull preserving part of the interorbital region, intertemporal bar, and occiput.

Locus Typicus—Dongxiaolongkou, Xinjiang, China.

Horizon—Guodikeng Formation (Upper Permian).

Status—Junior subjective synonym of *Turfanodon bogdaensis* Sun, 1973.

Remarks—Sun (1978) described *Striodon magnus* as a large new dicynodont characterized by a wide, low occiput, long, narrow intertemporal bar, and large pineal foramen within a depressed portion of the skull roof. King (1988) noted that this species might be referable to *Dicynodon*, but that the holotype was too incomplete to be certain. Lucas (1998a) transferred this species to *Dicynodon*, but later (Lucas, 2001) considered it a nomen dubium because of the incomplete type skull. The elongate, narrow intertemporal bar of IVPP V4694, with nearly complete postorbital-parietal overlap, is typical of Permian dicynodontoids, and is similar in both taxa of Chinese Permian dicynodontoids herein recognized as valid (*Jimusaria sinkianensis* and *Turfanodon bogdaensis*: in both taxa the intertemporal bar is longer and narrower than in *Dicynodon lacerticeps* of similar size

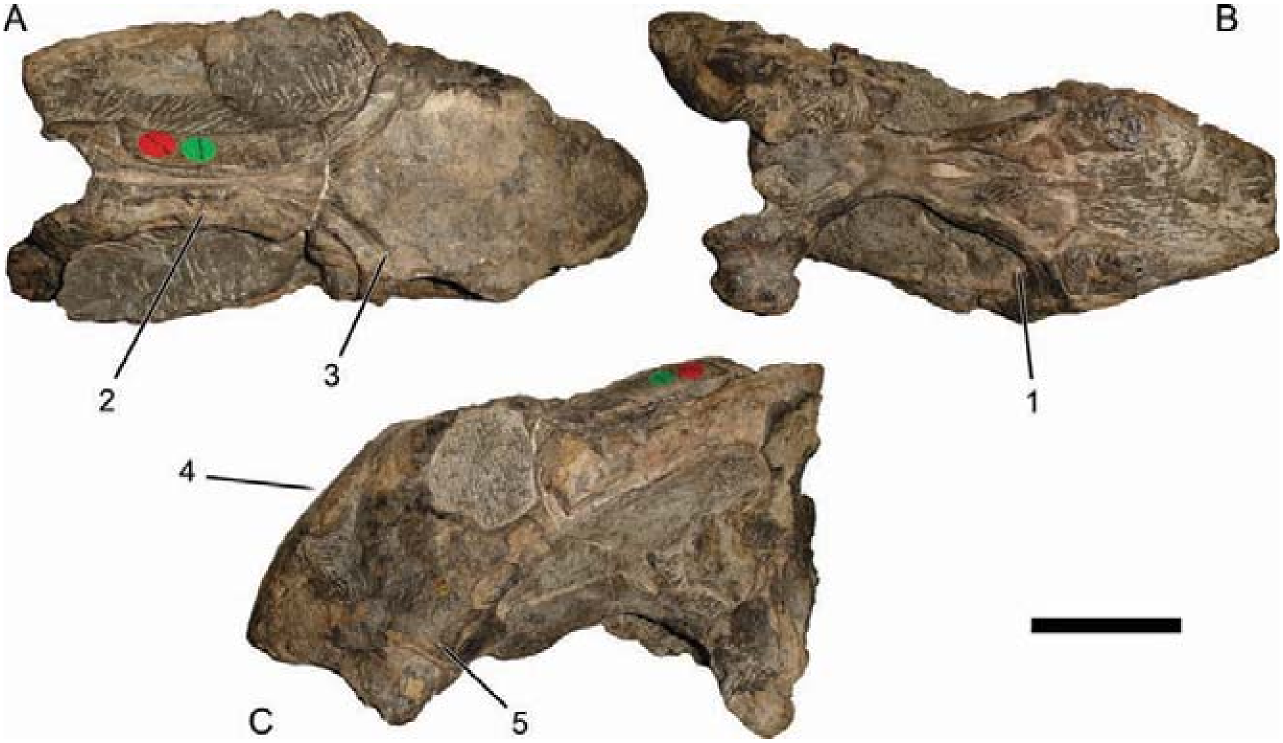

FIGURE 70. NHMUK 47047, the holotype of *Dicynodon leoniceps* (= *Daptocephalus leoniceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. *Daptocephalus leoniceps* can be distinguished from other dicynodontoids by the combination of a (2) long, extremely narrow intertemporal bar with nearly complete postorbital-parietal overlap, (3) thin, strap-like postfrontal, (4) steeply sloping snout profile, and (5) ventrally directed caniniform process. Scale bar equals 10 cm.

but shorter than in *Daptocephalus leoniceps* or *Dinanomodon gilli*). Of the two Chinese taxa, *Turfanodon bogdaensis* shares with *Striodon magnus* a depression of the skull roof in which the pineal foramen is situated; in the absence of any substantive characters distinguishing these species, they should be considered synonyms. The proportional differences in the occiput between the holotypes of *Striodon magnus* (IVPP V4694) and *Turfanodon bogdaensis* (IVPP V3241) (wide and low in the former, narrow and tall in the latter) can be attributed to different styles of taphonomic deformation—dorsoventral crushing in IVPP V4694 and lateral crushing in IVPP V3241.

Dicynodon marlothi (Broili and Schröder, 1936)

Holotype—BSP 1935 VIII 32, a complete, somewhat dorsoventrally crushed skull and partial lower jaw (Fig. 84).

Locus Typicus—Zuurplaas, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broili and Schröder (1936) characterized *Oudenodon marlothi* on the basis of the long, low skull, short snout, and well-developed caniniform process of the type skull. Von Huene (1940) included this species in the genus *Dicynodon* in his list of '*Cistecephalus*-Zone' tetrapods. Keyser (1975:53) noted that the "possibility of the name *Oudenodon marlothi* being synonymous with *Oudenodon baini* Owen deserves serious consideration." Brink (1986) and King (1988) listed this species as a junior synonym of *O. bainii*, and this approach is followed here. BSP 1935 VIII 32 is a well-preserved and nearly complete skull (some of the interorbital region and right palate are reconstructed with plaster) showing all the diagnostic features of *O. bainii*.

Dicynodon megalops (Owen, 1876)

Holotype—NHMUK 47061, a very poorly preserved, weathered skull missing parts of the temporal arches and snout (Fig. 85).

Locus Typicus—Steilkrans, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Owen (1876) distinguished *Oudenodon megalops* from other species of the genus by its large orbits with raised rims. Seeley (1898) included *O. megalops* in his subgenus *Aulacocephalus* along with the type species of *Oudenodon*, *O. bainii*. Broom (1913a) transferred this (and all other) species of *Oudenodon* to *Dicynodon*, although van Hoepen (1934) continued to recognize it as a valid species within *Oudenodon*. Keyser (1975) synonymized this species with *O. bainii*, and this synonymy has been recognized by all subsequent studies (e.g., Brink, 1986; King, 1988). NHMUK 47061 is a nearly complete but very poorly preserved skull. Most of the surface bone on the snout is missing, leaving a cast of the nasal passage beneath. The zygomatic arches, intertemporal bar, and premaxilla are broken off at the edges. Although the caniniform processes are broken off at their tips, their posterior portions are reasonably complete and demonstrate the lack of tusks and presence of postcaniniform crests in this specimen. The palatal region as a whole is badly damaged, but it is evident that the interpterygoid vacuity is relatively long for a dicynodont and the palatines are moderately rugose (source of the

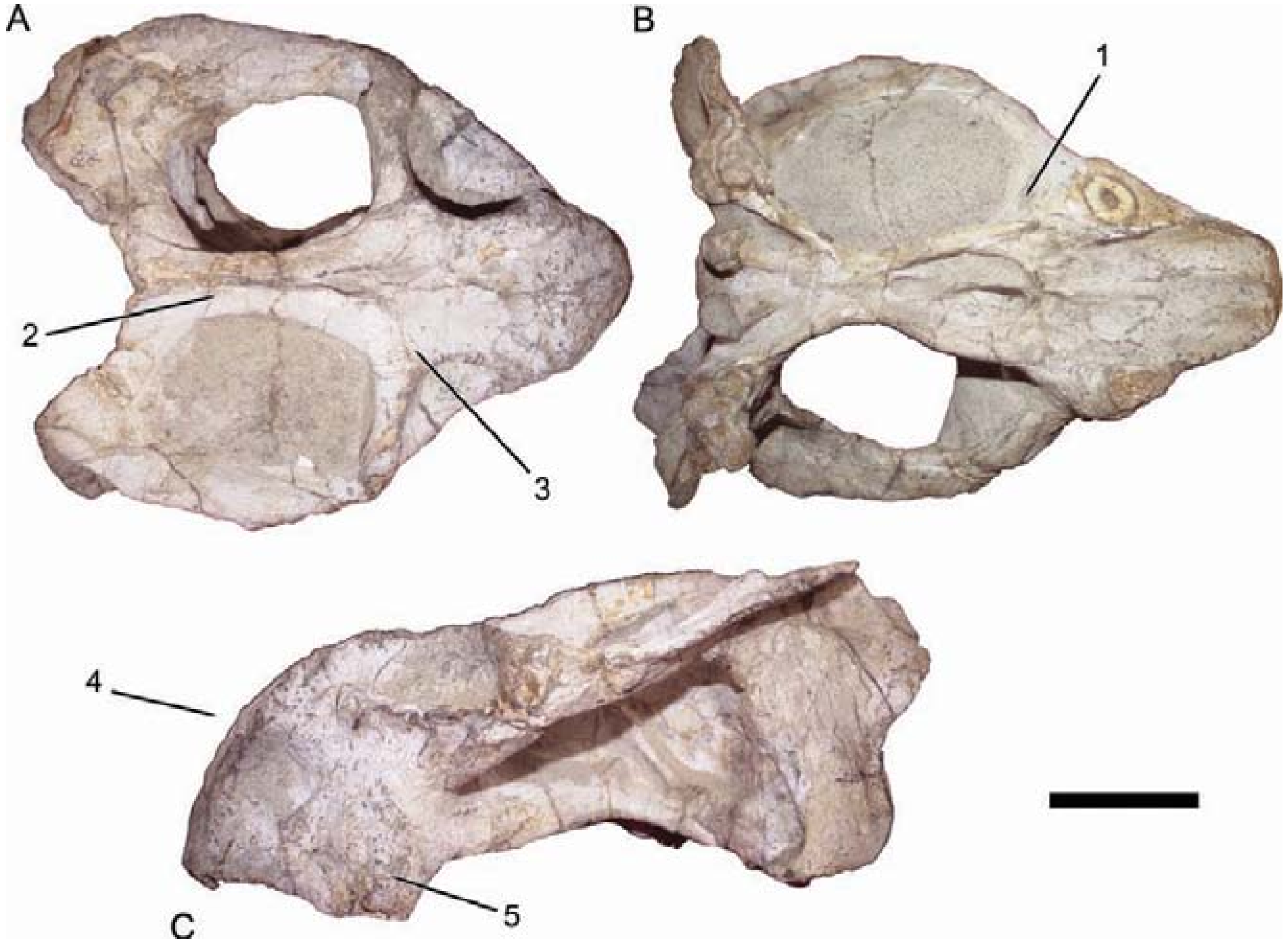

FIGURE 71. RC 96, the holotype of *Dicynodon leontocephalus* (= *Daptocephalus leoniceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *D. leoniceps* on the basis of the (2) long, extremely narrow intertemporal bar with nearly complete postorbital-parietal overlap, (3) thin, strap-like postfrontal, (4) steeply sloping snout profile, and (5) ventrally directed caniniform process. Scale bar equals 10 cm.

supposed 'palatine teeth' refuted by Broom [1912a]). Despite the poor quality of this specimen, enough parts of the skull are preserved to allow for a confident identification. The postcaniniform crests indicate that NHMUK 47061 is a cryptodont, the long interpterygoid vacuity indicates that it is an oudenodontid, and the total absence of dentition and short snout proportions indicate that it is a specimen of *Oudenodon bainii*.

Dicynodon megalorhinus (Broom, 1904b)

Holotype—SAM-PK-640, a poorly preserved skull missing the lower left portion of the snout (Fig. 86).

Locus Typicus—Prince Albert Road, Prince Albert, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Nomen dubium (*Emydops* sp.).

Remarks—Broom (1904b) described SAM-PK-640 as a new species of *Oudenodon*, *O. megalorhinus*, characterized by its relatively long snout and short temporal region compared to other species of the genus. Broom (1913a) transferred this species to *Dicynodon* as part of his synonymization of *Oudenodon* with that genus. Van Hoepen (1934) recognized that SAM-PK-640 was dissimilar from both *Oudenodon* and *Dicynodon*, and made it the type species of the new genus *Orophicephalus*, which also included *Dicynodon microrhynchus* and *Dicynodon pygmaeus* (both considered junior synonyms of *Pristerodon mackayi* herein). Toerien (1953), Haughton and Brink (1954), and King (1988) listed *D. megalorhinus* as a valid species of *Dicynodon*, but Brink (1986) considered it a synonym of *Diictodon feliceps*. SAM-PK-640 is a small, poorly preserved skull showing no diagnostic features of *Dicynodon lacerticeps*, *Oudenodon bainii*, or *Diictodon feliceps*. Rather, the embayment of the palatal rim anterior to the caniniform process, squared-off profile of occiput, and wide intertemporal region with broadly exposed parietals allow this specimen to be identified as *Emydops*. This specimen provides further evidence for the first appearance of *Emydops* in the *Tapinocephalus* AZ (Angielczyk et al., 2005a). In its current state, it is impossible to determine whether SAM-PK-640 represents a specimen of *Emydops arctatus* or *Emydops oweni*. Additional preparation will be required to identify species-specific characters in SAM-PK-640.

Dicynodon microdon Broom, 1936

Holotype—TM 267, a complete skull, somewhat weathered ventrally (Fig. 87).

Locus Typicus—Bethesda Road, Graaff-Reinet, South Africa.

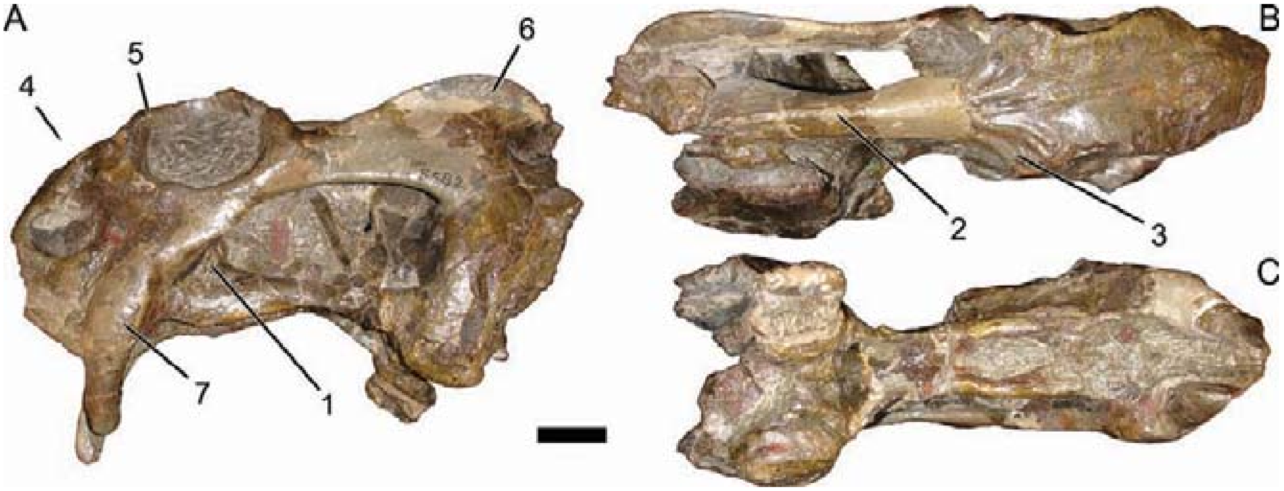

FIGURE 72. AMNH FARB 5582, the holotype of *Dicynodon leontops* (= *Daptocephalus leoniceps*), in left lateral (**A**), dorsal (**B**), and palatal (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *D*. *leoniceps* on the basis of the (2) long, extremely narrow intertemporal bar with nearly complete postorbital-parietal overlap, (3) thin, strap-like postfrontal, (4) steeply sloping snout profile, (5) rims around the orbits, (6) broadly rounded dorsal margin of the squamosal in lateral view, and (7) ventrally directed caniniform process. Scale bar equals 5 cm.

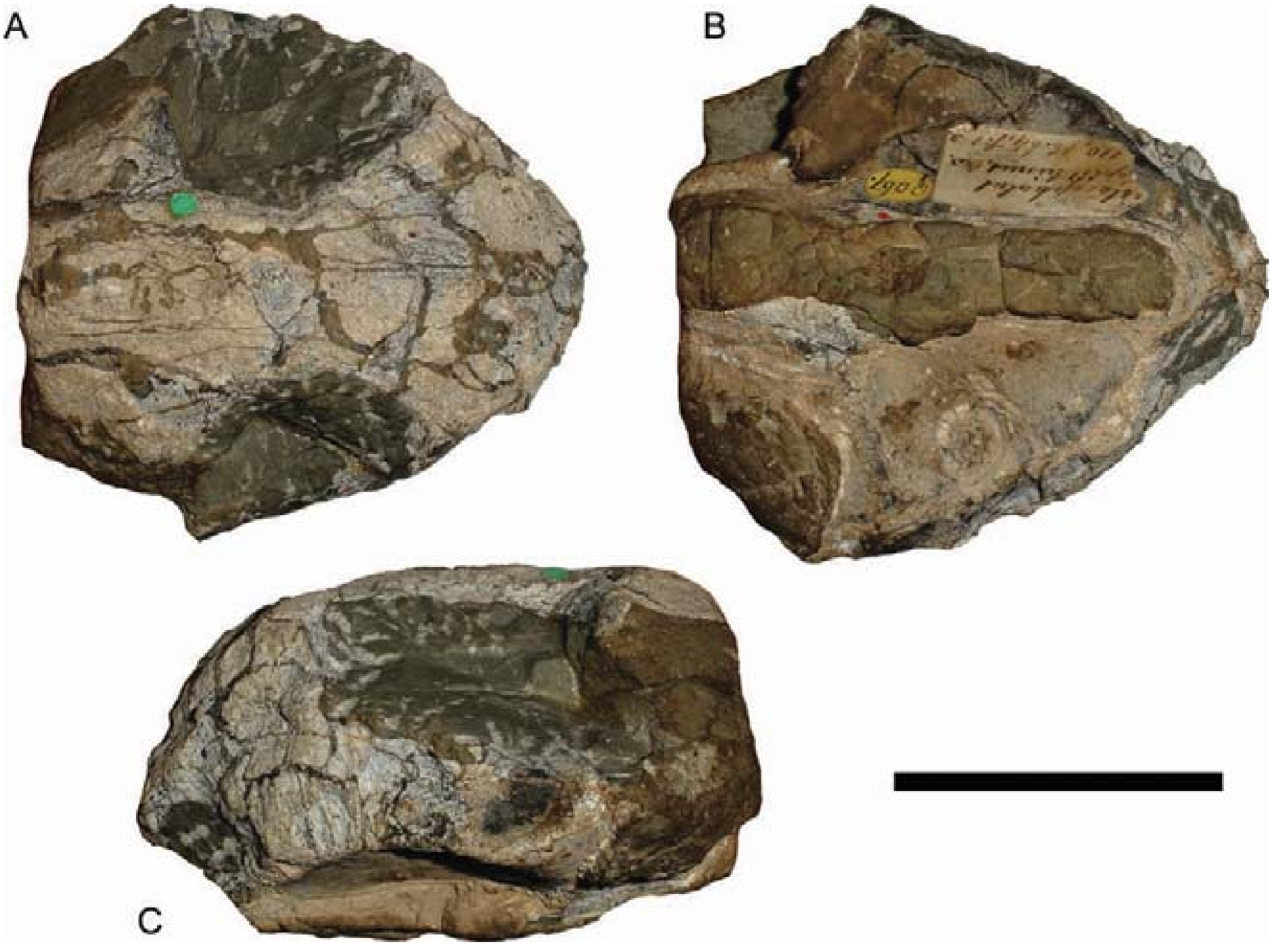

FIGURE 73. NHMUK 47067, the holotype of *Dicynodon leptorhinus* (*Kistecephalus leptorhinus*, *Baiopsis leptorhinus*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This poorly preserved specimen cannot be identified beyond Dicynodontia indet. Scale bar equals 5 cm.

FIGURE 74. AMG 407, the holotype of *Dicynodon leptoscelus* (*Dicranozygoma leptoscelus*) (**A**), a natural sandstone mold, and a cast made from this specimen (**B**). This fragmentary skeleton cannot currently be identified beyond Dicynodontia indet., although the shape of the squamosal suggests that this may be a cryptodont. Scale bar equals 10 cm.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Basilodon woodwardi* (Broom, 1921).

Remarks—Broom (1936) described *Dicynodon microdon* based on a slightly dorsoventrally compressed skull showing a very small canine root. Haughton and Brink (1954), Kitching (1977), Cluver and Hotton (1981), and King (1988) listed *D. microdon* as a valid species, although Brink (1986) considered it a synonym of *Dicynodon lacerticeps*. TM 267 is dissimilar from the typical *Dicynodon lacerticeps* morphotype: in *D. lacerticeps* specimens of similar size there is nearly complete postorbital-parietal overlap, whereas the parietal is exposed for the length of the intertemporal bar in TM 267. Also, all like-sized *D. lacerticeps* specimens have large, fully erupted tusks, although the possibility that this condition is pathological in TM 267 cannot be discounted. Finally, TM 267 lacks the characteristic tall, acutely angled lateral rami of the squamosal of *D. lacerticeps*. TM 267 is extremely similar to the holotype of *Dicynodon calverleyi* (RC 39), a specimen referred to *Basilodon woodwardi* herein. Diagnostic features of *B. woodwardi* exhibited by TM 267 include triangular depressions on the dorsal surface of the postorbital contribution to the postorbital bar and a broad intertemporal bar with extensive exposure of the parietals.

Dicynodon microrhynchus von Huene, 1931

Holotype—GPIT unnumbered, a poorly preserved skull (missing the zygomatic arches) and lower jaws (Fig. 88).

Locus Typicus—Kuilspoort, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Pristerodon mackayi* Huxley, 1868.

Remarks—Von Huene (1931) described *Dicynodon microrhynchus* on the basis of a small skull missing both temporal arches, and characterized this taxon by its very short snout. Van Hoepen (1934) included *D. microrhynchus* in the new genus *Orophicephalus* with *Dicynodon megalorhinus* (= *Emydops* sp.) and *Dicynodon pygmaeus* (= *Pristerodon mackayi*). King (1988) transferred this species to *Pristerodon* based on the leaf-shaped palatines, but Keyser (1993) considered it a nomen dubium based on the poor preservation of the holotype. Although the holotype of *D. microrhynchus* is poor, it preserves the most important diagnostic features of *Pristerodon* (leaf-shaped palatine pads, prominent, horizontal lateral dentary shelf, oblique row of multiple postcanine teeth). *Dicynodon microrhynchus* exhibits no unique characters that would distinguish it from *Pristerodon mackayi*.

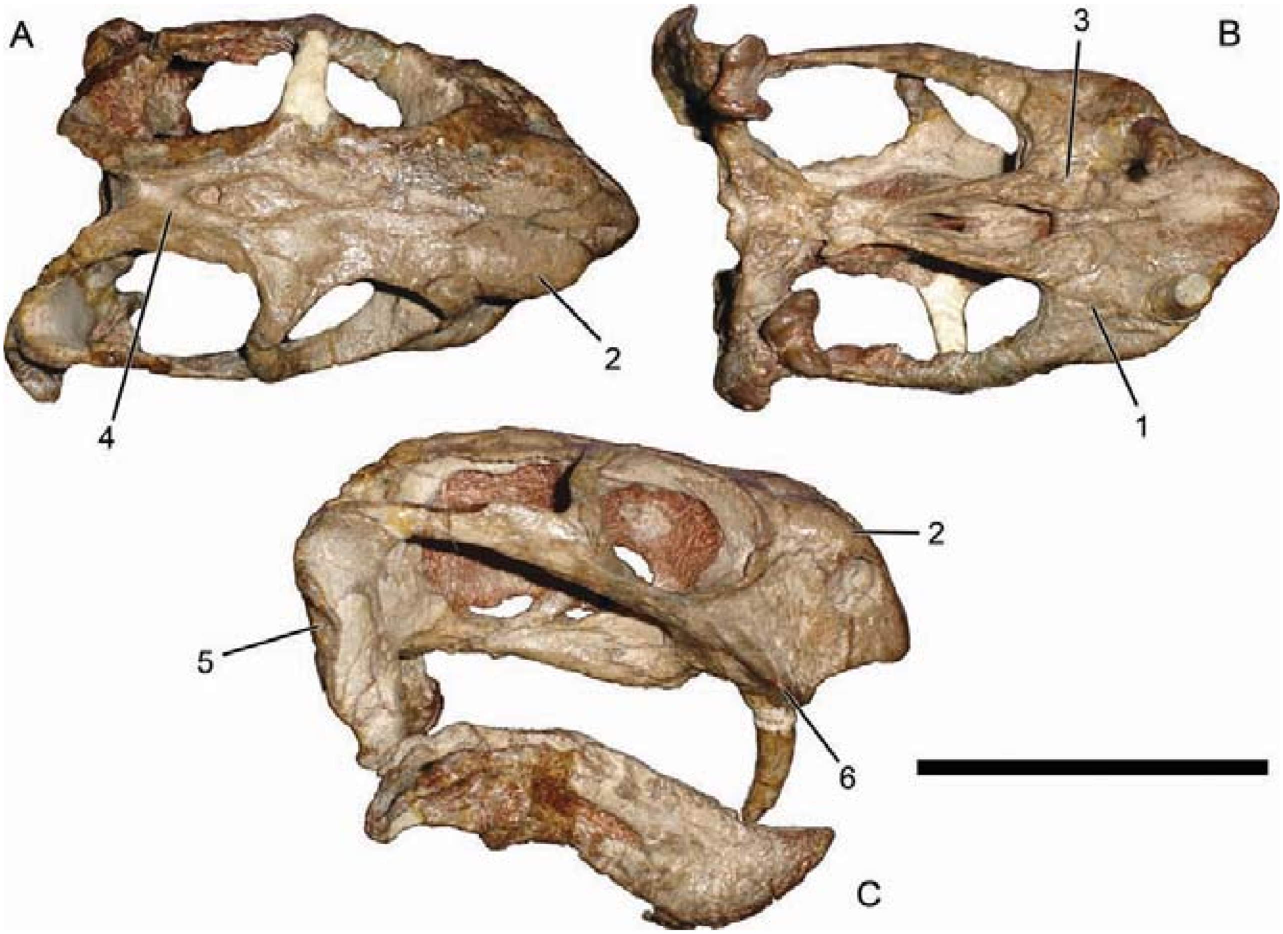

FIGURE 75. IVPP V7940, the holotype of *Dicynodon limbus* (= *Daqingshanodon limbus*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest, (2) paired nasal bosses overhanging the external nares, and (3) palatal surface of the palatine with a smooth anterior section flush with the secondary palate and a rugose, raised posterior section. *Daqingshanodon limbus* can be distinguished from *Keyseria benjamini* by the (4) relatively narrower intertemporal bar, with posterior constriction, and from all other dicynodonts by the (5) anterior curl of the quadrate ramus of the squamosal at midheight and (6) sharp ridge running anteroventrally from below orbit along the lateral surface of the caniniform process. Scale bar equals 5 cm.

Dicynodon microtrema Seeley, 1889

Holotype—NHMUK R868, an occiput (Fig. 89).

Locus Typicus—Tafelberg, Beaufort West, South Africa.

Horizon—?*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Tropidostoma dubium* (Owen, 1876).

Remarks—Refer to the entry on *Dicynodon dunnii* for information on this species.

Dicynodon milletti Broom, 1928

Holotype—MMK 4164, a dorsoventrally compressed skull (missing the left zygomatic arch), lower jaws (Fig. 90), and associated postcranial elements.

Locus Typicus—Sekretariskraal, Murraysburg, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1928) considered MMK 4164 to represent an animal very similar to *Dicynodon andrewsi* (= *Oudenodon bainii*), but described it as a new species (*Dicynodon milletti*) because it was found lower in section than the holotype of *D. andrewsi*. He also stated that *D. milletti* could be diagnosed by the acute angle between the skull roof and occipital plane. Van Hoepen (1934) included *D. milletti* in '*Aulacocephalodon*' (= *Aulacephalodon*) because of the broad skull and prominent nasal bosses of MMK 4164, despite the fact that it lacks tusks. Keyser (1975) synonymized *D. milletti* with *Oudenodon bainii*, noting that the apparent breadth of the skull and the sharp angle between skull roof and occiput are both artifacts of the intense dorsoventral compression this specimen has suffered. Subsequent studies (e.g., Brink, 1986; King, 1988) have upheld this synonymy, and it is maintained here.

Dicynodon moschops Broom, 1913c

Holotype—AMNH FARB 5325, a well-preserved skull missing the left squamosal (Fig. 91).

Locus Typicus—Oudeberg, Graaff-Reinet, South Africa.

Horizon—Probably *Dicynodon* Assemblage Zone (Upper Permian).

Status—Valid as *Pelanomodon moschops* (Broom, 1913c).

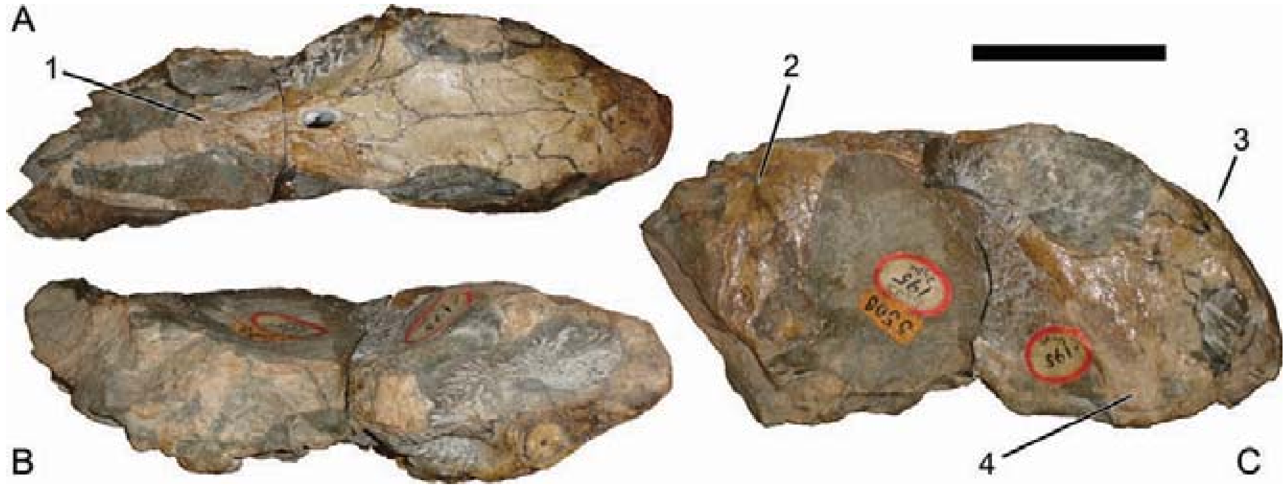

FIGURE 76. AMNH FARB 5508, the holotype of *Dicynodon lissops* (= *Daptocephalus leoniceps*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as *D. leoniceps* on the basis of the (1) long, extremely narrow intertemporal bar with nearly complete postorbital-parietal overlap, (2) broadly rounded dorsal margin of the squamosal in lateral view, (3) steeply sloping snout profile, and (4) ventrally directed caniniform process. Scale bar equals 5 cm.

Remarks—Broom (1913c) described *Dicynodon moschops* on the basis of a nearly complete, well-preserved skull missing only the left squamosal from Oudeberg. Broom distinguished *D. moschops* from other *Dicynodon* species by its extremely robust skull, ventrally angled snout (similar to but less extreme than the condition in *Lystrosaurus*), and flattened nasal bosses. Broom (1932) and van Hoepen (1934) included this species in '*Aulacocephalodon*' (= *Aulacephalodon*) because of similar skull proportions and strong development of the nasal bosses. Broom (1938) named a new genus, *Pelanomodon*, to refer to specimens

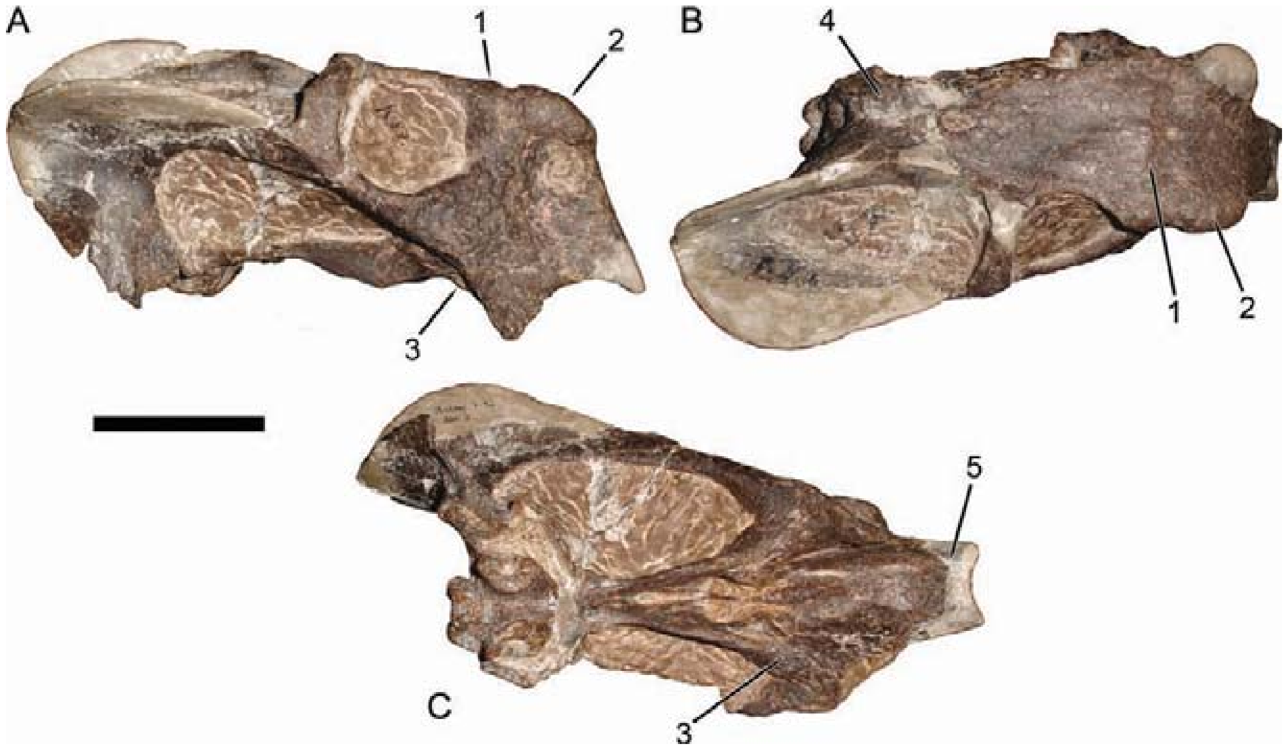

FIGURE 77. GPIT/RE/7186, the holotype of *Dicynodon locusticeps* (= *Geikia locusticeps*), in right lateral (**A**), dorsal (**B**), and ventral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (2) paired nasal bosses on the posterodorsal margins of the external nares and (3) postcaniniform crest, and as a geikiine on the basis of the (1) transverse snout ridge at the level of the prefrontals and (4) parietal exposure on the skull roof. This specimen can be identified as *Geikia* rather than *Aulacephalodon* or *Pelanomodon* on the basis of the (5) squared-off snout. Additionally, this specimen lacks a median ridge on the anterior surface of the snout, a cryptodontian synapomorphy that is present in other geikiids but absent in *Geikia*. Scale bar equals 5 cm.

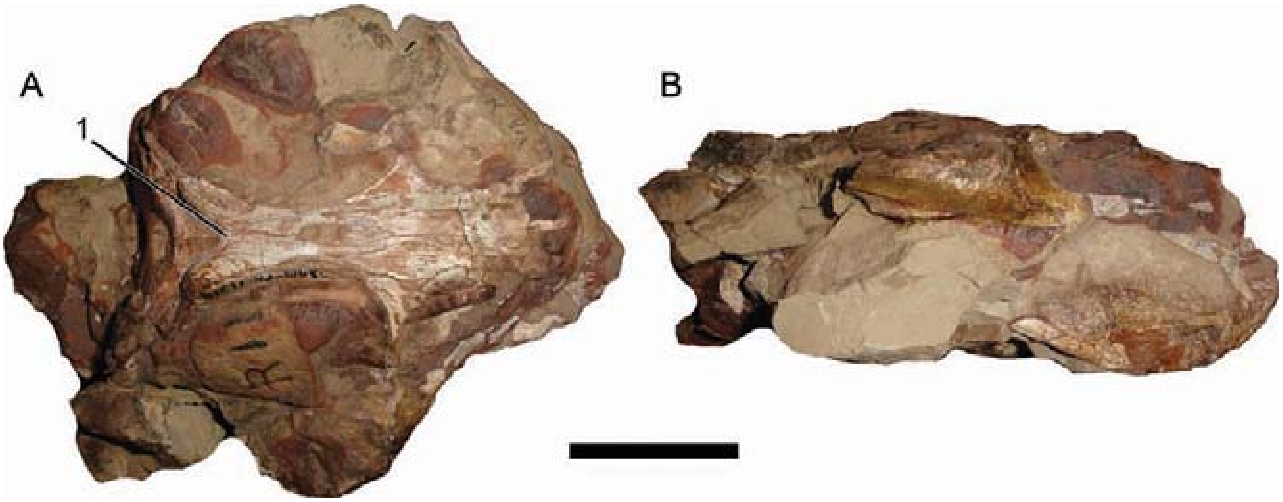

FIGURE 78. SAM-PK-11310, the holotype of *Dicynodon luangwanensis* (= *Oudenodon bainii*), in dorsal (**A**) and right lateral (**B**) views. This specimen is incompletely prepared, but it can be identified as an oudenodontid on the basis of the (1) postparietal contribution to the skull roof and as *O. bainii* on the basis of the lack of tusks. Scale bar equals 5 cm.

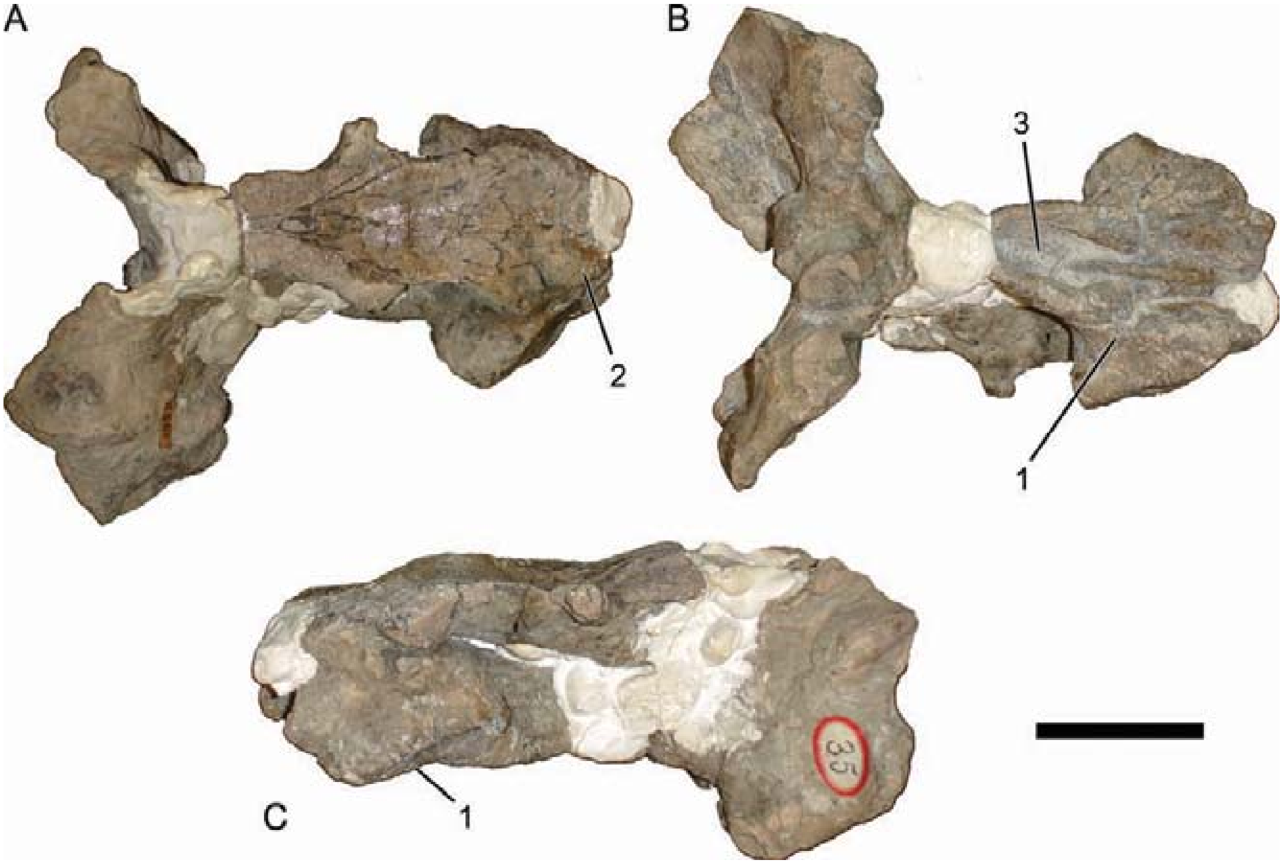

FIGURE 79. AMNH FARB 5501, the holotype of *Dicynodon lutriceps* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks. Scale bar equals 5 cm.

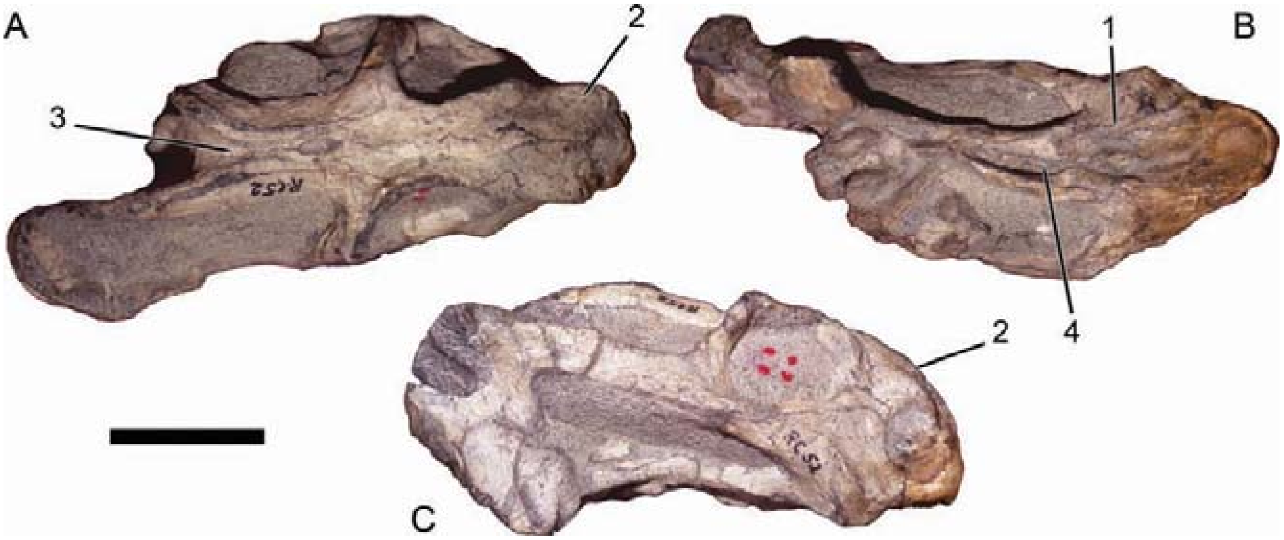

FIGURE 80. RC 52, the holotype of *Dicynodon maccabei* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

with an *Aulacephalodon*-like skull but lacking tusks. In addition to describing the new species *P. rubidgei* (type species of *Pelanomodon*), Broom transferred *D. moschops* to the new genus. Recent reviews of Permian dicynodonts (e.g., King, 1988) have retained *P. rubidgei* and *P. moschops* as separate species. The alpha taxonomy of geikiine cryptodonts remains a lingering problem for Permian dicynodont systematics. Although the monospecificity of *Aulacephalodon* is generally agreed upon and well supported by morphometric analyses (Tollman et al., 1981; although the synonymy of the aberrant *Aulacephalodon peavoti* with the type species *A. bainii* requires reinvestigation), the number of tuskless geikiine species is far less certain. The two species of *Pelanomodon* have traditionally been separated based on differences in size and shape of the snout bosses. Snout boss (nasal and prefrontal bosses) morphology is intraspecifically variable in some dicynodont species (e.g., *Oudenodon bainii*), but

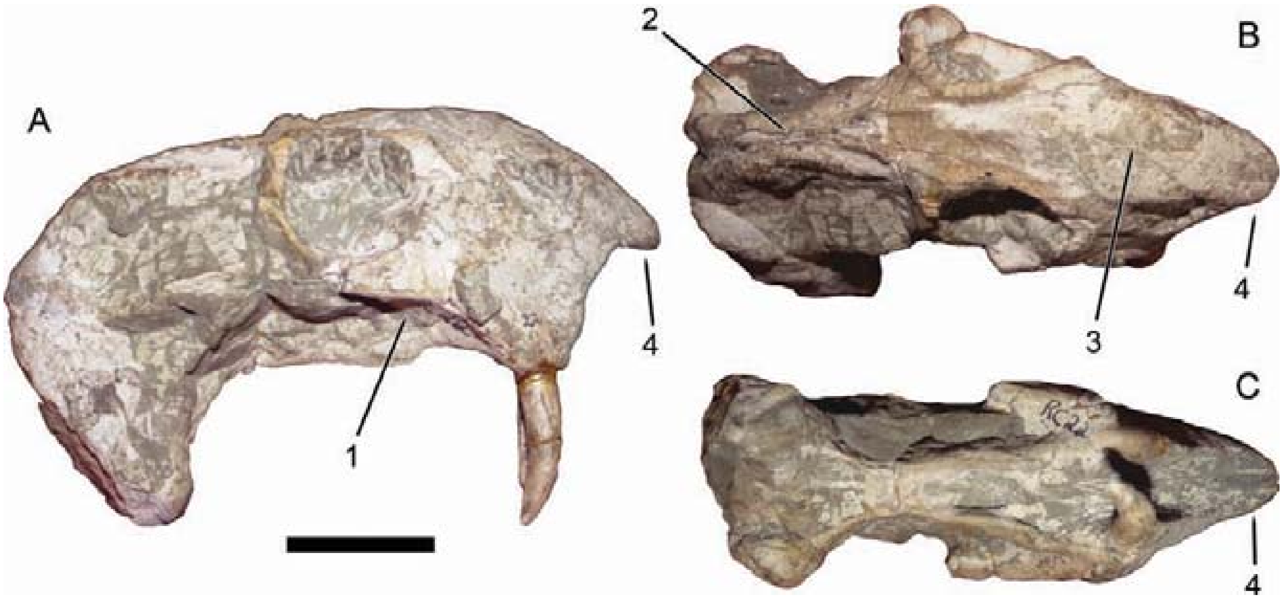

FIGURE 81. RC 22, the holotype of *Dicynodon macrodon* (= *Dinanomodon gilli*), in right lateral (**A**), dorsal (**B**), and palatal (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *Dinanomodon* on the basis of the (2) extremely narrow intertemporal bar, with closely appressed postorbitals almost completely overlapping the parietals, (3) elongate ascending process of the premaxilla nearly contacting an anterior process of the frontals, and (4) the elongate, sharply ‘hooked’ premaxillary tip. Scale bar equals 5 cm.

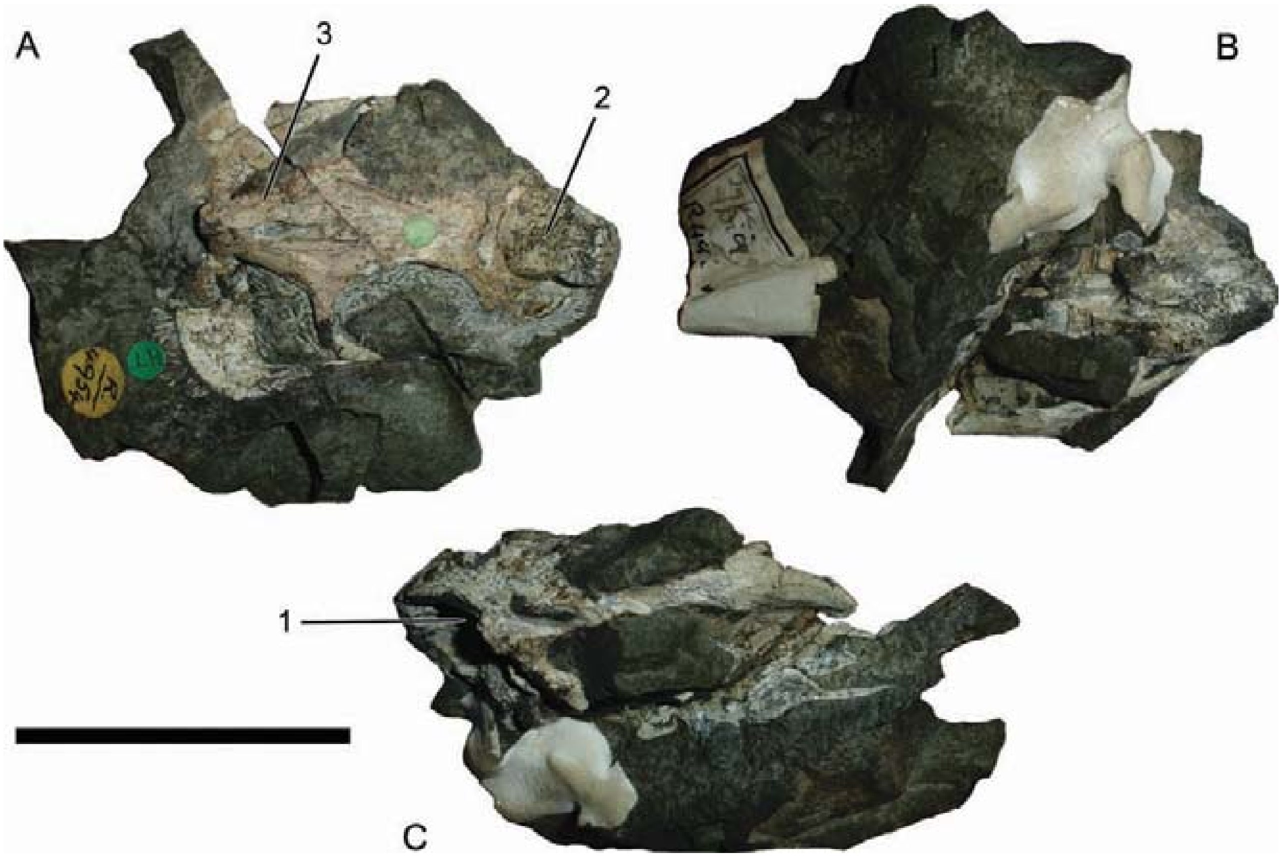

FIGURE 82. NHMUK R4954, the holotype of *Dicynodon macrorhynchus* (= *Diictodon feliceps*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch and (2) median boss on the snout and as *D. feliceps* on the basis of the (3) relatively narrow intertemporal bar with extensive postorbital-parietal overlap and absence of teeth. Scale bar equals 5 cm.

two distinct morphs are consistently observed in *Pelanomodon* specimens: one with large, extremely bulbous, distinct nasal and prefrontal bosses (*P. rubidgei*) and the other with weak, poorly developed bosses (*P. moschops*). The *P. rubidgei* morphology is observed only in large skulls, whereas the *P. moschops* morphology is observed in both large and small skulls. We suggest that, as has been argued for the closely related *Aulacephalodon* (Tollman et al., 1981), the snout bosses of *Pelanomodon* may be sexually dimorphic, with one sex (probably the male) developing large bosses as a secondary sexual feature and the other sex (probably the female) and juveniles with undeveloped bosses. Unfortunately *Pelanomodon* is a rare dicynodont, making a rigorous population-level study of potential dimorphism in this taxon currently impossible. Still, given that the difference in boss size is the only character that consistently separates the two species, and given its size distribution in known specimens, with no juveniles of the '*P. rubidgei*' morph, the most parsimonious explanation is that there is a single species of South African *Pelanomodon* showing boss dimorphism. As such, we consider *P. rubidgei* to be a junior synonym of *P. moschops*.

Dicynodon moutonae Broom, 1948

Holotype—MMK 5033, a nearly complete skull and disarticulated lower jaw (missing the posterior portion of the left mandibular ramus) (Fig. 92).

Locus Typicus—Ca. 10 miles southwest of Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1948) did not directly compare *Dicynodon moutonae* with particular other species of the genus, but did note that *D. moutonae* has a smaller maxilla and shorter stapes than most other *Dicynodon* species. Keyser (1975) synonymized this species with *Oudenodon bainii*, a measure followed by all subsequent workers (e.g., Brink, 1986; King, 1988). The maxilla of MMK 5033 is similar in size and shape to most specimens of *Oudenodon bainii*, and although the stapes is poorly exposed in this specimen, it appears indistinguishable from those of other oudenodontid specimens.

Dicynodon murrayi Huxley, 1859

Holotype—NHMUK R1291, a poorly preserved complete skull and lower jaws (Fig. 93).

Locus Typicus—Colesberg, north of Sneewberg Range, South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Valid as *Lystrosaurus murrayi* (Huxley, 1859).

Remarks—Huxley (1859) described NHMUK R1291 as a new species of *Dicynodon* (*D. murrayi*) distinguished from existing species by a right angle between the planes of the

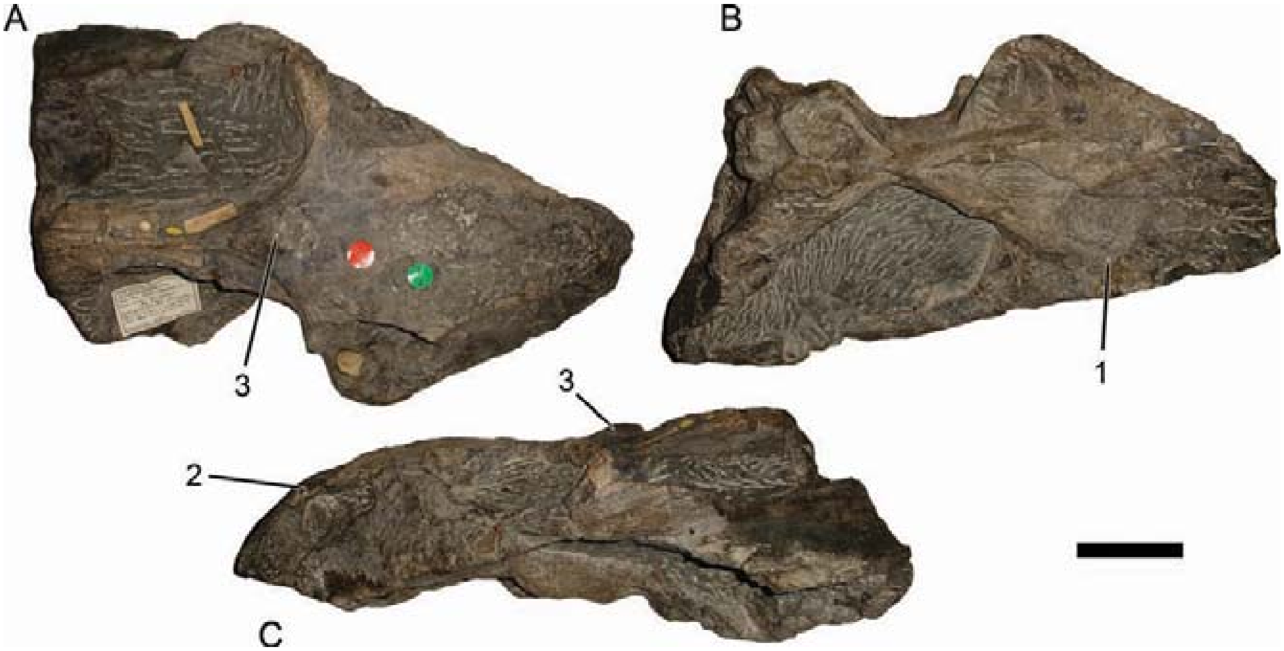

FIGURE 83. NHMUK 36252, the holotype of *Dicynodon magnus* (= *Rhachiocephalus magnus*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the nares and as a rhachiocephalid on the basis of the (2) elongate shape of the nasal bosses and (3) massive, anteriorly angled pineal boss. *Rhachiocephalus magnus* has a narrower, more attenuate snout in dorsal view than the similar *Kitchinganomodon crassus*. Scale bar equals 10 cm.

premaxilla-nasal and frontal-parietal, short parietal region, and proportional characters of the tusks, nares, and mandible. Huxley's (1859) first two characters are characteristic of most species of *Lystrosaurus* (with only *L. curvatus* lacking a distinct break between the facial and snout planes), and the relationship between *D. murrayi* and Owen's (1860b) *Ptychognathus* (= *Lystrosaurus*) was recognized by Lydekker (1890), who included this species in *Ptychosiagum* (a replacement name for *Ptychognathus*, which was preoccupied by a crustacean). Broom (1903a) noted that Cope's (1870a) *Lystrosaurus* has priority over *Ptychosiagum* to refer to this type of dicynodont, but did not explicitly transfer *D. murrayi* to *Lystrosaurus* until 1932. As the first-named species referable to *Lystrosaurus*, *L. murrayi* has been recognized as valid in all subsequent studies of dicynodont taxonomy (see, e.g., King, 1988). NHMUK R1291 is cracked and crushed but nearly complete, missing only parts of the edges of the temporal arches. Although somewhat weathered, it clearly exhibits the triplanar snout profile and prefrontal and median premaxillary ridges that distinguish the *L. murrayi* morphotype from other *Lystrosaurus* species (Grine et al., 2006).

Dicynodon mustoi Haughton, 1915

Holotype—SAM-PK-2674, a well-preserved skull (missing the right zygomatic arch) and lower jaws (Fig. 94).

Locus Typicus—Dunedin, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Haughton (1915) described SAM-PK-2674 as a new species of *Dicynodon*, printed as *Dicynodon mustonis* but in all copies crossed out and hand-written as '*Dicynodon mustoi*.' This is not sufficient to indicate intentional emendation, although the stated etymology (after Mr. Musto) may be taken to indicate that this was a lapsus calami. In all subsequent papers (e.g., Haughton, 1917), Haughton referred to this species as *D. mustoi*. Van Hoepen (1934) included this species in *Oudenodon*. Keyser (1975) stated that the holotype shows many features of *Oudenodon bainii*. He hesitated to officially synonymize *D. mustoi* with *O. bainii* because several important regions were still encased in matrix on the holotype, but noted that they would probably prove conspecific with further preparation. Brink (1986) and King (1988) listed *D. mustoi* as a junior synonym of *O. bainii*. Botha and Angielczyk (2007) included SAM-PK-2674 in their traditional morphometric analysis and supported its placement within *O. bainii*. This makes SAM-PK-2674 one of the earliest records of the species, one of the few specimens of *O. bainii* from the *Tropidostoma* AZ.

Dicynodon nanus Broom, 1936

Holotype—TM 268, a complete skull (Fig. 95).

Locus Typicus—Wimbledon, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom (1936) described *Dicynodon nanus* as one of the smallest known species of *Dicynodon* based on a tiny skull (3.86 cm dorsal length) from Wimbledon. Haughton and Brink (1954), Kitching (1977), and King (1988) listed *D. nanus* as a valid species of *Dicynodon*, but Brink (1986) listed it in the synonymy of *Diictodon feliceps*. We agree with Brink's (1986) referral—TM 268 exhibits a precaniniform notch, has a short intertemporal region (but even at this small size the intertemporal region is constricted, with extensive postorbital-parietal overlap), and completely lacks teeth. TM 268 is one of the best-preserved juvenile skulls of *Diictodon*.

FIGURE 84. BSP 1935 VIII 32, the holotype of *Dicynodon marlothi* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares and (2) postcaniniform crest and as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the (5) lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

Dicynodon nesemanni Broom, 1940a

Holotype—TM 1481, a skull missing much of the temporal arches, now lost.

Locus Typicus—Swagershoek, Graaff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1940a) did not directly compare *Dicynodon nesemanni* with any other species of the genus, but noted that it had a relatively large preparietal for *Dicynodon*. The loss of the holotype has rendered further study of this species difficult, but Broom's (1940a) description indicates that TM 1481 was probably a specimen of *Oudenodon bainii*. The lack of tusks, elongate but fairly broad intertemporal region (with continuous exposure of the parietals), and paired nasal bosses overhanging the nares are all consistent with identification as *Oudenodon*, as is the fact that Broom stated that this specimen compares favorably with *Dicynodon platyceps*, another synonym of *Oudenodon bainii*.

Dicynodon njalilus von Huene, 1942

Holotype—GPIT/RE/7110, a complete, well-preserved skull (Fig. 96), lower jaws, and most of the postcranium.

Locus Typicus—Njalila, Tanzania.

Horizon—Manda beds (Middle Triassic).

Status—Valid as *Tetragonias njalilus* (von Huene, 1942).

Remarks—*Dicynodon njalilus* was the last Middle Triassic dicynodont to be described as a new species within *Dicynodon* (von Huene, 1942). By this time, the distinction between *Dicynodon* sensu lato and *Kannemeyeria* had been recognized (Broom, 1913c), but more generalized Triassic dicynodonts (e.g., *D. njalilus*) as well as those represented largely by postcranial material (e.g., *Dicynodon turpior*) were still being referred to the expansive former genus. Cox (1965) recognized that this species was not referable to *Dicynodon*, and was instead closely related to *Shansiodon* from the Middle Triassic of China. Cruickshank (1967) removed *D. njalilus* from *Dicynodon* and made it the type species of the new genus *Tetragonias*. All subsequent authors have recognized *T. njalilus* as a valid species (e.g., King, 1988), although Lucas (1998b) included it within *Shansiodon*. GPIT/RE/7110 is one of the most thoroughly known Middle Triassic dicynodonts and includes a well-preserved skull, jaws, and most of the skeleton. This specimen is clearly a kannemeyeriiform rather than a '*Dicynodon*-grade' dicynodontoid based on the absence of the postfrontal. Although *T. njalilus* is considered valid here, shansiodontid alpha taxonomy requires further study: Surkov and Benton (2008) found individually coded *Tetragonias* specimens from the Manda beds to be paraphyletic with regards to Chinese *Shansiodon*.

Dicynodon nowacki von Huene, 1942

Holotype—GPIT/RE/7174, a nearly complete skull missing the right temporal arch and the tips of the caniniform processes (Fig. 97).

Locus Typicus—Kingori Mountain, Ruhuhu Basin, Tanzania.

Horizon—Usili Formation (Upper Permian).

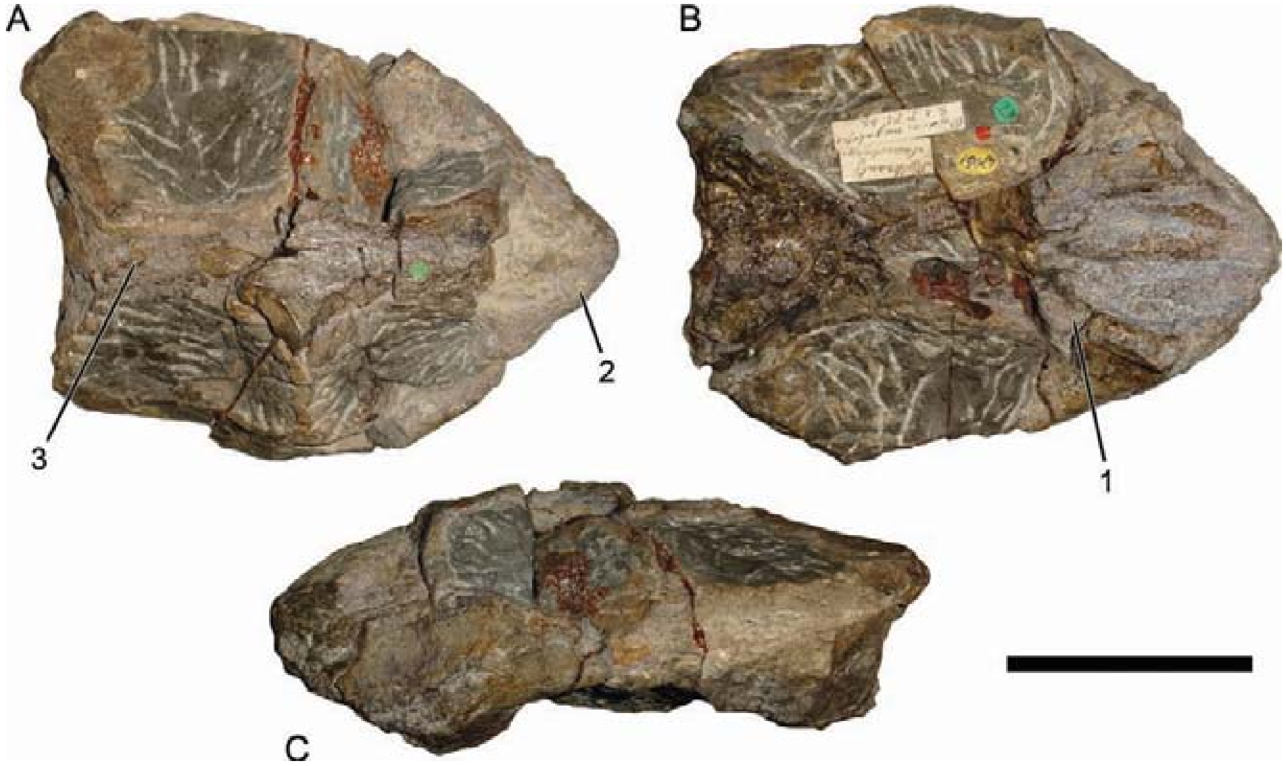

FIGURE 85. NHMUK 47061, the holotype of *Dicynodon megalops* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and relatively tall, short snout. Scale bar equals 5 cm.

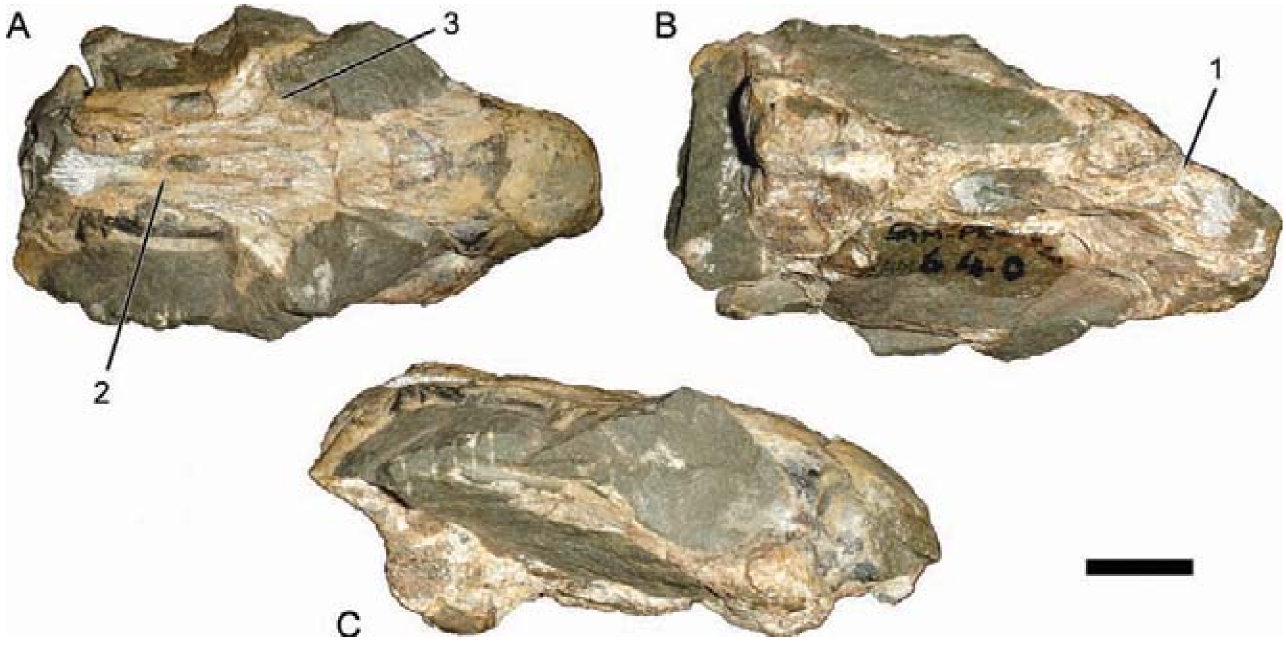

FIGURE 86. SAM-PK-640, the holotype of *Dicynodon megalorhinus* (= *Emydops* sp.), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) embayment of the palatal rim anterior to the caniniform process and as *Emydops* on the basis of the (2) broadly exposed parietals and (3) presence of the postfrontal. Scale bar equals 1 cm.

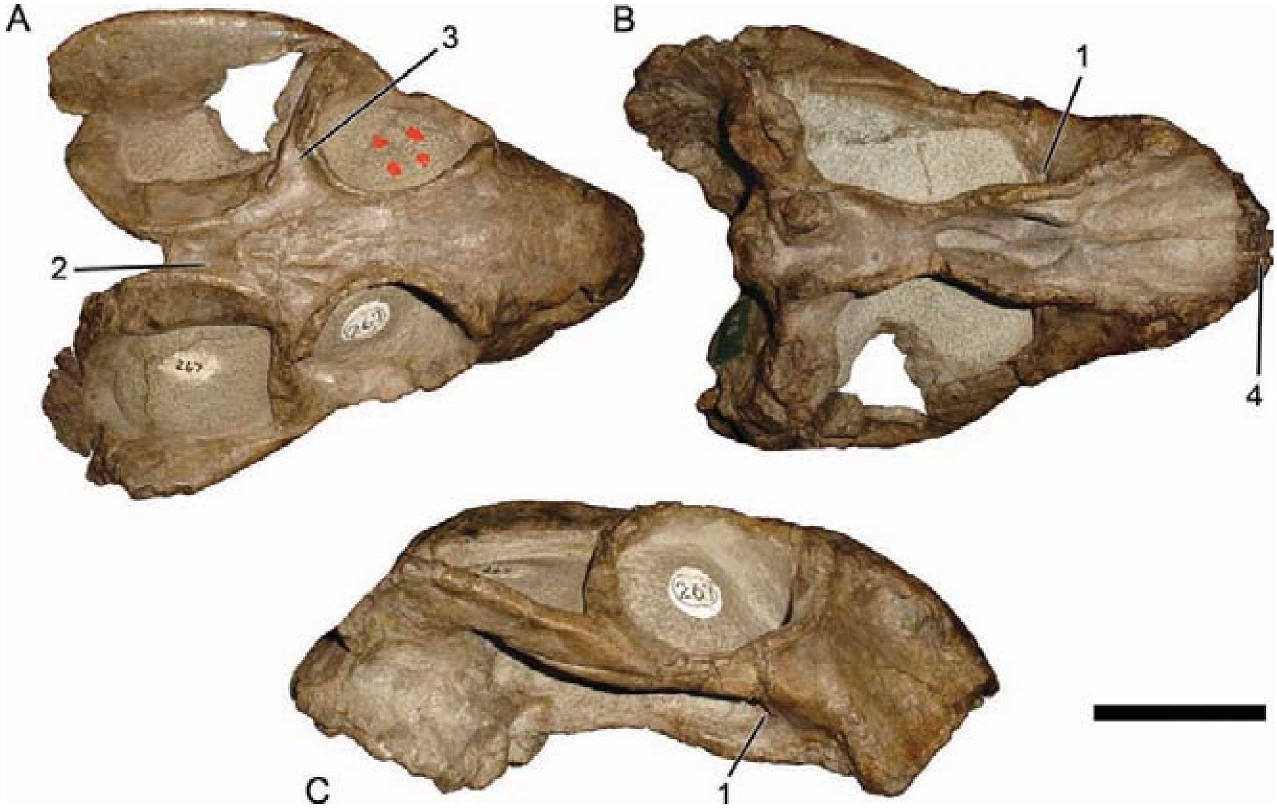

FIGURE 87. TM 267, the holotype of *Dicynodon microdon* (= *Basilodon woodwardi*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa, and as *B. woodwardi* on the basis of the (2) short, broad intertemporal bar with extensive exposure of the parietals, (3) triangular depression on the dorsal surface of the postorbital bar, and (4) blunt premaxillary tip. Scale bar equals 5 cm.

Status—Valid as *Dicynodontoides nowacki* (von Huene, 1942).

Remarks—Von Huene (1942) described *Dicynodon nowacki* based on a set of skulls (GPIT/RE/7173 [formerly K48], GPIT/RE/7174 [formerly K12], and GPIT K35) from Kingori Mountain. Cox (1959) made *D. nowacki* the type species of his new genus *Kingoria*. Angielczyk et al. (2009) synonymized *Kingoria* with *Dicynodontoides* (a course of action first suggested, but not formalized, by Cluver and Hotton [1981]), but retained *D. nowacki* as a distinct species, and it is recognized as valid here.

Dicynodon orientalis Huxley, 1865

Syntypes—GSI unnumbered, a series of fragmentary cranial and postcranial elements.

Locus Typicus—Damodar Basin, India.

Horizon—Panchet Formation (Lower Triassic).

Status—Junior subjective synonym of *Lystrosaurus murrayi* (Huxley, 1859).

Remarks—Huxley (1865) described *Dicynodon orientalis* on the basis of a series of fragmentary cranial and postcranial elements from the Early Triassic of India. Das Gupta (1922) transferred this species to *Lystrosaurus*, and Tripathi and Satsangi (1963) considered it to be a junior synonym of the common South African species *L. murrayi*, a position followed by subsequent authors (e.g., Colbert, 1974). Ray (2005) reviewed the Panchet Formation *Lystrosaurus* material, and demonstrated that only a single species is present, *L. murrayi*. Panchet Formation *Lystrosaurus* skulls show the triplanar snout profile and well-developed median snout ridge and prefrontal bosses characteristic of *L. murrayi*.

Dicynodon osborni Broom, 1921

Holotype—AMNH FARB 5598, a very dorsoventrally crushed skull missing the temporal arches (Fig. 98).

Locus Typicus—Wapadsberg, near New Bethesda Road, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Daptocephalus leoniceps* (Owen, 1876).

Remarks—Broom (1921) described this taxon as being from the *Lystrosaurus* AZ, but Kitching (1977) determined that this locality includes both *Dicynodon* and *Lystrosaurus* AZ exposures, with AMNH FARB 5598 originating from the former. Van Hoepen (1934) included *Dicynodon osborni* in his genus *Daptocephalus*. Haughton and Brink (1954), Kitching (1977), and King (1988) listed *D. osborni* as a valid species of *Dicynodon* (Cluver and Hotton [1981] did not address this species), but Brink (1986) considered it to be a junior synonym of *Dicynodon lacerticeps*. Although badly distorted, AMNH FARB 5598 displays several diagnostic features of the *Daptocephalus leoniceps* morphotype, including an extremely long, narrow intertemporal bar with nearly complete postorbital-parietal overlap, steeply angled snout profile, and ventrally directed caniniform processes. Distinctions in overall skull breadth and temporal arch shape between AMNH FARB 5598 and typical specimens of *D. leoniceps* can be attributed to taphonomic deformation in this

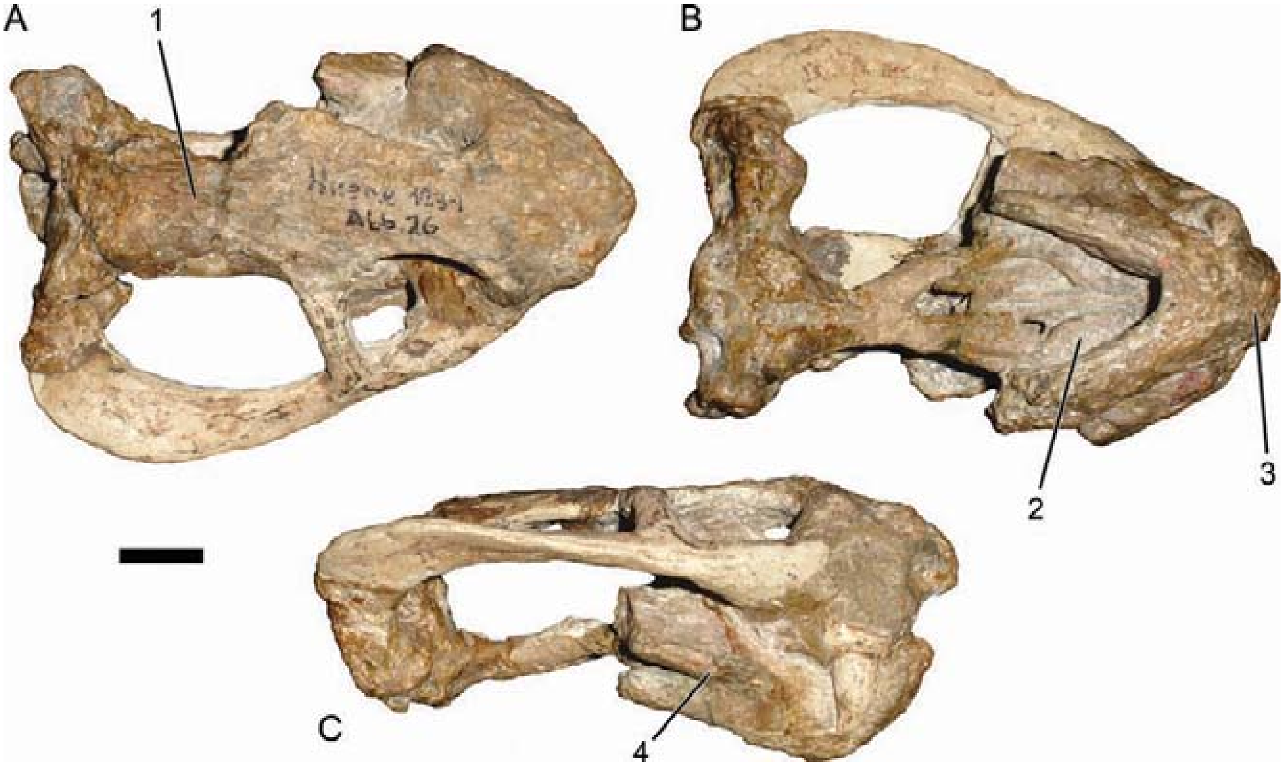

FIGURE 88. GPIT unnumbered, the holotype of *Dicynodon microrhynchus* (= *Pristerodon mackayi*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as *Pristerodon* on the basis of the (1) nearly equal width of the postorbitals and parietals in the intertemporal bar, (2) leaf-shaped palatine pads, (3) sharp, elongate mandibular symphysis, and (4) sharp lateral dentary shelf angled over the mandibular fenestra. Scale bar equals 1 cm.

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specimen, and *D. osborni* can be added to the synonymy of *D. leoniceps*.

Dicynodon oweni (Seeley, 1889)

Holotype—NHMUK 46075, two slabs containing natural molds of a partial dicynodont skeleton (dorsal vertebrae, thoracic ribs, forelimbs, part of the left hindlimb) (Fig. 99).

Locus Typicus—Sneewberg Range, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontia indet.).

Remarks—Owen (1876) initially figured portions of NHMUK 46075, labeling it as an indeterminate dicynodont, and later (1880) described the manus of this specimen as ?*Dicynodon*. Seeley (1889) argued that there is no evidence to demonstrate that this specimen represents a dicynodont, but probably does represent an anomodont (in Seeley's usage, a heterogeneous group mostly equivalent to non-mammalian Synapsida), and named it as a new taxon, *Eurycarpus oweni*. Lydekker (1889) maintained that Owen's (1880) generic attribution was correct, but upheld the species distinction as *Dicynodon oweni*. In his description of *Dicynodon* (= *Pelanomodon*) *moschops*, Broom (1913c) suggested that NHMUK 46075 could represent the postcranium of his new, skull-based species. Noting that the the type of *D. moschops* was found near the type locality of *E. oweni*, Broom (1913c:447) stated that, "it is not improbable that the skull I am now describing [AMNH FARB 5325, *D. moschops*] is the skull of the same species as the Poortjie specimen [NHMUK 46075, *E. oweni*]." Without any overlapping material between the two specimens, however, he concluded that, "it will never be possible to say with certainty to what species it [NHMUK 46075] belongs." Given the advances currently being made in the long-neglected field of dicynodont postcranial anatomy, the finality of Broom's dismissal may eventually prove overly pessimistic. That said, at present no postcranial characters preserved in NHMUK 46075 permit identification to species, and *Eurycarpus oweni* must be considered a nomen dubium.

Dicynodon pachyrhynchus (Jaekel, 1911)

Holotype—NHMUK R3742, a strongly anteroposteriorly crushed skull (broken off behind the orbits) and lower jaws (Fig. 100).

Locus Typicus—Unknown.

Horizon—?*Cynognathus* Assemblage Zone (Middle Triassic).

Status—Junior subjective synonym of *Kannemeyeria simocephala* (Weithofer, 1888).

Remarks—Jaekel (1911) described *Sagecephalus pachyrhynchus* as a new taxon of large dicynodont based on an extremely robust partial skull from an unknown Triassic locality. Broom (1913a) included this species within *Dicynodon* as *D. pachyrhynchus*, but Pearson (1924) considered it to be a distorted specimen of *Kannemeyeria*. Cruickshank (1970) agreed with the latter referral, and treated *S. pachyrhynchus* as a junior synonym of *Kannemeyeria simocephala*. This synonymy has been followed by all subsequent authors (e.g., King, 1988) and is upheld here.

Dicynodon parabreviceps Boonstra, 1938

Holotype—SAM-PK-11319, a partial skull missing the temporal arches (Fig. 101).

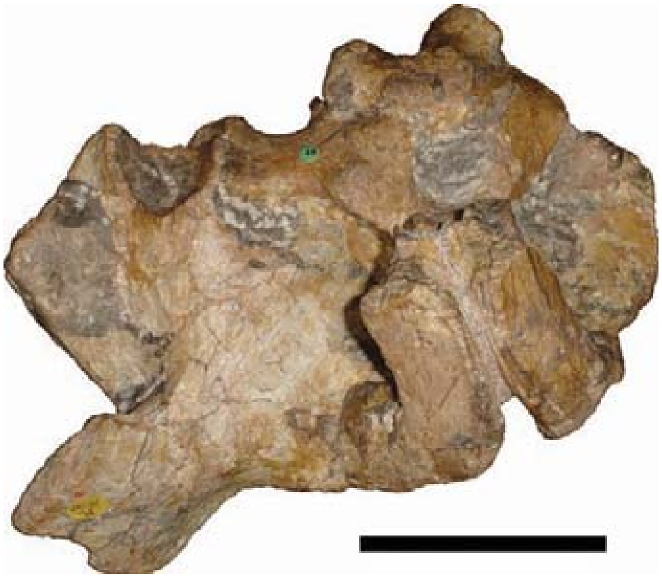

FIGURE 89. NHMUK R868, the holotype of *Dicynodon microtrema* (= *Tropidostoma dubium*), in dorsal view (anterior is up). This specimen is not by itself diagnostic for *Tropidostoma*, although we retain it as part of the hypodigm for that taxon in the absence of evidence suggesting otherwise. Scale bar equals 5 cm.

Locus Typicus—Luangwa Valley, Zambia.

Horizon—Upper Madumabisa Mudstone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Boonstra (1938) described *Dicynodon parabreviceps* based on a well-preserved skull exhibiting similar proportions to the South African *Dicynodon breviceps* (SAM-PK-2366, here considered a specimen of *Oudenodon bainii*). Keyser (1975) synonymized the four Luangwa Valley 'tuskless *Dicynodon*' (i.e., *Oudenodon*) species, but retained this group (under the senior name *Oudenodon luangwanensis*) as a distinct species from the South African *O. bainii*. Refer to the entry on *Dicynodon luangwanensis* for our rationale in referring the Zambian *Oudenodon* species to *O. bainii*.

Dicynodon pardiceps Owen, 1876

Holotype—NHMUK 47045, a poorly preserved, dorsoventrally crushed skull missing the right zygomatic arch (Fig. 102).

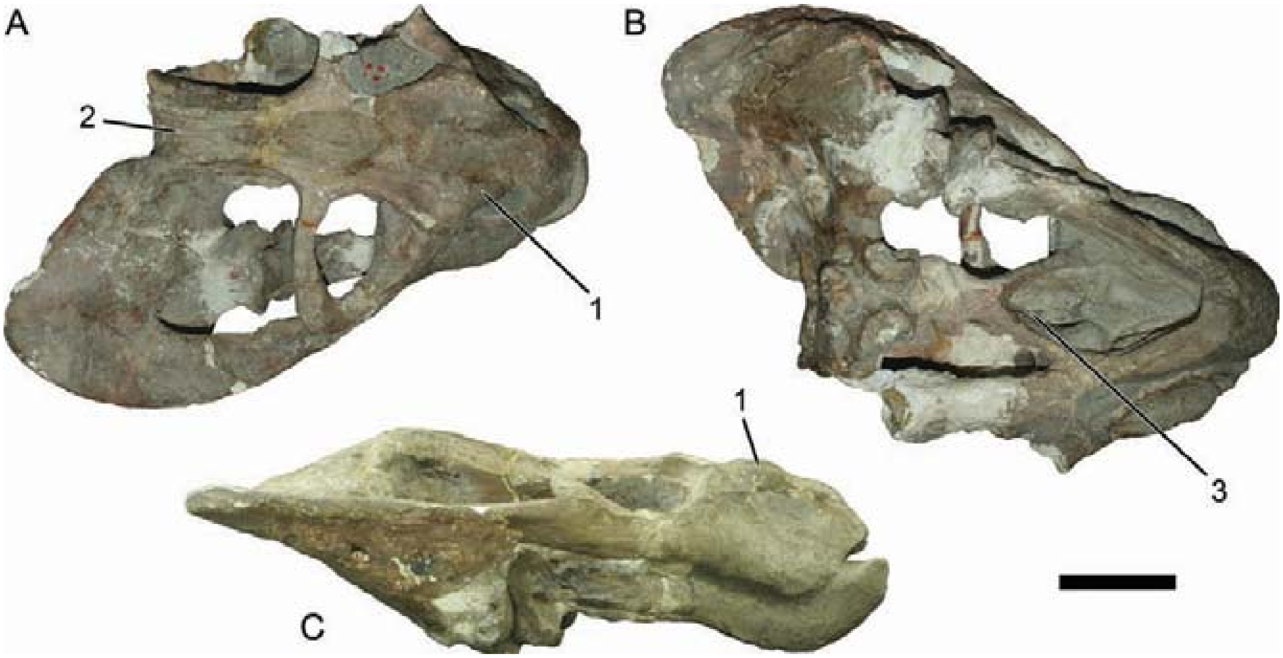

FIGURE 90. MMK 4164, the holotype of *Dicynodon milletti* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal and (3) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

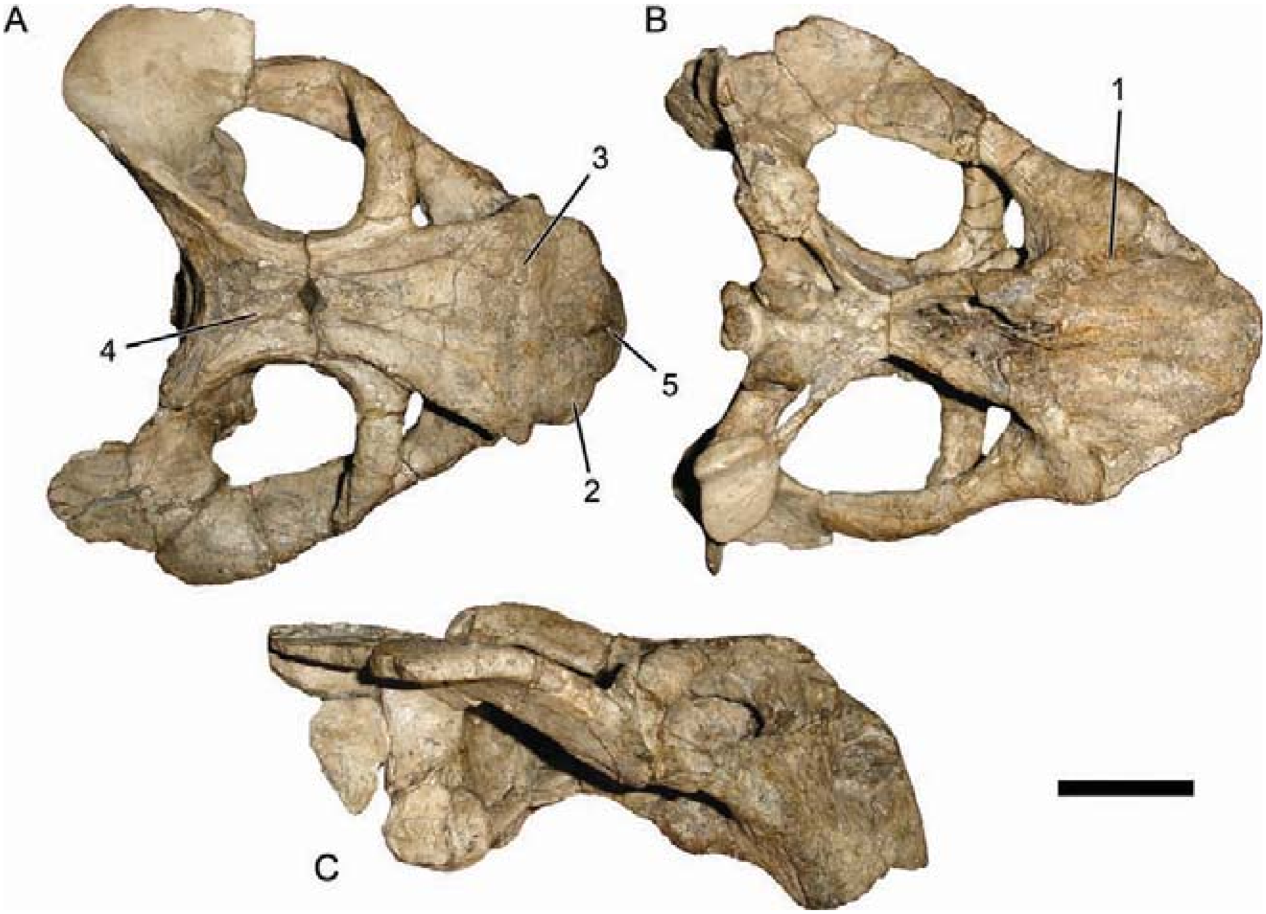

FIGURE 91. AMNH FARB 5325, the holotype of *Dicynodon moschops* (= *Pelanomodon moschops*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares and as a geikiine on the basis of the (3) transverse ridge running between the prefrontals and (4) broad exposure of the parietals in the intertemporal bar. *Pelanomodon* can be distinguished from *Aulacephalodon* and *Geikia* by the combination of a rounded premaxillary tip, (5) presence of a median ridge on the anterior dorsal surface of the premaxilla, and lack of tusks. Scale bar equals 5 cm.

Locus Typicus—Fort Beaufort, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodon lacerticeps* Owen, 1845.

Remarks—Owen (1876) described *Dicynodon pardiceps* as a large species similar to *Dicynodon leoniceps*. Most subsequent studies of this taxon have emphasized its similarity to *D. leoniceps*—van Hoepen (1934) included both species in *Daptocephalus*, and Broom (1932) considered them synonymous, a referral followed by Haughton and Brink (1954) and King (1988). NHMUK 47045 has an narrow intertemporal bar, but it is unusually short (shorter than the pretemporal region) for a large specimen of *D. leoniceps*. The snout and squamosal profile in lateral view are also atypical for *D. leoniceps*, with a gradual, very weakly biplanar snout profile and acutely angled squamosal rami, with a posterodorsal flange on the squamosal, as in *Dicynodon lacerticeps*. It is possible that these peculiarities are attributable to taphonomic distortion due to strong dorsoventral compression in this specimen, but this specimen also has an unusually broad, squared-off premaxillary tip as in *D. lacerticeps*. At present, the best interpretation of this specimen is as a large adult *D. lacerticeps* rather than *Daptocephalus*.

Dicynodon parvidens Owen, 1876

Holotype—NHMUK 47062, a sagittally sectioned skull and lower jaws in a nodule (Fig. 103).

Locus Typicus—Steilkrans, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Probable junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Owen (1876) described *Dicynodon parvidens* based on an unprepared nodule cut and polished in sagittal section. Because of the poor state of preparation of the holotype, this species has largely been ignored by subsequent workers, although Brink (1986) lists it as a synonym of *Dicynodon lacerticeps*. NHMUK 47062 is still almost entirely encased in matrix, with only the left and right tusks, right temporal arch, and parts of the interorbital and intertemporal regions exposed externally. This nodule has been split along the sagittal plane of the skull and polished, showing some of the internal anatomy of the skull in section but unfortunately few features of phylogenetic import. That said, based on the apparent presence of a precaniniform notch on the right side of the skull and convergence of the postorbitals in the short intertemporal region, we tentatively identify this specimen as an individual of *Diictodon feliceps*. This identification could easily

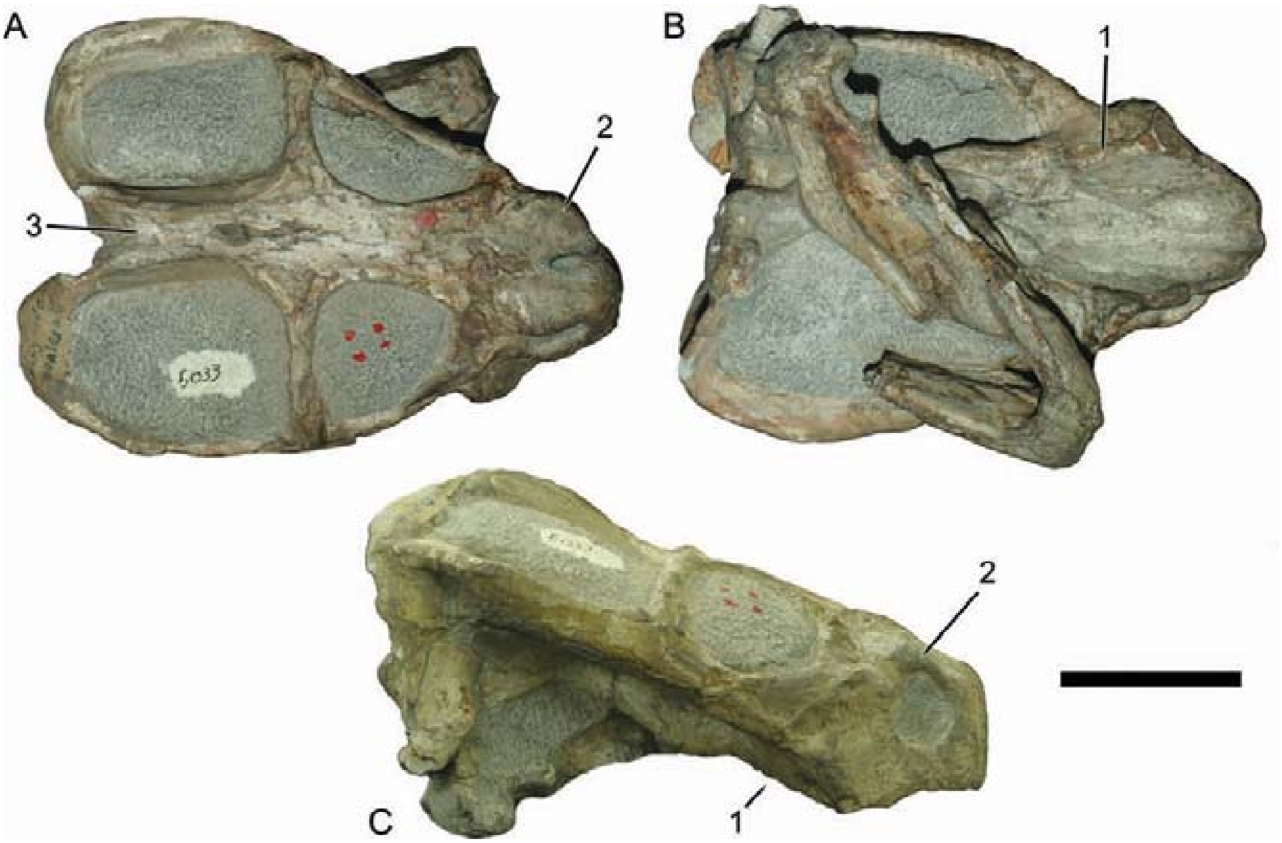

FIGURE 92. MMK 5033, the holotype of *Dicynodon moutonae* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

be confirmed by minor additional preparation of the lateral surface of the skull, although we understand that preparation of another *Diictodon* skull may not be a high priority in the field of therapsid paleontology.

Dicynodon planus Broom, 1913c

Holotype—AMNH FARB 5549, a poorly preserved partial skull (Fig. 104).

Locus Typicus—Kuilspoort, Beaufort West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1913c) described *Dicynodon planus* on the basis of a partial skull from Kuilspoort. He distinguished it from other species of *Dicynodon* by its relatively longer, narrower snout and small, laterally directed nares. Van Hoepen (1934) included *D. planus* in *Oudenodon* in the subgenus *Mastocephalus*, and Keyser (1975) considered it a junior synonym of *Oudenodon bainii*. Subsequent studies have supported this assessment (e.g., Kitching, 1977; Brink, 1986; King, 1988) and it is maintained here.

Dicynodon platyceps Broom, 1913c

Holotype—AMNH FARB 5542, a nearly complete skull (missing portions of the temporal arches) and lower jaws (Fig. 105).

Locus Typicus—New Bethesda, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1913c) described *Dicynodon platyceps* on the basis of a nearly complete skull missing the temporal arches from New Bethesda. Broom considered *D. platyceps* to be most similar to *Dicynodon megalops* (= *Oudenodon bainii*) and *Dicynodon leptorhinus* (indeterminate), but distinguished it from the latter taxon on the basis of its relatively smaller postfrontal. In addition to the type skull, Broom (1913c) referred a number of additional specimens from the type locality to *D. platyceps*. Van Hoepen (1934) included *D. platyceps* in *Oudenodon* in the subgenus *Mastocephalus*, and Keyser (1975) considered it a junior synonym of *Oudenodon bainii*. Subsequent studies have supported this assessment (e.g., Kitching, 1977; Brink, 1986; King, 1988) and it is maintained here.

Dicynodon platyfrons Broom, 1932

Holotype—ELM unnumbered, a partial, dorsoventrally crushed skull missing the tip of the snout and portions of both temporal arches, now lost.

Locus Typicus—Kwezana, Victoria East, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

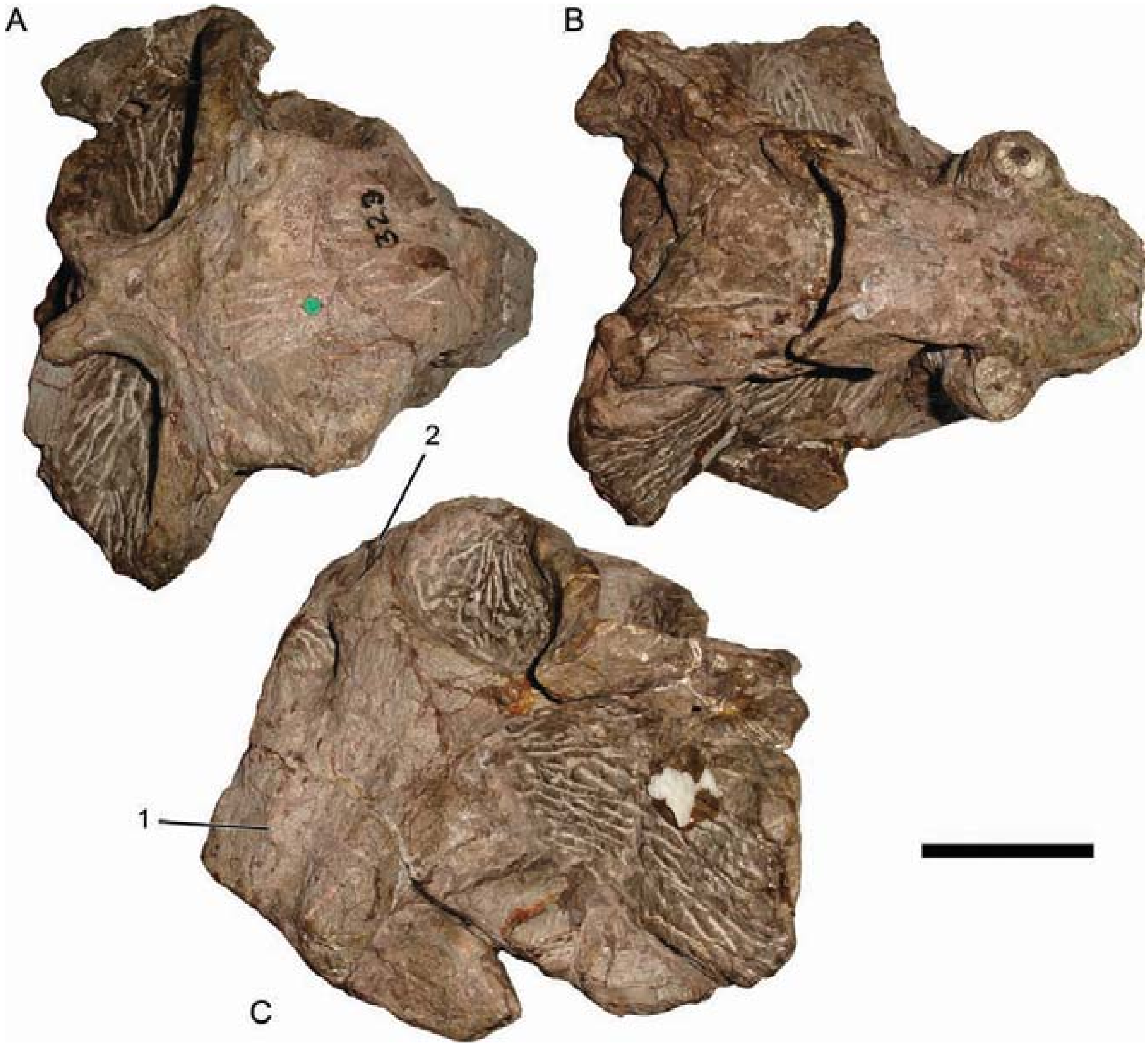

FIGURE 93. NHMUK R1291, the holotype of *Dicynodon murrayi* (= *Lystrosaurus murrayi*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a lystrosaurid on the basis of the (1) tall, strongly deflected snout. The most obvious feature distinguishing *L. murrayi* from other species in the genus is the (2) triplanar skull profile, broken into distinct naso-premaxillary, naso-frontal, and fronto-parietal planes. Scale bar equals 5 cm.

Remarks—Broom (1932) described *Dicynodon platyfrons* based on a highly flattened skull from Victoria East, an area of uncertain stratigraphy but considered by Kitching (1977) to represent *Cistecephalus* AZ rocks. Van Hoepen (1934) included *D. platyfrons* in *Oudenodon* in the subgenus *Mastocephalus*, and Keyser (1975) considered it a junior synonym of *Oudenodon bainii*. Subsequent studies have supported this assessment (e.g., Kitching, 1977; Brink, 1986; King, 1988) and it is maintained here. The holotype of this species could not be found in recent searches of the ELM collections, but Broom's (1932) original description and Keyser's (1975) notes on the specimen detail several diagnostic featues of *O. bainii*, including the lack of tusks, small, ovoid nasal bosses overhanging the nares, and broad intertemporal region.

Dicynodon prognathus (Owen, 1860b)

Holotype—NHMUK 47059, the anterior half of a ventrally sheared skull and lower jaws (Fig. 106).

Locus Typicus—Mildenhall, Fort Beaufort, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Owen (1876) distinguished *Oudenodon prognathus* from the type species *O. bainii* based on the forward position and angulation of the caniniform process. Seeley (1898) included this species and other 'prognathous' *Oudenodon* (including *O. magnus*) in the subgenus *Rhachiocephalus*. Broom (1913a) transferred all *Oudenodon* species (including *O. prognathus*) to

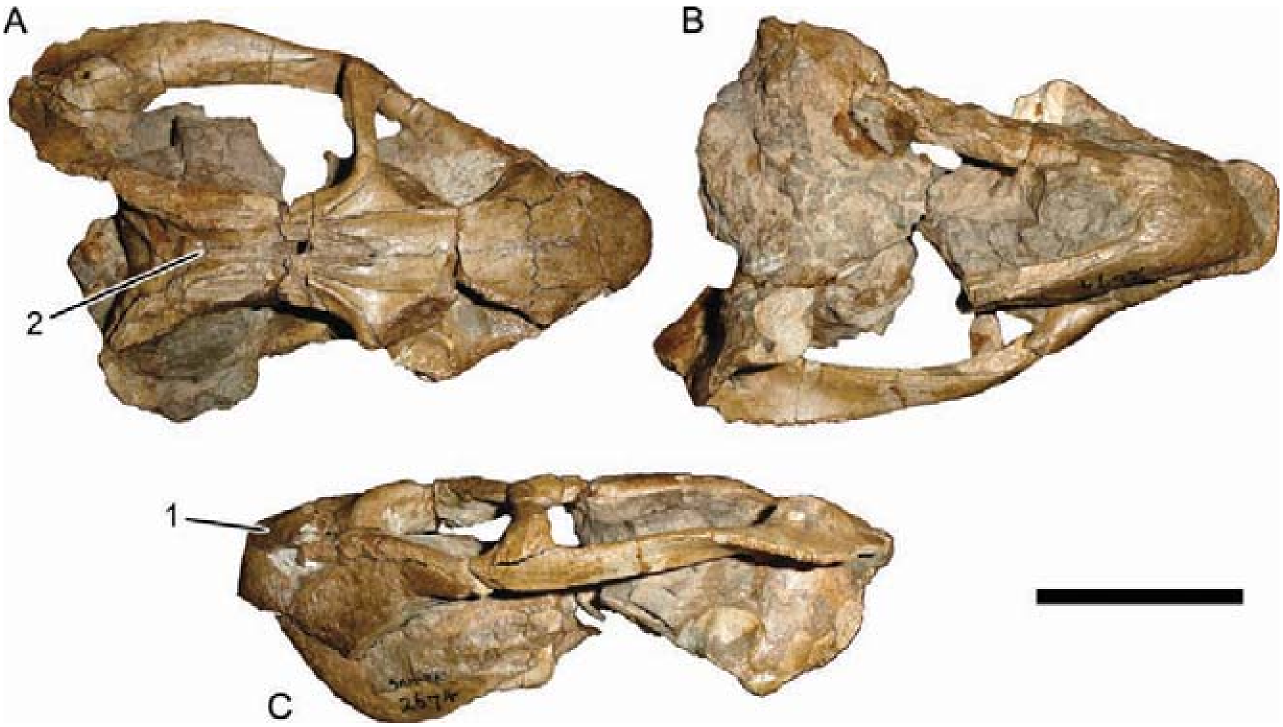

FIGURE 94. SAM-PK-2674, the holotype of *Dicynodon mustoi* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

Dicynodon, but van Hoepen (1934) retained *O. prognathus* in *Oudenodon*. Keyser (1975) argued that the diagnostic featues of *O. prognathus* given by Owen (1860b) are the result of dorsoventral compression, and that this species is synonymous with *Oudenodon bainii*. Subsequent studies have supported this assessment (e.g., Kitching, 1977; Brink, 1986; King, 1988) and it is maintained here.

Dicynodon pseudojouberti Boonstra, 1948

Holotype—SAM-PK-774, a complete skull, now lost.

Locus Typicus—Prince Albert Road, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Nomen dubium (*Emydops* sp.).

Remarks—Boonstra (1948) reexamined the dicynodonts of the *Tapinocephalus* AZ, focusing on a large collection (over a hundred skulls) in the South African Museum labeled as *Dicynodon jouberti* (currently considered a synonym of *Diictodon feliceps*, see entry on this species). Among these many specimens Boonstra recognized several skulls that could not be referred to *D. jouberti*, and separated these out as three new taxa: the pylaecephalid *Robertia broomiana* (based on the holotype SAM-PK-11761 and numerous referred specimens, and later to become the best-known *Tapinocephalus* AZ-restricted dicynodont), the enigmatic *Koupia koupensis* (based on the lost holotype SAM-PK-11796), and *Dicynodon pseudojouberti*. *Dicynodon pseudojouberti* was erected on the basis of a complete skull from Prince Albert Road collected by J. A. Cairncross in 1905. Additionally, Boonstra (1948) listed two 'cotypes' (= paratypes) for this species, the skulls SAM-PK-775 and 776, both from 'the Koup,' collected by J. R. Joubert in 1881. Cluver and Hotton (1981) transferred this species to *Diictodon* and King (1988) maintained it as a valid species of *Diictodon*, but Brink (1986) and Sullivan and Reisz (2005) considered it a junior synonym of *Diictodon feliceps*. SAM-PK-774 is currently represented solely by two uninformative skull fragments, and the rest of the skull is presumed lost. The paratype SAM-PK-775 (Fig. 107), however, is highly informative, and the elongate intertemporal bar with broadly exposed parietals and lack of a precaniniform notch indicate that it is not a specimen of *Diictodon feliceps*. Rather, the intertemporal morphology, squared-off occiput, and presence of an embayment in the palatal rim anterior to the caniniform process indicate that this is a specimen of *Emydops*. The morphology of SAM-PK-775 agrees with the description and figure Boonstra (1948) gave for the holotype, and as such we consider *Dicynodon pseudojouberti* referable to *Emydops*. In its current state, it is impossible to determine whether SAM-PK-775 represents a specimen of *Emydops arctatus* or *Emydops oweni*. Additional preparation will be required to identify species-specific characters in SAM-PK-775.

Dicynodon psittacops Broom, 1912b

Holotype—AMNH FARB 5534, a dorsoventrally crushed skull (missing the temporal arches), lower jaws, and most of the postcranium (Fig. 108).

Locus Typicus—Beaufort West Commonage, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom (1912b) described *Dicynodon psittacops* on the basis of a nearly complete skeleton (missing the ribs and tail) from Beaufort West Commonage. He justified the creation of this new species on geographic and stratigraphic grounds. Van Hoepen (1934) retained this species in *Dicynodon* sensu stricto

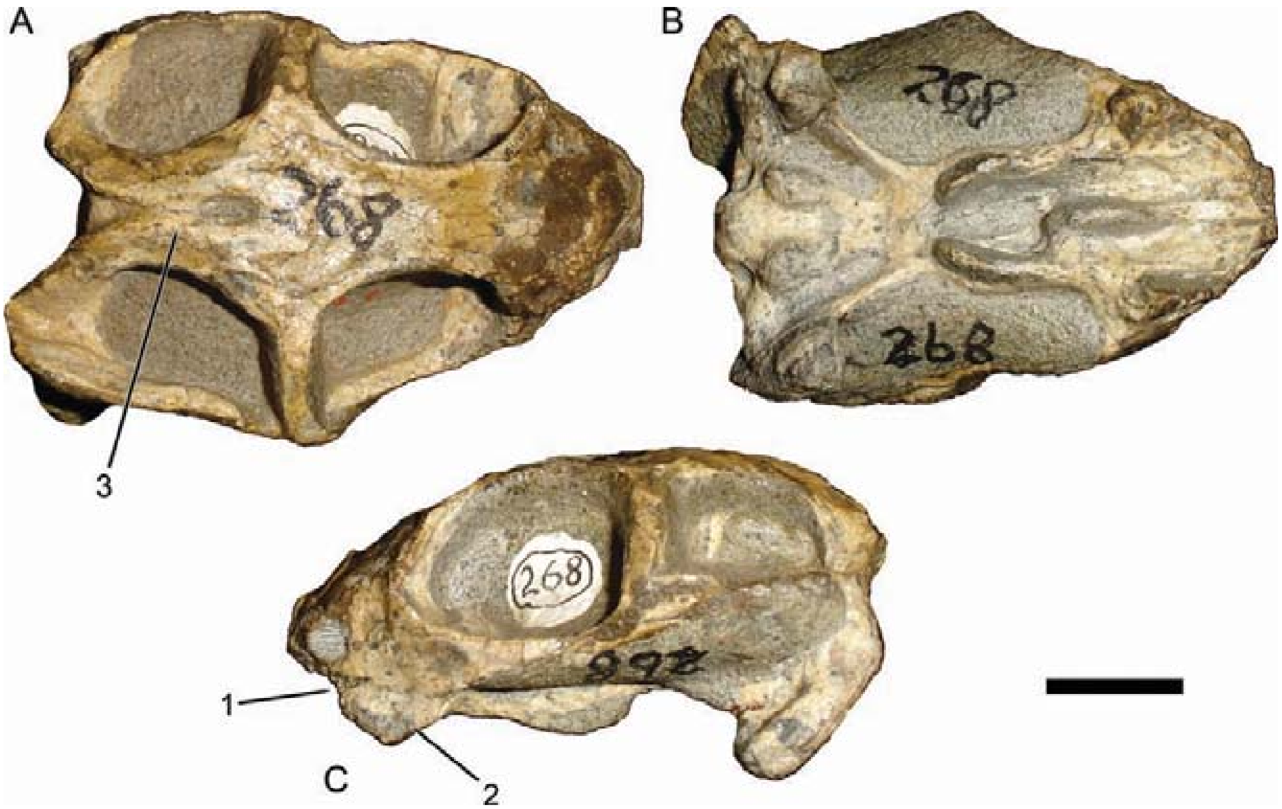

FIGURE 95. TM 268, the holotype of *Dicynodon nanus* (= *Diictodon feliceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch and (2) ventral surface of the caniniform process at level of anterior margin of orbits and as *D*. *feliceps* on the basis of the (3) relatively narrow intertemporal bar with extensive postorbital-parietal overlap and lack of teeth. Scale bar equals 1 cm.

(together with *D*. *lacerticeps* and *D*. *feliceps*). Cluver and Hotton (1981) transferred this species to *Diictodon* (see also King, 1988), and Sullivan and Reisz (2005) synonymized it with *Diictodon feliceps*. Brink (1986) considered *D*. *psittacops* to be a nomen dubium. The skull of AMNH FARB 5534 is highly dorsoventrally compressed and poorly prepared, but the presence of a distinct precaniniform notch, short intertemporal bar with nearly complete postorbital-parietal overlap, and absence of teeth are sufficient to identify this specimen as *Diictodon feliceps*.

Dicynodon pygmaeus Broom and Haughton, 1917

Holotype—SAM-PK-2664, a complete skull and mandibular symphysis still mostly embedded in matrix (Fig. 109).

Locus Typicus—Dunedin, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Pristerodon mackayi* Huxley, 1868.

Remarks—Broom and Haughton (1917:123) described *Dicynodon pygmaeus* as the smallest known species of the genus (dorsal skull length 5.4 cm in the holotype), arguing that, as “two or three specimens were obtained from the same locality of about similar size, it seems probable that the specimen represents a small species rather than a young individual.” In addition to small size, they diagnosed *D*. *pygmaeus* on the basis of its broad intertemporal region and relatively small squamosals. Van Hoepen (1934) included *D*. *pygmaeus* in the new genus *Orophicephalus* with *D*. *megalorhinus* (= *Emydops* sp.) and *D*. *microrhynchus* (= *Pristerodon mackayi*). Cluver and Hotton (1981) transferred *D*. *pygmaeus* to *Diictodon*, retaining it as a valid species. King (1988) synonymized it with *Diictodon testudirostris*, noting that both species are from the same locality and their original descriptions list no characters that separate them. Brink (1986) listed *D*. *pygmaeus* as a junior synonym of *Diictodon feliceps*, but Sullivan and Reisz (2005) noted that SAM-PK-2664 requires further preparation and that its assignment to *Diictodon* is questionable. Only the dorsal skull roof and part of the mandibular symphysis of this specimen have been prepared, although the caniniform processes and parts of the squamosals are exposed laterally. The intertemporal region is relatively short, as in *Diictodon*, but unlike that taxon the parietals are exposed throughout the length of the intertemporal bar. The parietal exposure is significantly narrower than in *Emydops*, but is consistent with the condition in *Pristerodon*. The presence of a row of six postcanines in the maxilla provides further evidence that *D*. *pygmaeus* is synonymous with *Pristerodon mackayi*.

Dicynodon raniceps (Owen, 1876)

Holotype—NHMUK R1650, a dorsoventrally crushed skull (missing the edges of the orbits and temporal fenestrae) and lower jaws (Fig. 110).

Locus Typicus—East London area, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Pristerodon mackayi* Huxley, 1868.

Remarks—Owen (1876) diagnosed *Oudenodon raniceps* based on its small size, extremely short snout, and skull wider than

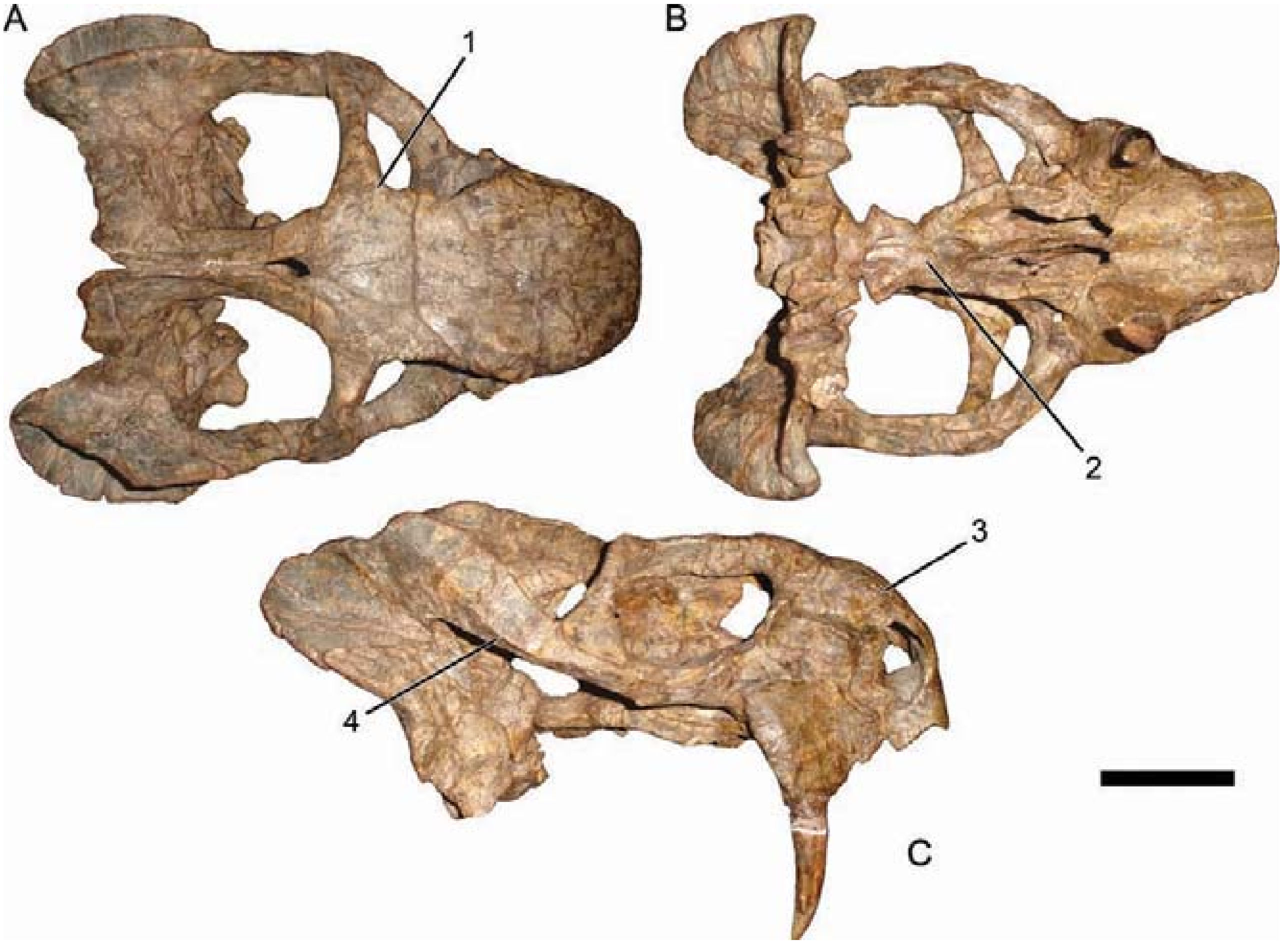

FIGURE 96. GPIT/RE/7110, the holotype of *Dicynodon njalilus* (= *Tetragonias njalilus*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be recognized as a kannemeyeriiform on the basis of the (1) absence of a postfrontal and (2) absence of converging keels on the posterior portion of the anterior pterygoid rami and as a shansiodontid on the basis of (3) nasal bosses present as paired swellings near the dorsal or posterodorsal margin of the external nares and (4) a prominent ridge on the lateral surface of the temporal arch. *Tetragonias njalilus* has traditionally been distinguished from other shansiodontids on the basis of postcranial characters. Scale bar equals 5 cm.

long. Following his belief that *Oudenodon* represents the female of *Dicynodon*, Broom (1913a) put *O*. *raniceps* in the new combination *Dicynodon raniceps*. Upon actually examining the holotype, however, Broom (1913c) concluded that it represented a specimen of *Pristerodon mackayi*, and synonymized the two species. Later, he reinstated it as a distinct species of *Pristerodon* (1915b), the approach followed by Haughton and Brink (1954) and King (1988). Keyser (1993) considered NHMUK R1650 to be identifiable as *Pristerodon*, but considered the species to be a nomen dubium because of the poor quality of the holotype. The diagnostic 'leaf-shaped' palatine pads of *P. mackayi* are not visible in NHMUK R1650 because the palate is largely unprepared. Nevertheless, the combination of a prominent, horizontally oriented lateral dentary shelf, rows of tall, roughly denticulated maxillary and dentary postcanines, short intertemporal bar with consistent parietal exposure and posterior contribution by the postparietal, and absence of a 'shovel-shaped' dentary symphysis (the presence of which is diagnostic of emydopoids) allows this specimen to be confidently identified as *Pristerodon mackayi*.

Dicynodon rectidens Owen, 1876

Holotype—NHMUK 47057, a poorly preserved ventral portion of the snout and anterior portion of the lower jaws (Fig. 111).

Locus Typicus—Near Fort Beaufort, South Africa.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Bidentalia indet.).

Remarks—Owen (1876) described *Dicynodon rectidens* on the basis of an anterior skull fragment (NHMUK 47057) and an apparently associated block of postcranial elements (NHMUK 47058). Broom (1932) considered *D. rectidens* to be a synonym of *Dicynodon leoniceps*. Because of the poor quality of the holotype, *D. rectidens* has been largely ignored by subsequent workers, and its status was not addressed by Kitching (1977), Cluver and Hotton (1981), or King (1988). Brink (1986) listed it as a synonym of *Dicynodon lacerticeps* without discussion. The highly incomplete nature of NHMUK 47057 makes identification difficult. The general shape of the snout is consistent with *Daptocephalus leoniceps*, as suggested by Broom (1932). The long, tall

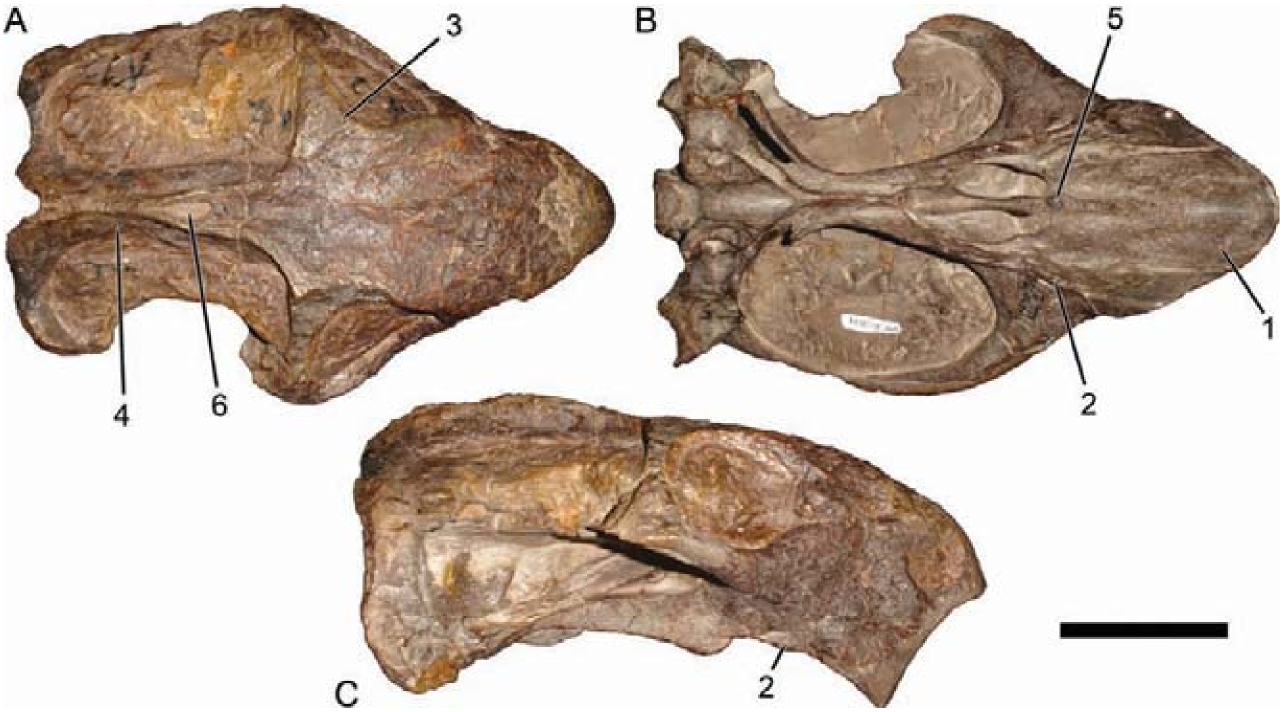

FIGURE 97. GPIT/RE/7174, the holotype of *Dicynodon nowacki* (= *Dicynodontoides nowacki*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) palatal surface of the premaxilla with a groove-like depression with a rounded anterior end and a (2) postcaniniform keel, as a kistecephalian on the basis of the (3) absence of the postfrontal, and as a kingoriid on the basis of the (4) postorbitals sloping slightly ventrolaterally, overlapping the parietals except for a narrow exposure of the latter as a sagittal crest and (5) relatively wide mid-ventral plate of the vomer. This specimen can be identified as *Dicynodontoides* rather than *Kombuisia* based on the (6) elongate, well-developed pineal foramen. *Dicynodontoides nowacki* is distinguished from the South African species *D. recurvidens* on the basis of postcranial morphology and larger average size (Angielczyk et al., 2009). Scale bar equals 5 cm.

mandibular symphysis of NHMUK 47057 is unusual for Permian dicynodontoids, but is typical of cryptodonts, and the massive tusks suggest that this could be a specimen of *Aulacephalodon bainii*. However, the transversely narrow premaxilla is at odds with the typical morphology of *Aulacephalodon*. This species is best regarded as a nomen dubium; it is a large bidentalian of some kind but cannot be identified to a lower taxonomic level with confidence.

Dicynodon recurvidens Owen, 1876

Holotype—NHMUK 47091, a nearly complete skull (missing the temporal arches) and lower jaws (Fig. 112).

Locus Typicus—Fort Beaufort, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Valid as *Dicynodontoides recurvidens* (Owen, 1876).

Remarks—Owen (1876) diagnosed *Dicynodon recurvidens* based on its strongly recurved tusks. Lydekker (1890) suggested that this species may represent the juvenile of *Dicynodon leoniceps*. Accordingly, van Hoepen (1934) transferred this species to *Daptocephalus*, but Cluver and Hotton (1981) included it in *Kingoria*, a referral followed by King (1988). Brink (1986) listed *D. recurvidens* as a junior synonym of *Dicynodon lacerticeps* without comment. NHMUK 47091 is a nearly complete and, for an Owen specimen, reasonably well-prepared skull. The dorsal surface of the skull is badly sheared leftwards, the interorbital region is badly cracked, and the temporal arches are broken off, but the temporal region, lateral surface of the snout, and mandible are well preserved. Based on the absence of postfrontals, presence of extensive postorbital overlap of the parietals on the intertemporal bar, parietals forming a slight ridge dorsally, postcaniniform keel, shovel-like mandibular symphysis, well-developed lateral dentary shelf, and occlusion of the mandibular fenestra, Angielczyk et al. (2009) referred this specimen to *Dicynodontoides*, a designation that is maintained here. As the oldest nominal species of *Dicynodontoides*, *D. recurvidens* has seniority to refer to the South African species of this genus.

Dicynodon richardi Broom, 1940b

Holotype—RC 41 (TM 4041), a poorly prepared skull missing the right temporal arch (Fig. 113).

Locus Typicus—Wimbledon, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1940b) described *Dicynodon richardi* as a new species very similar to *Dicynodon allani* (= *Oudenodon bainii*) from the same locality, but distinguished by the greater overlap of the parietals by the postorbitals on the intertemporal bar. This specimen was lost some time after its description, hindering further study. King (1988) listed it as a valid species of *Dicynodon* and Brink (1986) listed it as a junior synonym of *Diictodon feliceps* without comment. During a recent trip to Ditsong, the National Museum of Natural History (formerly the Transvaal Museum), we rediscovered the holotype of *D. richardi*, relabeled as TM 4041. This specimen agrees in all respects with Broom's (1940b) description (including length of the skull and areas of damage) and bears the quadruple red diamond traditionally used to identify a holotype in South African collections. Examination of TM 4041 reveals that this specimen represents an

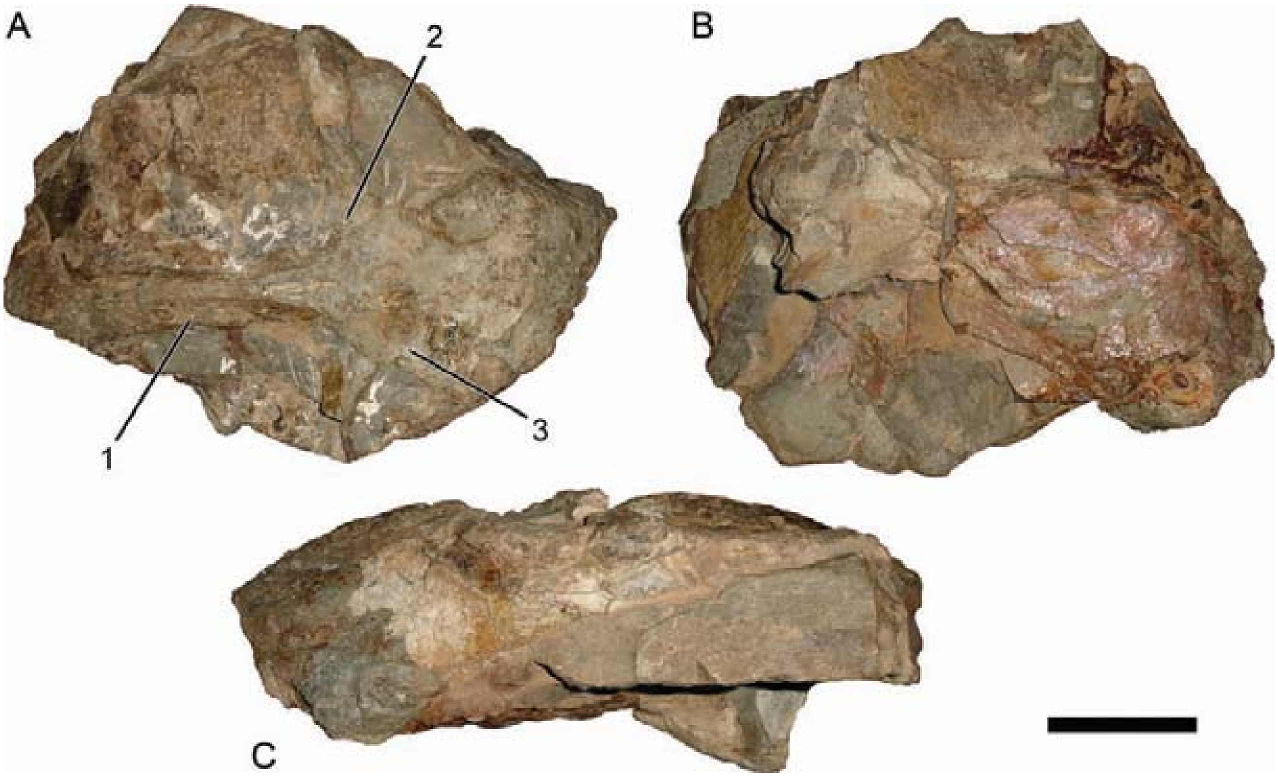

FIGURE 98. AMNH FARB 5598, the holotype of *Dicynodon osborni* (= *Daptocephalus leoniceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. Although very poorly preserved, this specimen can be identified as *D*. *leoniceps* on the basis of the (1) long, extremely narrow intertemporal bar, (2) thin, strap-like postfrontals, and (3) wide interorbital region. Scale bar equals 10 cm.

individual of *Oudenodon bainii*: it is tuskless, has a low pineal foramen flush with the skull roof, and has small, ovoid nasal bosses overhanging the nares. Broom's (1940b) chief diagnostic character of this species, extent of postorbital overlap on the intertemporal bar, is both variable with ontogeny in *Oudenodon* (larger skulls have a higher degree of overlap) and variable as a result of taphonomic deformation. The condition in RC 41 is well within the range of intertemporal variation observed in *O*. *bainii*.

Dicynodon roberti Boonstra, 1938

Holotype—SAM-PK-11325B, a poorly preserved skull missing the temporal arches and occiput (Fig. 114).

Locus Typicus—Luangwa Valley, Zambia.

Horizon—Upper Madumabisa Mudstone (Upper Permian).

Status—Junior subjective synonym of *Syops vanhoepeni* (Boonstra, 1938).

Remarks—Boonstra (1938) described *Dicynodon roberti* based on two skulls, one (SAM-PK-11325B, the holotype) preserving the snout and intertemporal bar, and the other (SAM-PK-11325A, the paratype) preserving only the caniniform processes and snout tip. King (1988) listed *D*. *roberti* as a valid species of *Dicynodon*. Brink (1986) considered it of uncertain position, listing the synonymy of this species as '?'. SAM-PK-11325A and SAM-PK-11325B show the same unusual combination of characters: low, elongate precanine region of the snout

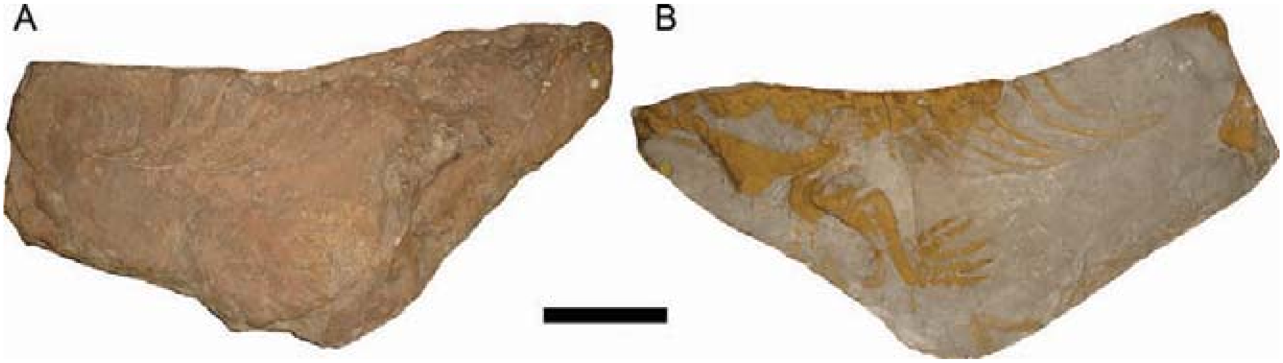

FIGURE 99. NHMUK 46075, the holotype of *Dicynodon oweni* (*Eurycarpus oweni*) (**A**), a natural sandstone mold, and a cast made from it (**B**). This specimen is not identifiable beyond Dicynodontia indet. Scale bar equals 10 cm.

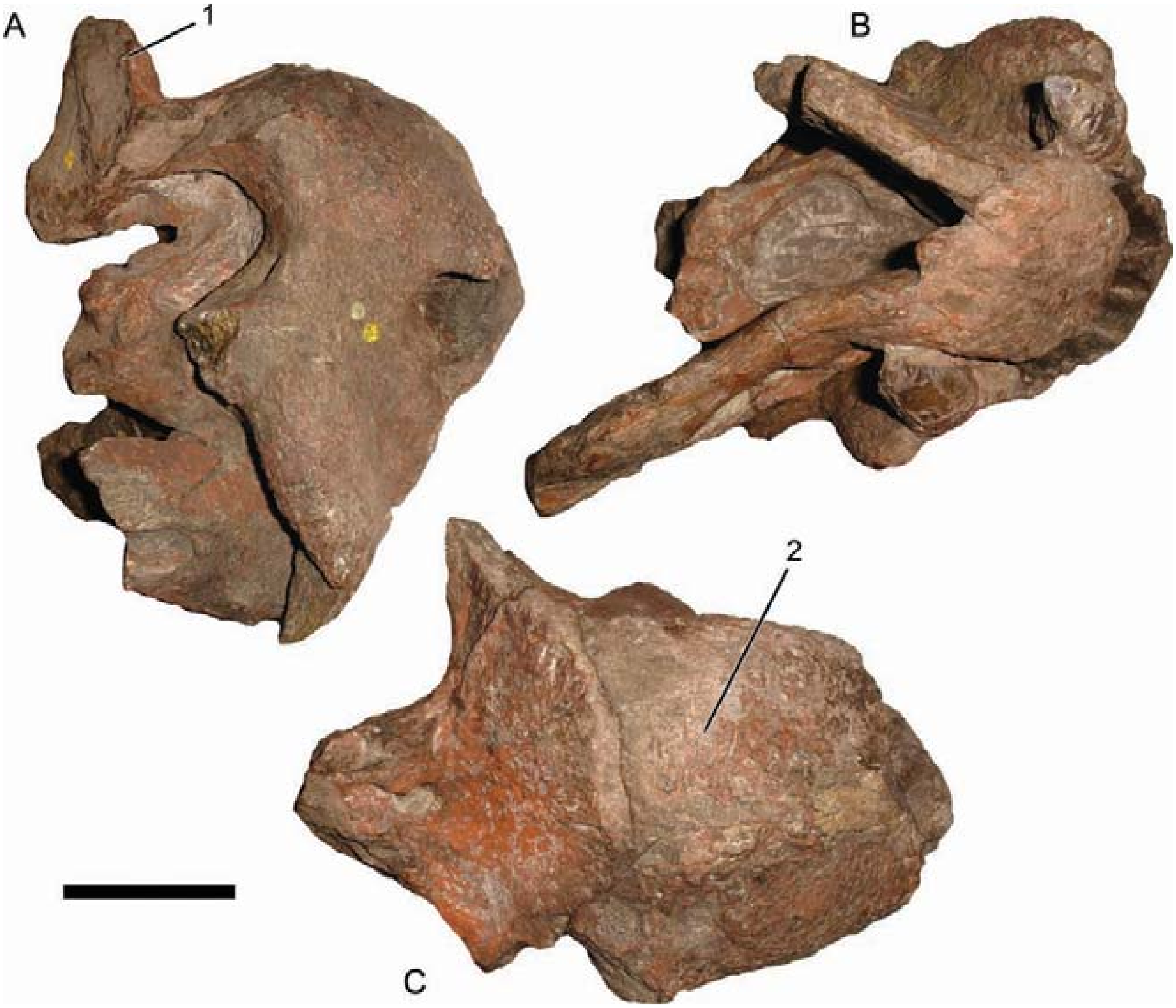

FIGURE 100. NHMUK R3742, the holotype of *Dicynodon pachyrhynchus* (= *Kannemeyeria simocephala*), in right lateral (**A**), ventral (**B**), and dorsal (**C**) views. This specimen can be identified as *Kannemeyeria* on the basis of its (1) steeply angled sagittal crest (further accentuated by deformation, however) at a plane above that of the snout and (2) swollen nasals forming a median ridge. Scale bar equals 10 cm.

(but without a prominently 'hooked' tip as in *Dinanomodon gilli*), paired grooves on the anterodorsal surface of the premaxillae, a lateral ridge on the premaxillary-maxillary suture (as in *Oudenodon*), strongly anteriorly canted caniniform processes and tusks, and palatal rim with an embayment anterior to the canine, followed by tapering premaxillary edges terminating in a strongly squared-off tip (giving the premaxillae a trapezoidal shape in palatal view). Among dicynodonts, this combination of characters is otherwise observed only in another nominal species of *Dicynodon* from the Luangwa Valley, "*D*." (*Syops*) *vanhoepeni*, and we consider these species synonymous, giving priority to *D*. *vanhoepeni*. SAM-PK-11325A additionally shares with the holotype of *D*. *vanhoepeni* (SAM-PK-11311) a characteristic snout profile, with a distinct break in slope between the nasal and premaxillary planes. Importantly, SAM-PK-11325B (the only specimen to preserve postorbital portions of the skull) demonstrates that this species had a long, narrow intertemporal bar with nearly complete postorbital-parietal overlap, as in many Permian dicynodontoids, and a pineal foramen set in a depressed region of the skull roof, as in *Turfanodon bogdaensis*.

Dicynodon robertsi Broom, 1948

Holotype—TM 1598, a partial skull (missing the postorbital region except for the intertemporal bar) and lower jaws (Fig. 115).

Locus Typicus—"A beach in the Transkei" (Broom, 1948:610), South Africa.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1948:611) described *Dicynodon robertsi* as one of the few *Dicynodon* species in which the skull is "nearly as broad as long." He considered this new species most similar to *Dicynodon helenae* from Zambia (here considered a synonym of *Oudenodon bainii*) and to a lesser degree *Dicynodon*

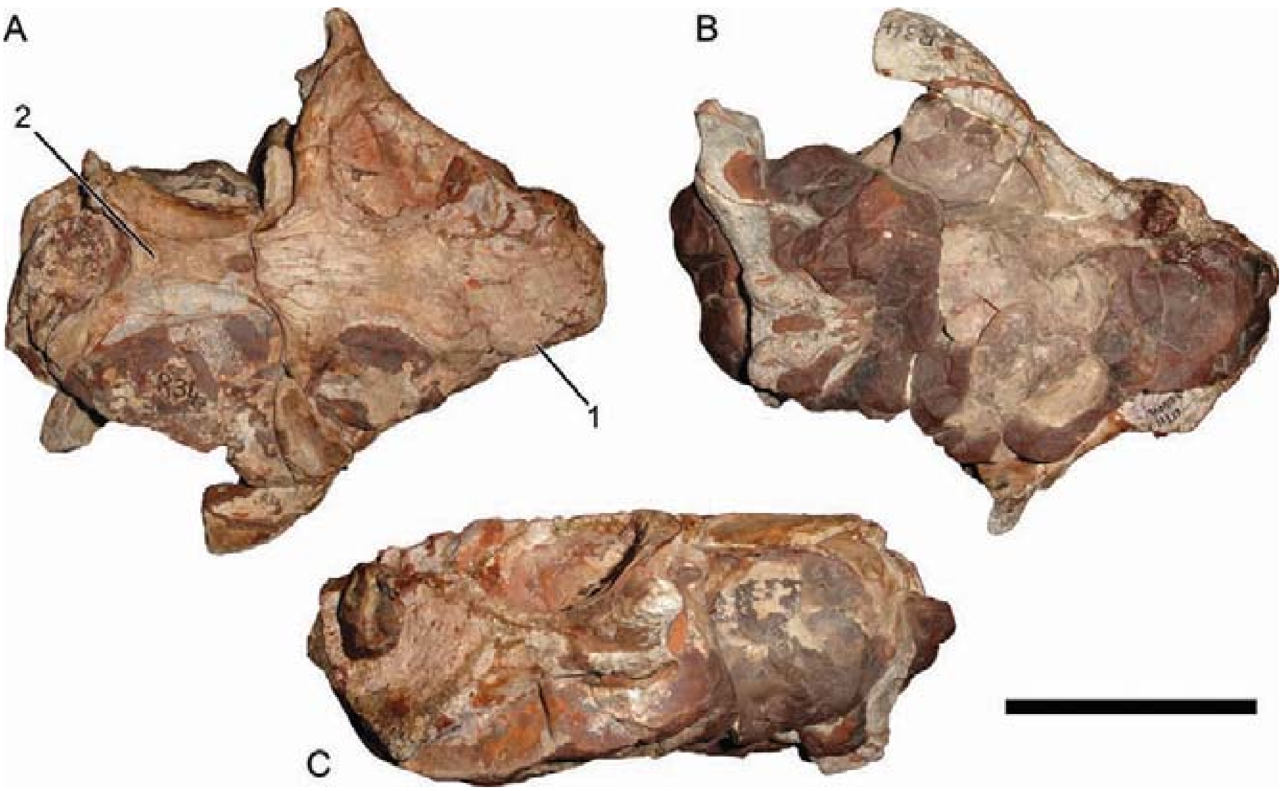

FIGURE 101. SAM-PK-11319, the holotype of *Dicynodon parabreviceps* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 10 cm.

corstorphinei (= *O. bainii*), but distinguished from the former by a broader snout and larger orbits and from the latter by a narrower snout and and broader temporal region. Keyser (1975) synonymized this species with *Oudenodon bainii*, a referral maintained by Brink (1986), King (1988), and the current study.

Dicynodon robustus Broom, 1932

Holotype—ELM unnumbered, a complete skull, now lost.

Locus Typicus—Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1932) considered *Dicynodon robustus* to be most closely related to *Dicynodon vanderbyli* (= *Oudenodon bainii*). Van Hoepen (1934) included this species in *Oudenodon* in the subgenus *Mastocephalus*. King (1988) listed *D. robustus* as a valid species of *Dicynodon*. Although the type skull is currently lost, Broom's (1932) description and figures of this specimen suggest that it was an individual of *Oudenodon bainii*. According to Broom (1932), this specimen was tuskless, with narrow parietal exposure in the intertemporal bar and small, ovoid nasal bosses overhanging the nares.

Dicynodon rogersi Broom and Haughton, 1917

Holotype—SAM-PK-2356, a partial skull missing most of its left side (Fig. 116).

Locus Typicus—The Kloof, Nieuweveld, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Tropidostoma dubium* (Owen, 1876).

Remarks—Broom and Haughton (1917) described *Dicynodon rogersi* based on a partial skull initially identified as the tusked male of *Dicynodon kolbei* (= *Oudenodon bainii*). They removed this specimen from *D. kolbei* based on the longer snout, poorly developed nasal bosses, shorter orbit, broader temporal bar, broader postfrontal, and broader preparietal. Keyser (1973) argued that SAM-PK-2356 represents a specimen of *Tropidostoma*, a referral supported by morphometric analysis (Botha and Angielczyk, 2007) and maintained here.

Dicynodon rosmarus Cope, 1870b

Holotype—An isolated, recurved tooth, now lost.

Locus Typicus—Wheatley copper mine, Phoenixville, Pennsylvania, U.S.A.

Horizon—Lockatong member, Newark Supergroup (Upper Triassic).

Status—Nomen dubium (Phytosauria?).

Remarks—Cope (1870b) briefly described the first North American species of *Dicynodon*, *D. rosmarus*, based on a large, isolated tooth showing strong recurvature in the private collection of the Wheatley mining family. The entirety of Wheatley's Triassic fossil collection was later purchased by Cope, and eventually donated to the AMNH. Von Huene (1921) makes no mention of *Dicynodon rosmarus* in his otherwise exhaustive survey of this collection, and it seems that if indeed the *D. rosmarus* tooth was ever a part of the AMNH collections, it had been lost

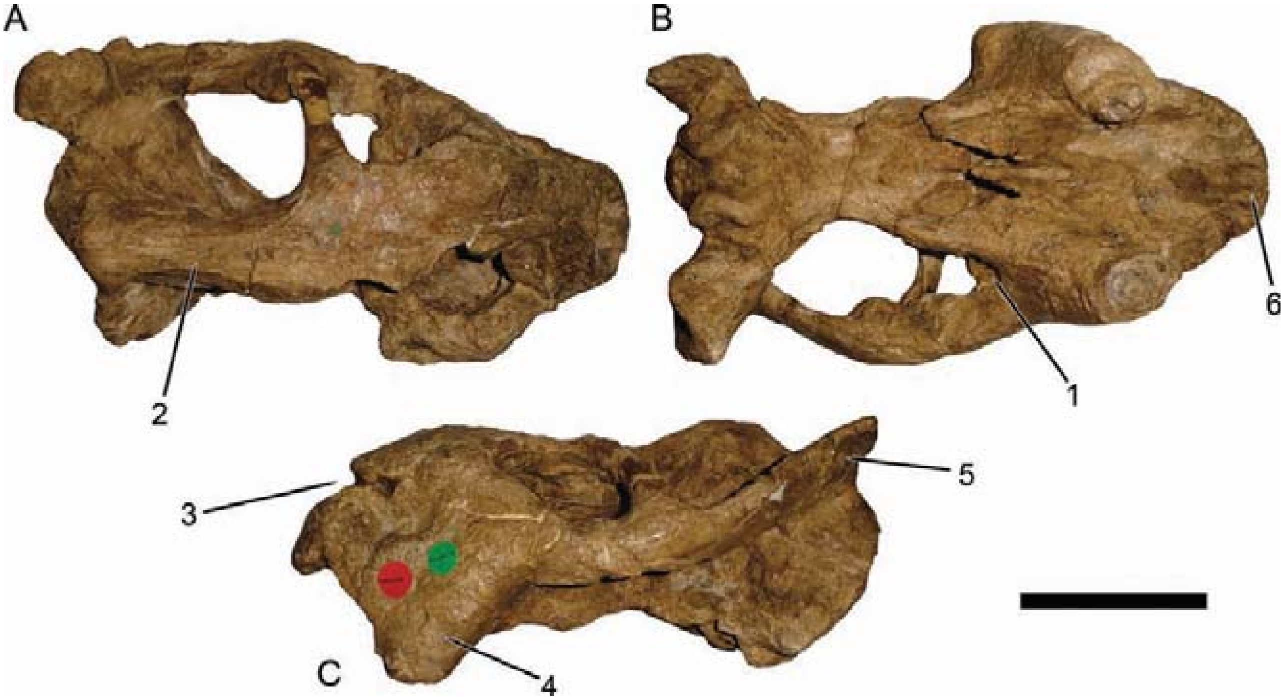

FIGURE 102. NHMUK 47045, the holotype of *Dicynodon pardiceps* (= *Dicynodon lacerticeps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *D. lacerticeps* on the basis of the (2) narrow but relatively short intertemporal bar, (3) gradually sloping snout profile, (4) anteriorly directed caniniform process, (5) acutely angled squamosal rami in lateral view, and (6) broad premaxillary portion of the palate with a squared-off tip. Scale bar equals 10 cm.

by that time. A thorough search of the AMNH Wheatley collection (including unaccessioned specimens) failed to locate any dental specimens corresponding to Cope's (1870b) description of *Dicynodon rosmarus*, and the other major repositories of Cope types (ANSP and USNM) also lack any records of this taxon. No dicynodont material of any kind is present in the AMNH Wheatley collection; the dental material from the Wheatley collection is almost entirely phytosaurian, and it is possible that *D. rosmarus* was as well. The enlarged teeth in the terminal rosette of phytosaurs would fit Cope's (1870b) description better than any Triassic dicynodont tusks, which tend to be only weakly recurved. However, as the original description is rather vague, and in the absence of figures and apparent loss of the type specimen, identification of *D. rosmarus* as a phytosaur is speculative, and its true

FIGURE 103. NHMUK 47062, the holotype of *Dicynodon parvidens* (= ?*Diictodon feliceps*), in left lateral (**A**), right medial (**B**), right lateral (**C**), and left medial (**D**) views. Although this specimen is too poorly prepared to be certain of its identification, the short, narrow intertemporal region and apparent precaniniform notch exposed on the right side of the skull strongly suggest that it is an individual of *Diictodon feliceps*. Scale bar equals 1 cm.

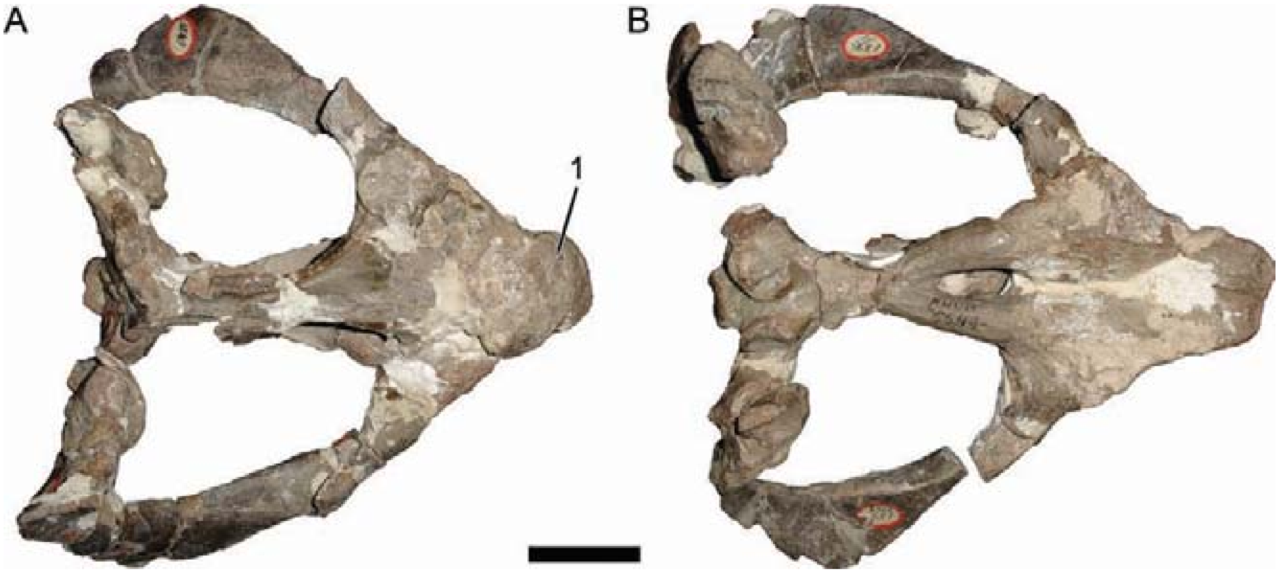

FIGURE 104. AMNH FARB 5549, the holotype of *Dicynodon planus* (= *Oudenodon bainii*), in dorsal (**A**) and palatal (**B**) views. This specimen can be identified as a cryptodont on the basis of (1) paired nasal bosses overhanging the nares and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

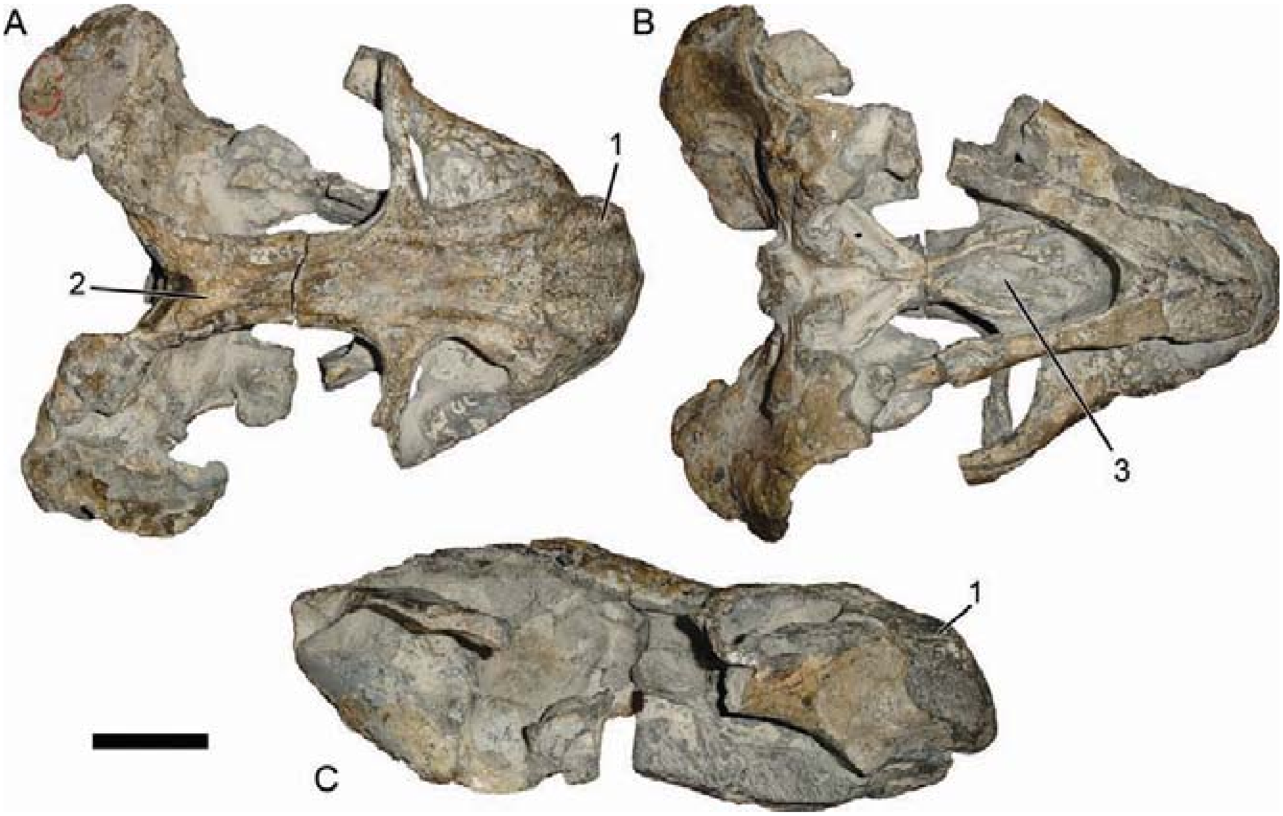

FIGURE 105. AMNH FARB 5542, the holotype of *Dicynodon platyceps* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (2) dorsal skull roof exposure of the postparietal and (3) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 10 cm.

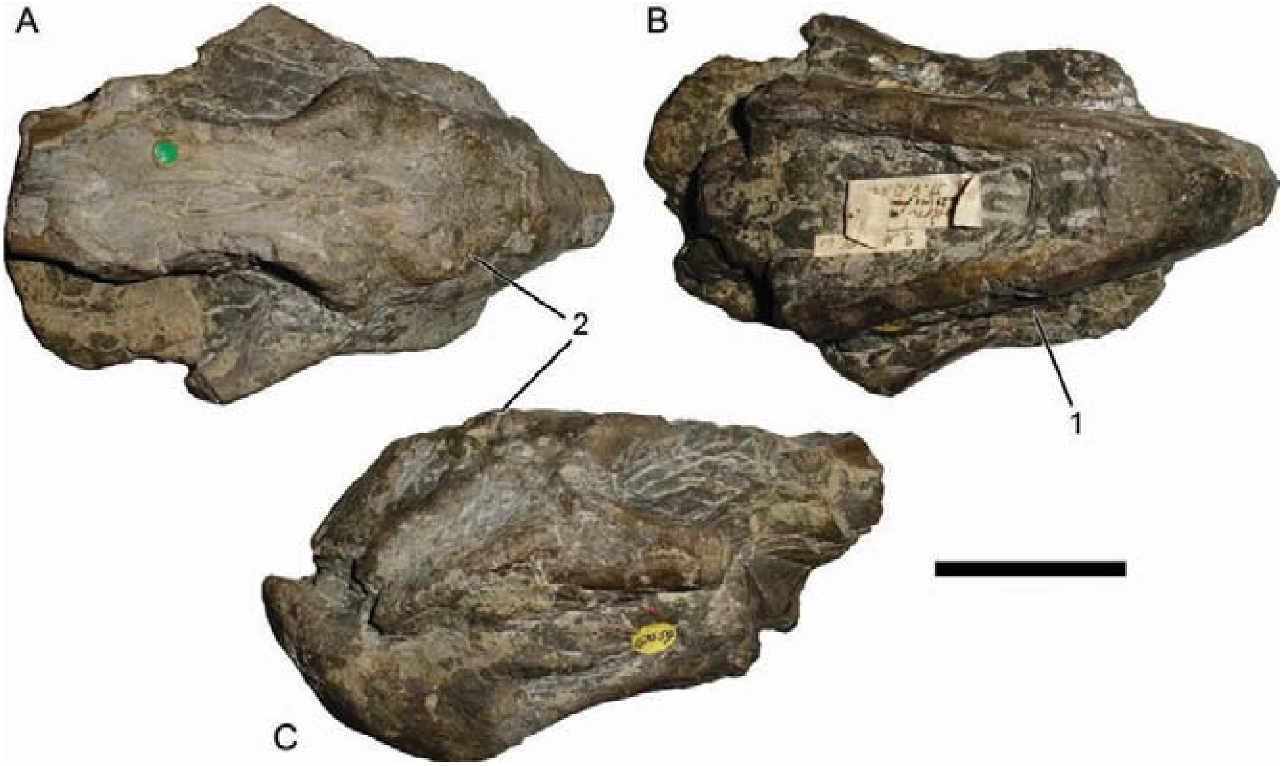

FIGURE 106. NHMUK 47059, the holotype of *Dicynodon prognathus* (= *Oudenodon bainii*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares. The relatively small, ovoid nasal bosses, absence of tusks, and snout proportions allow this specimen to be identified as *O. bainii*. Scale bar equals 5 cm.

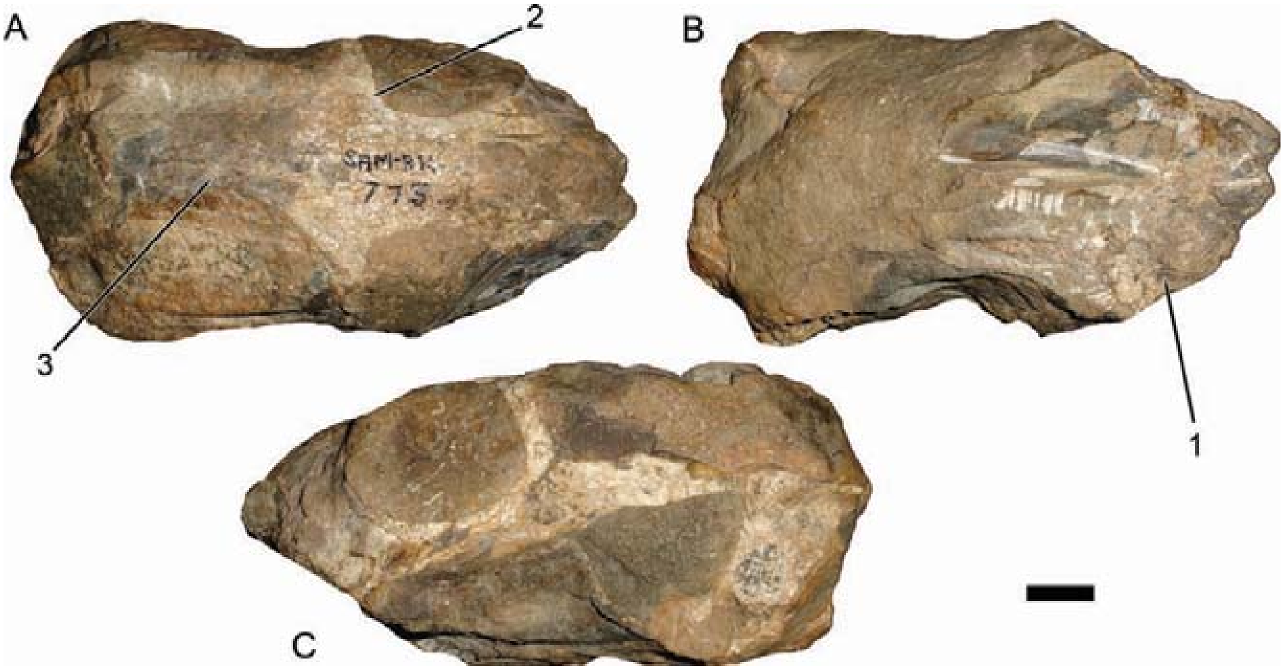

FIGURE 107. SAM-PK-775, the paratype of *Dicynodon pseudojouberti* (= *Emydops* sp.), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) embayment of the palatal rim anterior to the caniniform process and as *Emydops* on the basis of the (2) presence of the postfrontal and (3) broadly exposed parietals. Scale bar equals 1 cm.

FIGURE 108. AMNH FARB 5534, the holotype of *Dicynodon psittacops* (= *Diictodon feliceps*). This specimen can be identified as a pylaecephalid by the precaniniform notch (not figured) and as *D. feliceps* by the narrow intertemporal bar with extensive postorbital-parietal overlap and lack of teeth. Scale bar equals 5 cm.

identity will likely never be known. This taxon must be considered a nomen dubium.

Dicynodon rossicus (Amalitzky, 1922)

Holotype—PIN 2005/3, a badly distorted skull (Fig. 117).

Locus Typicus—Sokolki, Arkhangelsk Region, Kotlasskii District, Russia.

Horizon—Upper Vyatkian substage, Tatarian series (Upper Permian).

Status—Junior subjective synonym of *Vivaxosaurus trautscholdi* (Amalitzky, 1922).

Remarks—Amalitzky (1922) described two new species of the otherwise Scottish dicynodont genus *Gordonia* from the Upper Permian of Russia: *G. annae* and *G. rossica*. Sushkin (1926) considered *G. rossica* to be a junior synonym of *Dicynodon trautscholdi*, but von Huene (1940) retained it as valid, albeit within *Dicynodon* as *D. rossicus*. Subsequent authors (Efremov, 1940; King, 1988; Ivakhnenko et al., 1997; Angielczyk and Kurkin, 2003a; Ivakhnenko, 2003) have followed Sushkin's (1926) referral, and the synonymy of *G. rossica* and *D. trautscholdi* is upheld here. Although PIN 2005/3 is highly distorted, the autapomorphic caniniform morphology of *D. trautscholdi* (narrow and anteriorly directed, with a rounded anterior lobe) is visible in this specimen.

Dicynodon rubidgei Broom, 1932

Holotype—NHMUK 47081, a laterally sheared skull and right lower jaw (Fig. 118).

Locus Typicus—Graaff-Reinet, South Africa.

Horizon—*Cistcephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom (1932) described *Dicynodon rubidgei* based on a small skull with heavy weathering of the anterior palate. Van Hoepen (1934) included *D. rubidgei* in the new genus *Pylaecephalus* along with *Dicynodon ictinops*, *Dicynodon macrorhynchus*, *Dicynodon sollasi*, and *Dicynodon testudirostris* (all currently considered synonyms of *Diictodon feliceps*). Cluver and Hotton (1981) transferred *D. rubidgei* to *Diictodon* (see also King, 1988), and Brink (1986) and Sullivan and Reisz (2005) considered it a junior synonym of *Diictodon feliceps*. The dorsal surface of NHMUK 47081 is badly sheared leftwards, and the snout and anterior palate are poorly preserved. Most bones of the skull are intact, however, with clear sutures. No tusks are present. Although damaged, the right caniniform process appears to have a precaniniform notch; this, coupled with the lack of postcanine teeth and short, posterior overlap of the parietals by the postorbitals, indicates that this is a specimen of *Diictodon feliceps*.

Dicynodon scheepersi Broom, 1948

Holotype—RC 95, a well-preserved skull missing the right postorbital bar (Fig. 119).

Locus Typicus—The 3rd Drift, Adendorp, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Rhachiocephalus magnus* (Owen, 1876).

Remarks—Broom (1948) described *Dicynodon scheepersi* as a large species of *Dicynodon*, comparable to *Dicynodon rogersi* (= *Tropidostoma dubium*) and *Dicynodon whaitsi* (= *Odontocyclops whaitsi*) but distinguished by a narrower parietal region. Broom noted that this species has a large pineal foramen with a raised rim. Haughton and Brink (1954) and King (1988) listed *D. scheepersi* as a valid species of *Dicynodon*, but Keyser (1975) noted that it was very similar to species Broom (1948) described as *Platycyclops* (which Keyser [1975] considered synonymous with *Rhachiocephalus*). Brink (1986) listed *D. scheepersi* as a junior synonym of *Rhachiocephalus magnus* without comment. RC 95 is tuskless, and displays the narrow, triangular snout, elongate nasal and prefrontal bosses, and massive pineal boss diagnostic for *R. magnus*.

Dicynodon schroederi Toerien, 1953

Holotype—BP/1/2235, a poorly preserved skull missing the temporal arches (Fig. 120).

Locus Typicus—Kleinwaterval, Prince Albert, South Africa.

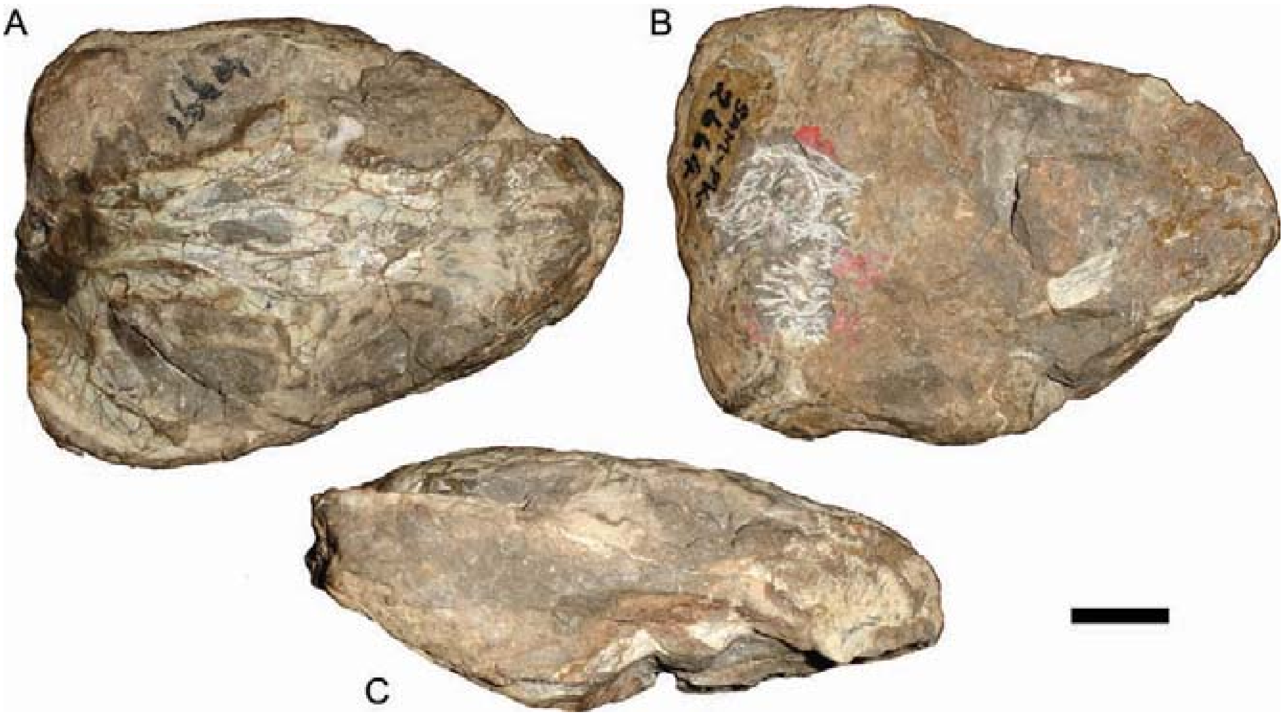

FIGURE 109. SAM-PK-2664, the holotype of *Dicynodon pygmaeus* (= *Pristerodon mackayi*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. The poor preparation of this specimen complicates identification, but the combination of postcanines, the clear absence of a precaniniform notch, and nearly equal contributions by the postorbitals and parietals to the width of the intertemporal indicate that this specimen probably represents *P. mackayi*. Scale bar equals 1 cm.

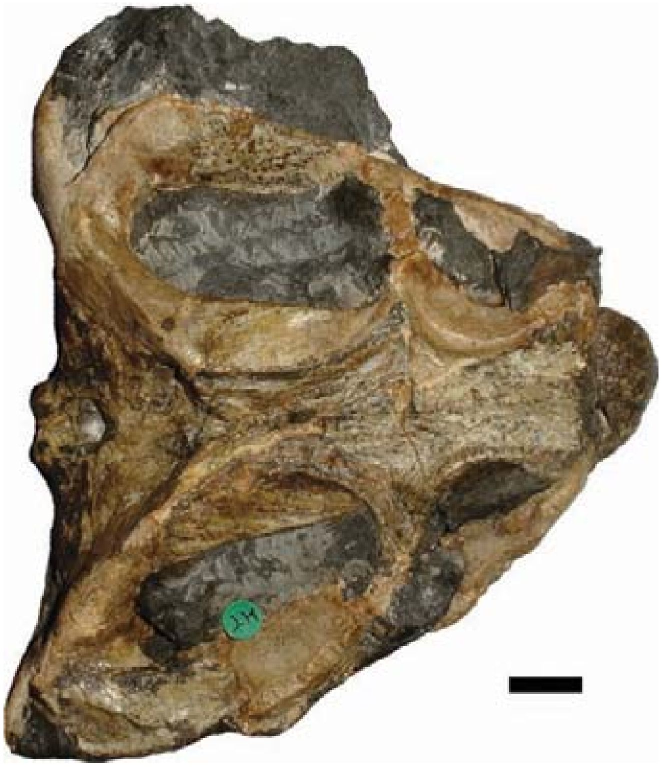

FIGURE 110. NHMUK R1650, the holotype of *Dicynodon raniceps* (= *Pristerodon mackayi*), in dorsal view. This specimen has postcanines and the intertemporal bar morphology characteristic of *Pristerodon*, with postorbitals and parietals of nearly equal width (unlike in *Emydops*, in which the parietals are significantly wider). Scale bar equals 1 cm.

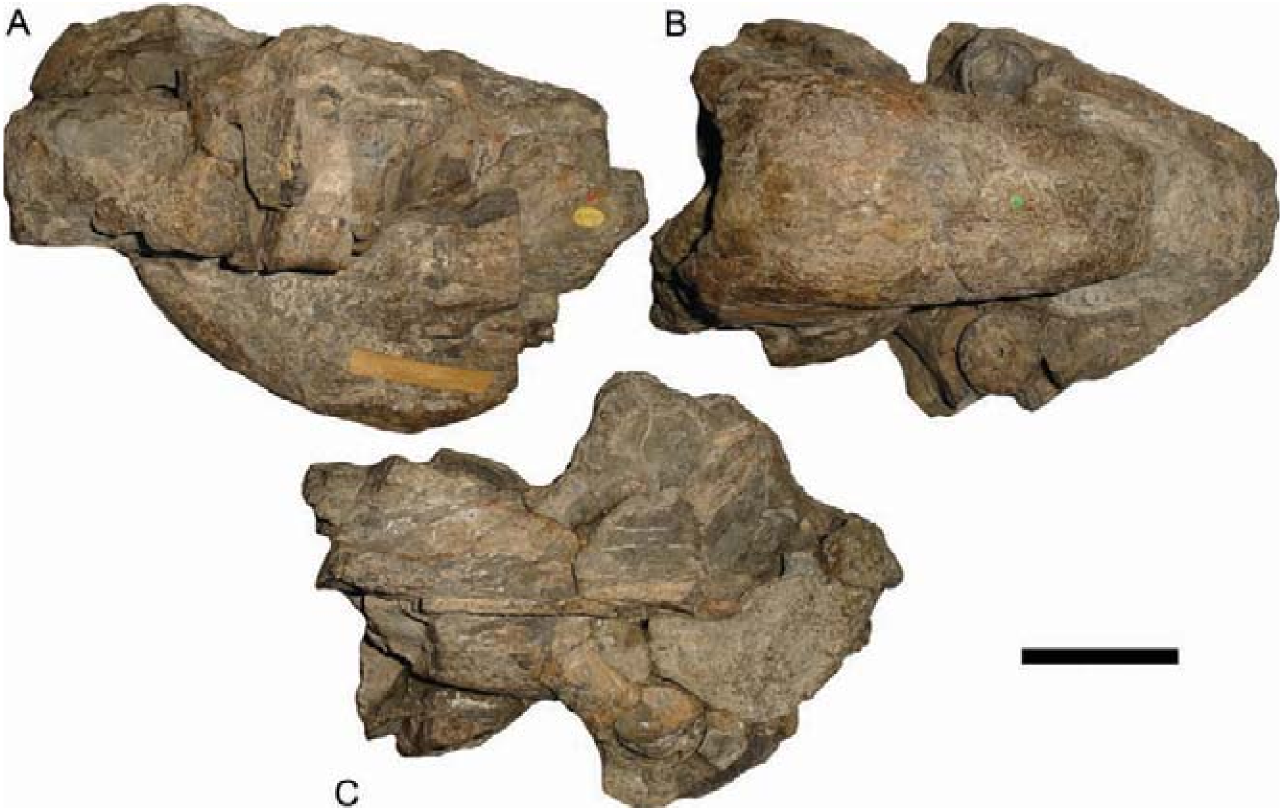

FIGURE 111. NHMUK 47057, the holotype of *Dicynodon rectidens*, in left lateral (**A**), ventral (**B**), and dorsal (**C**) views. This specimen is highly incomplete, and may represent an individual of *Aulacephalodon bainii* or *Daptocephalus leoniceps*. Scale bar equals 5 cm.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Robertia broomiana* Boonstra, 1948.

Remarks—Toerien (1953) described *Dicynodon schroederi* based on a pair of small skulls (the other is BP/1/286) from *Tapinocephalus* AZ exposures in Kleinwaterval. Haughton and Brink (1954), Kitching (1977), and King (1988) listed *D. schroederi* as a valid species of *Dicynodon*, but Brink (1986) listed it as a junior synonym of *Diictodon feliceps* without comment. BP/1/2235 is recognizable as a pylaecephalid by the presence of a precaniniform notch and median snout ridge, but the broad intertemporal bar (with consistent parietal exposure) and presence of postcanines indicates that this specimen represents *Robertia broomiana* rather than *Diictodon feliceps*. With regards to the rarer Karoo pylaecephalids, the anteroposteriorly narrow postorbital bar of BP/1/2235 rules out identification as *Eosimops newtoni* (Angielczyk and Rubidge, in press), and the broad intertemporal bar also rules out identification as *Prosictodon dubei* (Angielczyk and Rubidge, 2010).

Dicynodon schwarzi Broom, 1919

Holotype—AMG 2817, a nearly complete skull missing part of the edges of the temporal arches (Fig. 121).

Locus Typicus—12 miles northwest of Pearston, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1919) described *Dicynodon schwarzi* on the basis of a skull originally identified as *Oudenodon bainii*. Upon further study, Broom considered the parietal region of AMG 2817 to be different enough from NHMUK 36232 (the holotype of *O. bainii*) to warrant specific distinction. Broom (1919) cited the elongate posterior processes of the frontals and deep groove between the parietals as particular features distinguishing *D. schwarzi* from *O. bainii* and most other species of *Dicynodon*. Keyser (1975) considered AMG 2817 to fall within the range of variation observed for *O. bainii*, and synonymized the two species. Subsequent studies have supported this assessment (e.g., Kitching, 1977; Brink, 1986; King, 1988) and it is maintained here.

Dicynodon scopulusa (Sun, 1978)

Holotype—IVPP V4695, a partial snout, lower jaw, and partial forelimb.

Locus Typicus—Gongbangou, Xinjiang, China.

Horizon—Quanzijie Formation (Upper Permian).

Status—Uncertain (see below).

Remarks—Sun (1978) described *Kunpania scopulusa* based on a fragmentary snout missing the tips of the premaxillae and caniniform processes and a lower jaw broken off posterior to the mandibular fenestra. King (1988) noted the similarity between this taxon and *Dicynodon*, but tentatively maintained it as separate based on the lateral position of a groove on the dentary. Lucas (1998a, 2001) considered *Kunpania* to be synonymous with *Dicynodon*, but retained it as a valid species in the new combination *D. scopulusa*, distinguished by the long mandibular fenestra,

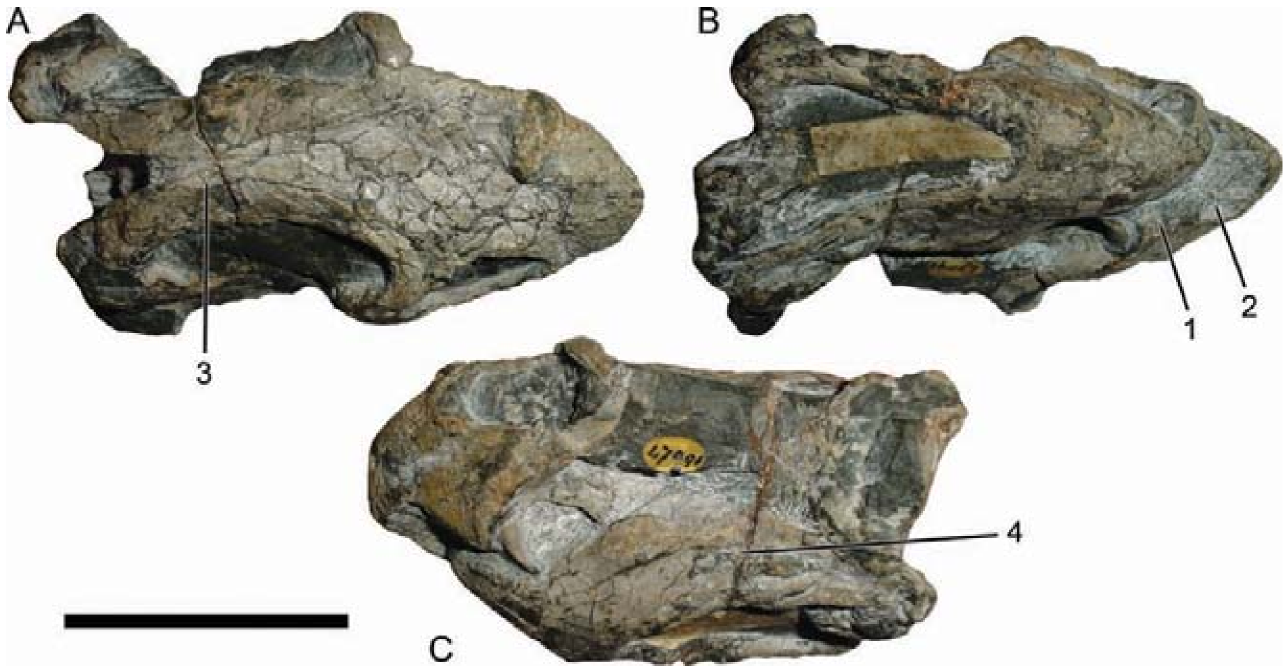

FIGURE 112. NHMUK 47091, the holotype of *Dicynodon recurvidens* (= *Dicynodontoides recurvidens*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as an emydopoid on the basis of the (1) embayment of the palatal rim anterior to the caniniform process and (2) palatal surface of the premaxilla with a groove-like depression with a rounded anterior end, and as a kingoriid on the basis of the (3) postorbitals sloping slightly ventrolaterally, overlapping the parietals except for a narrow exposure of the latter as a sagittal crest, and (4) restriction of the mandibular fenestra. *Dicynodontoides recurvidens* is distinguished from the Tanzanian species *D. nowacki* on the basis of postcranial morphology, smaller average size, and greater frequency of tusks (Angielczyk et al., 2009). Scale bar equals 5 cm.

lateral dentary shelf, and fossa dorsal to the shelf. Lucas (2005a) later considered this species to be a nomen dubium. The snout fragment of IVPP V4695 shares with *Jimusaria sinkianensis* the strong anterior angulation of the caniniform process, which is not attributable to deformation in this specimen. The morphology of the lateral dentary shelf in IVPP V4695 also corresponds closely with that of the holotype of *J. sinkianensis* (IVPP 341407), being a prominent, dorsoventrally narrow ridge running horizontally over the length of the mandibular fenestra. However, IVPP V4695 represents a much larger animal than IVPP 341407. Because IVPP 341407 appears to be an adult skull (as indicated by the large tusks, small preparietal, long, narrow intertemporal bar,

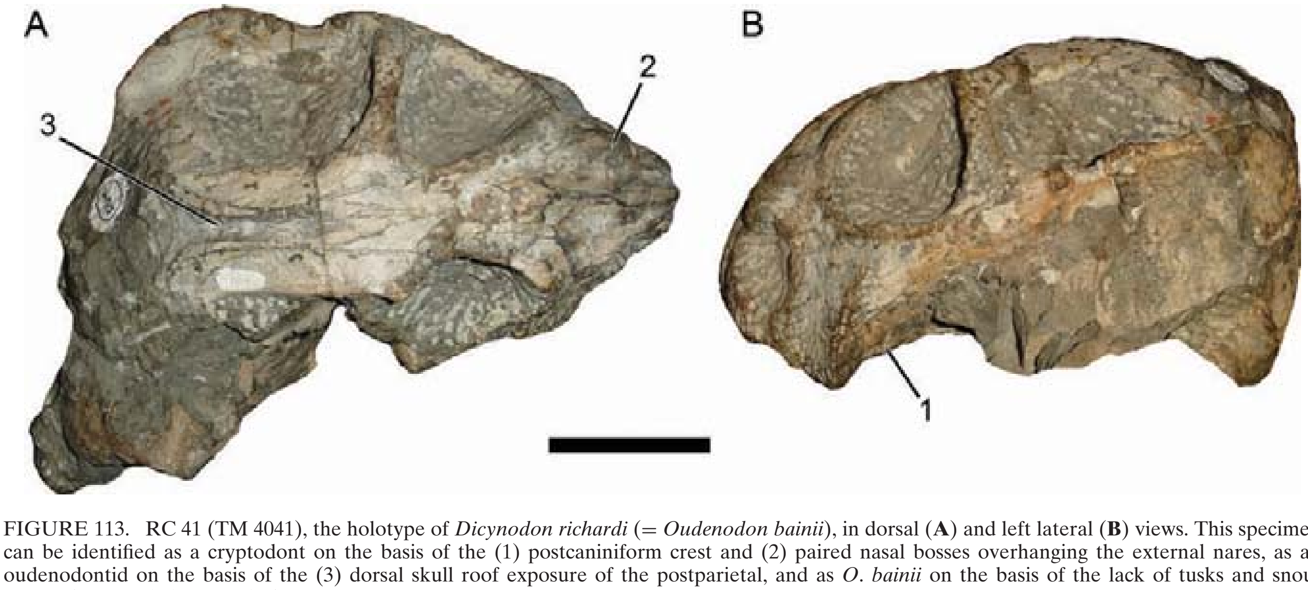

FIGURE 113. RC 41 (TM 4041), the holotype of *Dicynodon richardi* (= *Oudenodon bainii*), in dorsal (**A**) and left lateral (**B**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

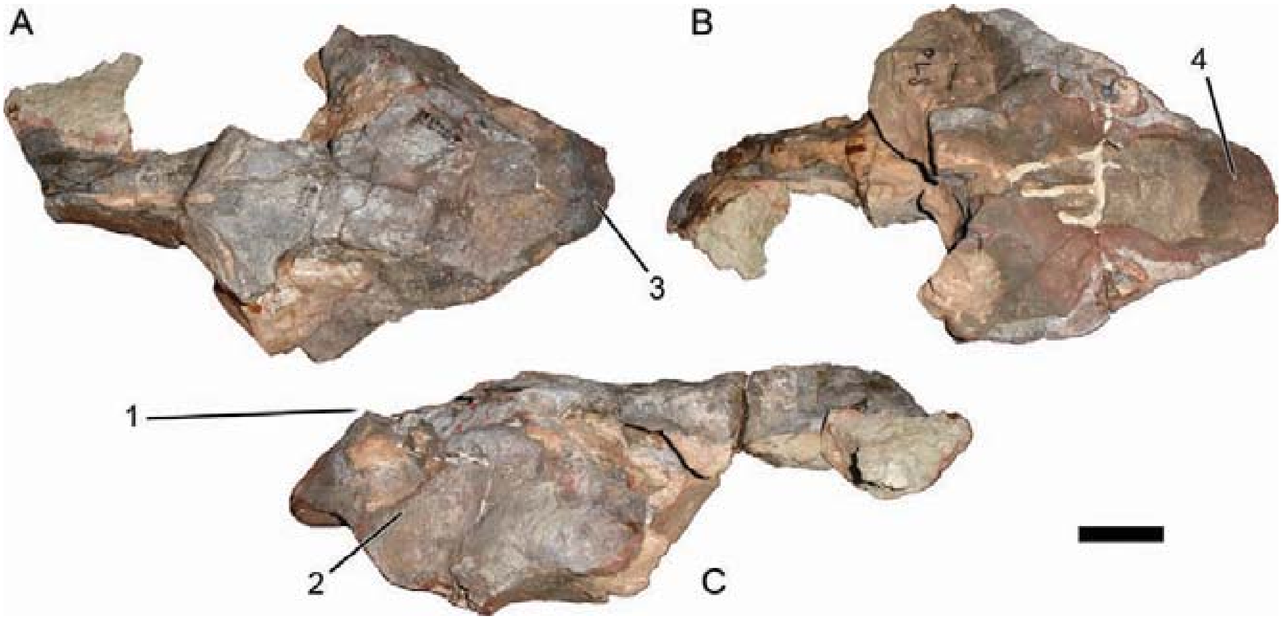

FIGURE 114. SAM-PK-11325B, the holotype of *Dicynodon roberti* (= *Syops vanhoepeni*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as *S. vanhoepeni* on the basis of the (1) distinct break in slope of the snout between the nasal and premaxilla above the external naris, (2) ridge on the lateral surface of the premaxillary-maxillary suture, (3) paired depressions on the anterodorsal surface of the premaxilla, and (4) elongate premaxillary portion of the palate with squared-off tip. Scale bar equals 5 cm.

and sutural closure), it is unlikely that these two skulls represent part of the growth series of a single taxon. Unfortunately, the type material of *D. scopulusa* is too fragmentary to be certain that it is distinct—no autapomorphies can be found in the available cranial material. It may represent a valid taxon, but further research and ideally new material is required.

Dicynodon seeleyi Broili, 1908

Holotype—A partial postcranium including the pelvic girdle, now lost.
Locus Typicus—Gryskop, Middelburg, South Africa.
Horizon—?*Lystrosaurus* Assemblage Zone (Lower Triassic).
Status—Nomen dubium (probably *Lystrosaurus* sp.).
Remarks—Broili (1908) named *Dicynodon seeleyi* on the basis of a fragmentary postcranial skeleton of a dicynodont, preserving part of the axial column and pelvic girdle. Although the dorsal margin of the ilium is incomplete, making it impossible to determine whether the characteristic 'scalloped' morphology of *Lystrosaurus* is present, in general shape the iliac blade agrees closely with the condition in *Lystrosaurus*. In the absence of further information or rediscovery of the holotype, this referral must be considered uncertain, and *D. seeleyi* must be considered a nomen dubium.

Dicynodon sidneyi Broom, 1940b

Holotype—RC 44, a laterally crushed skull missing the temporal arches (Fig. 122).
Locus Typicus—Wellwood, Graaff-Reinet, South Africa.
Horizon—*Dicynodon* Assemblage Zone (Upper Permian).
Status—Possible junior subjective synonym of *Pelanomodon moschops* (Broom, 1913c).
Remarks—Broom (1940b) described *Dicynodon sidneyi* as having an exceptionally long, relatively narrow intertemporal bar, short snout, no tusks, and expanded nasals with bosses over the nares. This species was not addressed by Cluver and Hotton (1981) or King (1988), although Brink (1986) listed it as a junior synonym of *Diictodon feliceps* without comment. RC 44 is not a specimen of *Diictodon*: it has a lengthy intertemporal bar, prominent, paired nasal bosses overhanging the nares, and lacks a precaniniform notch. Based on the nasal boss morphology and presence of a well-developed postcaniniform crest, RC 44 is identifiable as a cryptodont, and the presence of a transverse ridge across the snout at the level of the prefrontals identifies it as a geikiine. Based on the absence of tusks, we tentatively identify RC 44 as a juvenile specimen of *Pelanomodon moschops*. However, the extremely narrow intertemporal region, with extensive postorbital-parietal overlap, is at odds with the usual condition in geikiines. Adult specimens of *Aulacephalodon*, *Geikia*, and *Pelanomodon* all exhibit broad exposure of the parietals in the intertemporal bar. RC 44 has suffered from lateral compression, which probably exaggerated the narrowness of the intertemporal bar in this specimen, but this is not sufficient to account for the nearly complete overlap of the parietals. Intriguingly, a narrow intertemporal bar is also observed in the problematic holotype of *Propelanomodon devilliersi* (BP/1/485), a tuskless specimen displaying several geikiine synapomorphies (see entry on *Dicynodon tylorhinus*) but generally considered to be distinct from *Pelanomodon* and *Geikia* (e.g., Keyser, 1975; King, 1988; Maisch, 2003). The highly characteristic nasal boss morphology of *Propelanomodon* is not observed in RC 44, however, which is similar in snout morphology to the holotype of *Pelanomodon moschops* (AMNH FARB 5325). It should be noted that although the relative width of the intertemporal bar and degree of exposure of the parietals generally decreases with size in dicynodonts (markedly so in Permian dicynodontoids, in which the adults have nearly complete postorbital-parietal overlap), in small (presumably juvenile) specimens of *Aulacephalodon* (e.g., BP/1/763, the holotype of *Proaulacocephalodon miltoni*) the intertemporal bar is proportionally narrower than in large adults. More research on ontogenetic variation in geikiines is required; this clade may be

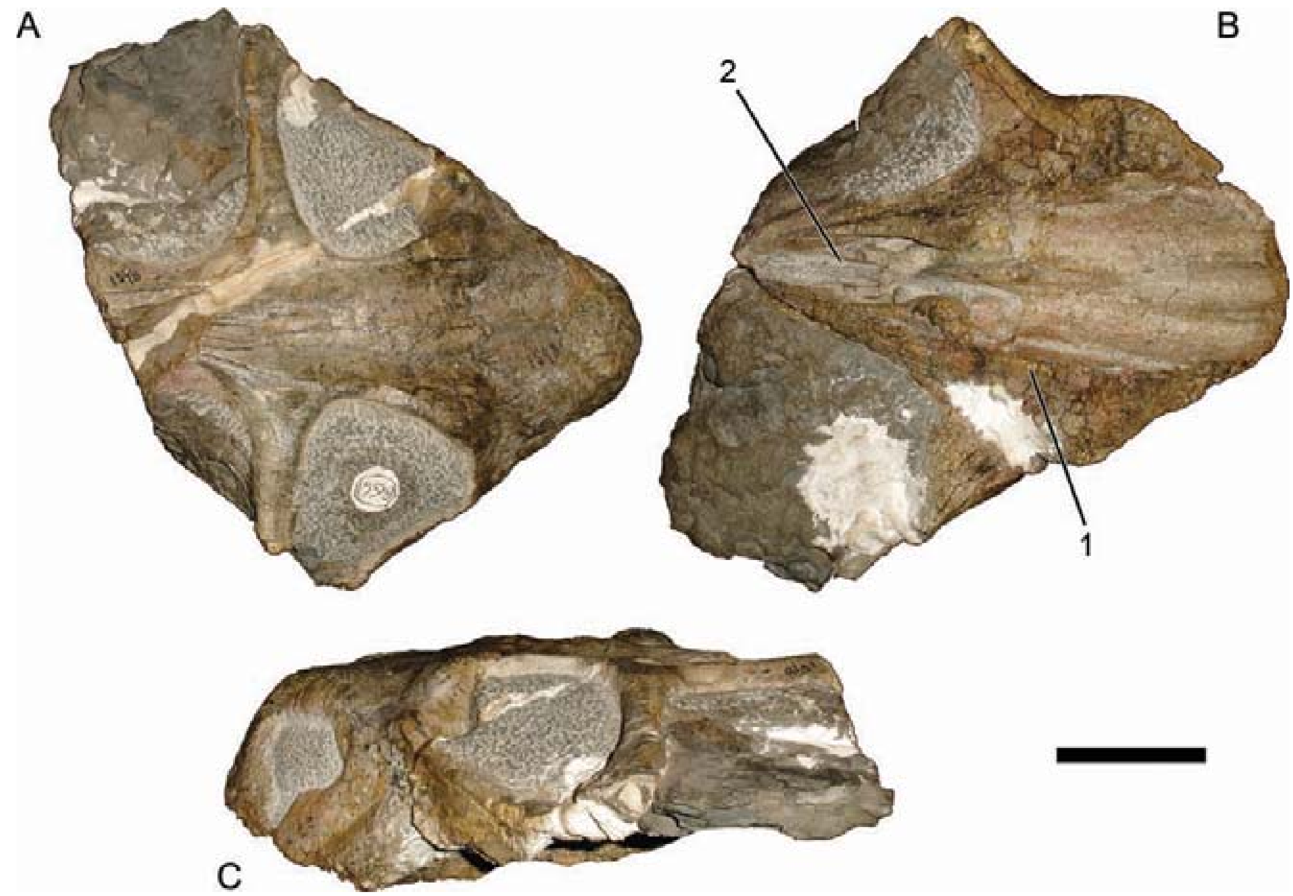

FIGURE 115. TM 1598, the holotype of *Dicynodon robertsi* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest, as an oudenodontid on the basis of the (2) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

characterized by a reverse trend in intertemporal width during growth compared to most dicynodonts.

Dicynodon simocephalus Weithofer, 1888

Holotype—NMW 8178, the right side of a skull (Fig. 123).

Locus Typicus—Unknown (but noted as probably Dwarsvlei, Aliwal North, by Cruickshank [1970]), South Africa.

Horizon—?*Cynognathus* Assemblage Zone (Middle Triassic).

Status—Valid as *Kannemeyeria simocephala* (Weithofer, 1888).

Remarks—Weithofer (1888) described the first specimen of a large Middle Triassic dicynodont from South Africa as the new species *Dicynodon simocephalus*. In the description of *Dicynodon strigops*, Broom (1913b) refers to the large *Dicynodon* species of the *Cynognathus* Zone, and later (1915a) listed *Kannemeyeria* as a subgenus of *Dicynodon*: *Dicynodon* (*Kannemeyeria*) *simocephalus*. Broom (1913c) first combined *D. simocephalus* with Seeley's (1909) genus *Kannemeyeria*, named for a fragmentary skull (NHMUK R3593, holotype of *Kannemeyeria proboscoides*) that Seeley believed would have housed a mobile proboscis (the large, open nares of the holotype are the result of breakage, however). Subsequent researchers have universally considered *Kannemeyeria* a valid taxon distinct from *Dicynodon* (see King, 1988), although the orthography of the type species name has varied between the original *K. simocephalus* and the correct gender agreement of *K. simocephala* (because *Kannemeyeria* is a feminine name). We utilize the latter, in accordance with Article 34.2 of the International Code of Zoological Nomenclature (ICZN, 1999).

Dicynodon sinkianensis Yuan and Young, 1934

Holotype—IVPP 341407, a well-preserved skull (missing the left temporal arch) and lower jaws (Fig. 124).

Locus Typicus—Northern foot of Tienshan, Xinjiang, China.

Horizon—Guodikeng Formation (Upper Permian).

Status—Valid as *Jimusaria sinkianensis* (Yuan and Young, 1934).

Remarks—Yuan and Young (1934) described *Dicynodon sinkianensis* (often misspelled *sinkiangensis* in the literature) as the first species of *Dicynodon* from China. Sun (1963) made *D. sinkianensis* the type species of a new genus, *Jimusaria*, and later (Sun, 1973) added the similar *J. taoshuyuanensis* to this genus. King (1988) returned *D. sinkianensis* to *Dicynodon*, with *J. taoshuyuanensis* as a synonym, a referral supported by Lucas (1998a, 2001). *Jimusaria sinkianensis* can be distinguished from the other valid taxon of Xinjiang Permian dicynodontoid, *Turfanodon bogdaensis*, by its more elongate, mediolaterally narrow, gradually sloping snout, lengthy median exposure of the nasals separating the frontals and premaxilla on the dorsal surface of the snout, absence of a depression anterior to the pineal

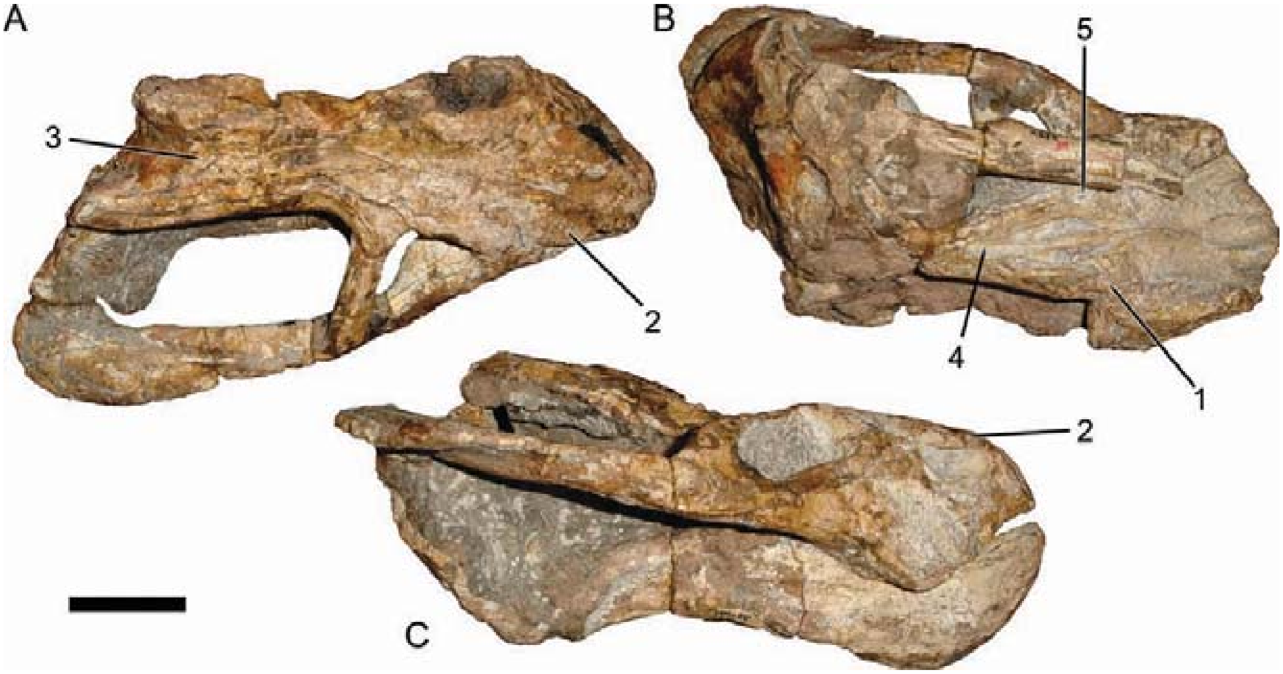

FIGURE 116. SAM-PK-2356, the holotype of *Dicynodon rogersi* (= *Tropidostoma dubium*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *Tropidostoma* on the basis of the tusks, (5) postcanine teeth, and snout proportions. Scale bar equals 5 cm.

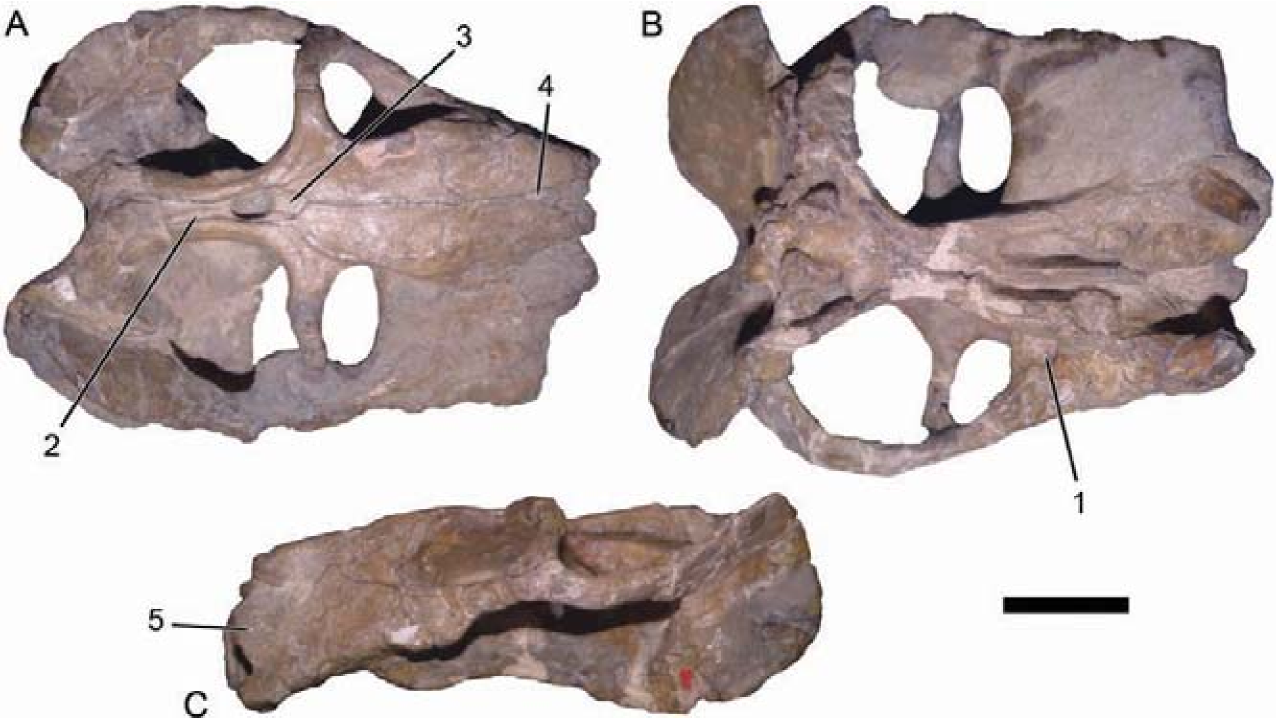

FIGURE 117. PIN 2005/3, the holotype of *Dicynodon rossicus* (= *Vivaxosaurus trautscholdi*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa, and as *V. trautscholdi* on the basis of the (2) short intertemporal bar with narrow but consistent exposure of the parietals, (3) a depression on the preparietal at the anterior edge of the pineal foramen, (4) an elongate ascending process of the premaxilla, and a (5) anteriorly directed caniniform process with rounded anterior lobe. Scale bar equals 5 cm.

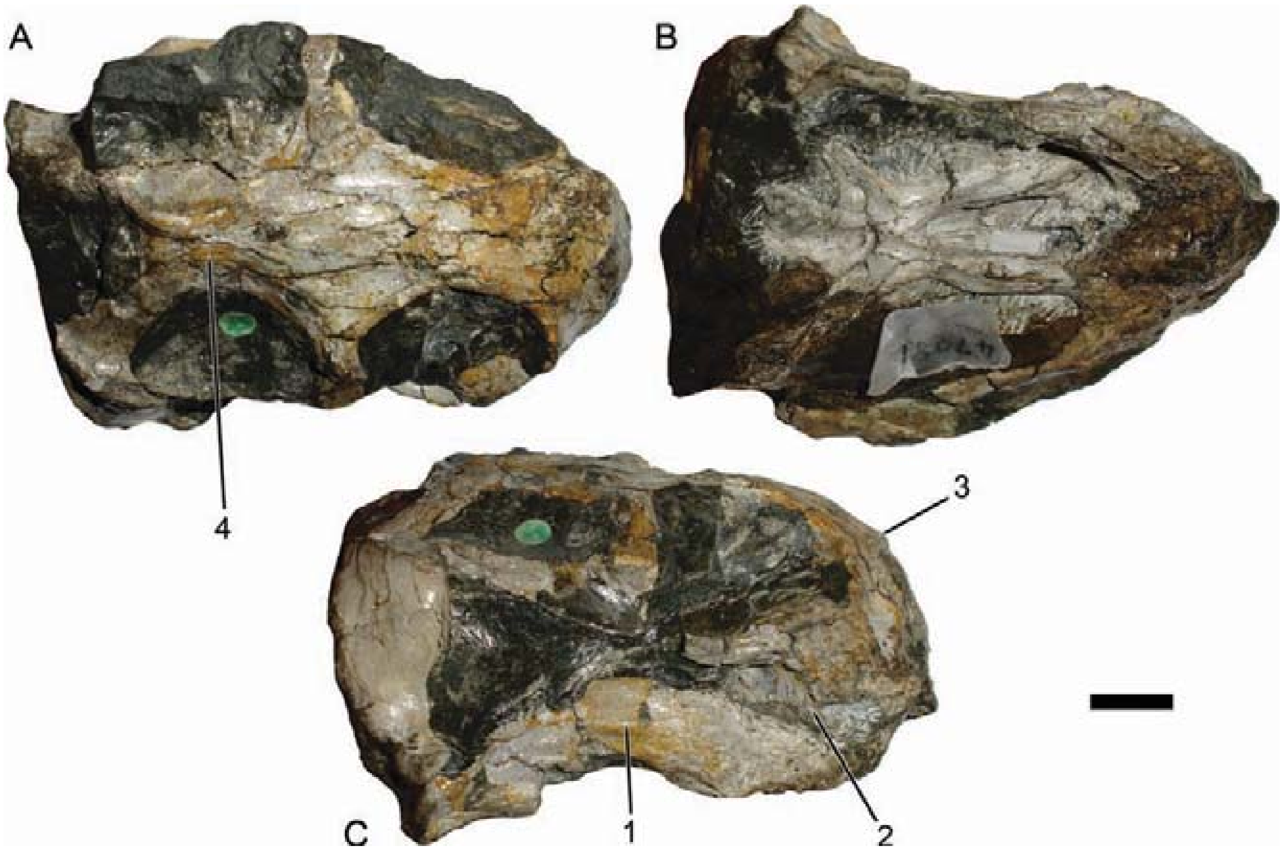

FIGURE 118. NHMUK 47081, the holotype of *Dicynodon rubidgei* (= *Diictodon feliceps*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) sharp lateral dentary shelf, (2) ventral margin of caniniform proces at the level of the anterior edge of the orbit, and (3) median snout boss and as *D. feliceps* on the basis of the (4) narrow intertemporal bar with extensive postorbital-parietal overlap and lack of teeth. Scale bar equals 1 cm.

foramen, exposure of the postfrontals in the dorsal skull roof, and anteroposteriorly narrower, more acutely angled squamosal rami in lateral view. *Jimusaria sinkianensis* can be distinguished from other dicynodontoids (except *Daptocephalus leoniceps*) by the arcuate grooves on the postorbitals at the anteromedial edge of the temporal fenestrae. *Jimusaria sinkianensis* differs from *D. leoniceps* by its relatively short intertemporal bar, acutely angled squamosal rami, and gradually sloping snout that narrows anterior to the orbits in dorsal view. We agree with King (1988) in regarding *Jimusaria taoshuyuanensis* as a junior synonym of *J. sinkianensis*—the snout and intertemporal morphology of these species are indistinguishable, showing all the characters that distinguish this taxon from *Turfanodon*. Among extrabasinal Permian dicynodontoids *J. sinkianensis* is most similar to *Dicynodon lacerticeps*, but differs from that taxon in the mediolaterally narrower snout and morphology of the lateral dentary shelf (an elongate horizontal ridge in *J. sinkianensis*, without a prominent, rounded swelling at the anterodorsal border of the mandibular fenestra).

Dicynodon sollasi Broom, 1921

Holotype—SAM-PK-7420, a dorsoventrally crushed complete skull and lower jaws (Fig. 125).

Locus Typicus—Biesjiespoort, Victoria West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom (1921) recognized a close similarity between *Dicynodon sollasi* and *Dicynodon feliceps*, *Dicynodon ictidops*, and *Dicynodon testudiceps* (all considered to represent a single species, *Diictodon feliceps*, herein). He distinguished *D. sollasi* from *D. feliceps* based on the more delicately built skull and thinner tusks, from *D. testudiceps* based on the lesser degree of overlap of the parietals by the postorbitals, and from *D. ictidops* by the smaller preparietal. Van Hoepen (1934) included *D. sollasi* in his new genus *Pylaecephalus* (including several species currently considered synonymous with *Diictodon feliceps*, albeit not *D. feliceps* itself, which he retained in *Dicynodon*). Cluver and Hotton (1981) transferred *D. sollasi* to *Diictodon*, and King (1988) retained it as the distinct species *Diictodon sollasi*. Brink (1986) and Sullivan and Reisz (2005) considered *D. sollasi* to represent a junior synonym of *D. feliceps*, and this approach is followed here. SAM-PK-7420 is a dorsoventrally compressed but well-preserved and well-prepared skull and lower jaws, exhibiting the 'saddle shape' observed in dicynodont skulls that have suffered proportionally greater compression of the orbitotemporal region than the more robust snout and occiput. SAM-PK-7420 displays a combination of characters diagnostic for *D. feliceps*, including the short intertemporal region with extensive postorbital-parietal overlap, a prominent median nasal boss, median ridge on anterior surface of snout, a distinct precaniniform notch, lack of postcanine teeth, and dentary table present as elongate grooved surface on the dorsal surface of the dentary bordered laterally by a low ridge and medially by a tall, thin, dorsally convex blade.

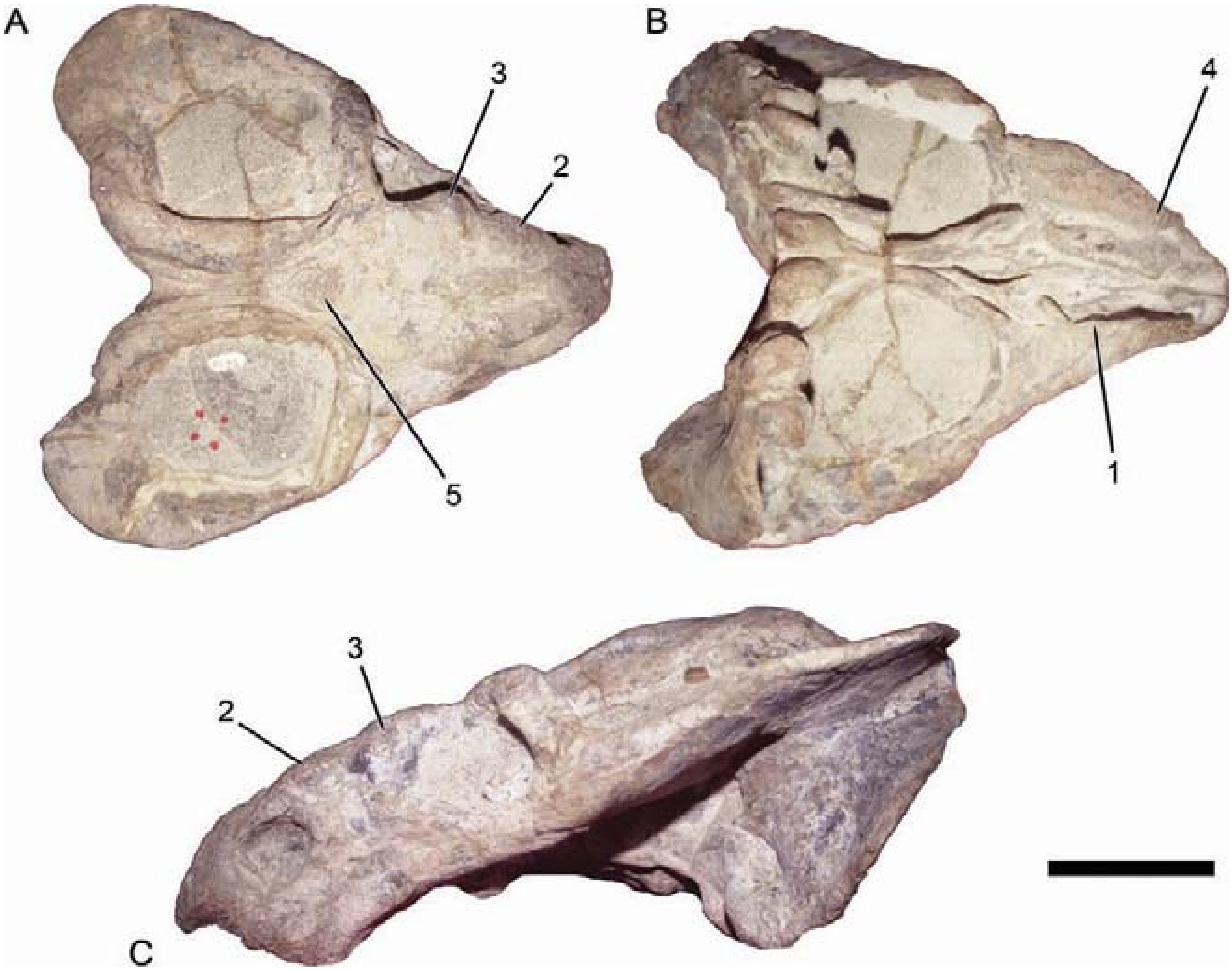

FIGURE 119. RC 95, the holotype of *Dicynodon scheepersi* (= *Rhachiocephalus magnus*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses, as a rhachiocephalid on the basis of the (2) elongate nasal bosses and (3) well-developed prefrontal bosses, (4) lack of tusks, and (5) rugose, massive, anteriorly angled pineal boss. This specimen can be identified as *Rhachiocephalus* rather than *Kitchinganomodon* based on the elongate, attenuate snout. Scale bar equals 10 cm.

Dicynodon strigiceps Owen, 1845

Holotype—NHMUK 47060, a weathered snout (Fig. 126).

Locus Typicus—Tarka prolongation of the Winterberg Range, South Africa.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontia indet.).

Remarks—Owen (1845) distinguished *Dicynodon strigiceps* from other species of the new genus by its remarkably short snout and forward-facing orbits. Owen (1876) later transferred this species to *Oudenodon* based on the (probable) lack of tusks, and Seeley (1898) included it in *Oudenodon* in the subgenus *Aulacocephalus* along with the type species *O. bainii*. Given the exceedingly poor preservation and incomplete nature of the holotype, most subsequent authors (e.g., Broom, 1932; Keyser, 1975; Brink, 1986) have considered *D. strigiceps* a nomen dubium. NHMUK 47060 is a weathered, poorly prepared skull fragment comprising the snout and anterior orbital region. The dorsal margins of the orbits and ventral margin of the premaxilla are broken off. The snout is short, deep, and bulbous; no discrete nasal bosses or snout ridges are evident (the snout is uniformly swollen in the nasal region), although this may be an artifact of overpreparation. No tusks appear to be present, although only the right caniniform process is intact enough to state that with any confidence. Only the premaxillary portion of the palate is preserved, but this area is too poorly prepared to interpret—part of the median posterior premaxillary ridge is visible, but all other structures have been chiseled away. Based on the apparent lack of tusks and general shape of the snout, this specimen is probably an individual of *Oudenodon bainii*. However, because the preserved portion of this skull lacks any discrete characters that permit definitive identification as an oudenodontid (much less *O. bainii* itself), *D. strigiceps* must be considered a nomen dubium. None of the synapomorphies diagnosing the major dicynodont subclades can be observed in NHMUK 47060, which should be regarded as Dicynodontia indet.

Dicynodon strigops Broom, 1913b

Holotype—AMNH FARB 5581, a badly weathered partial skull with the snout tip ground off (Fig. 127).

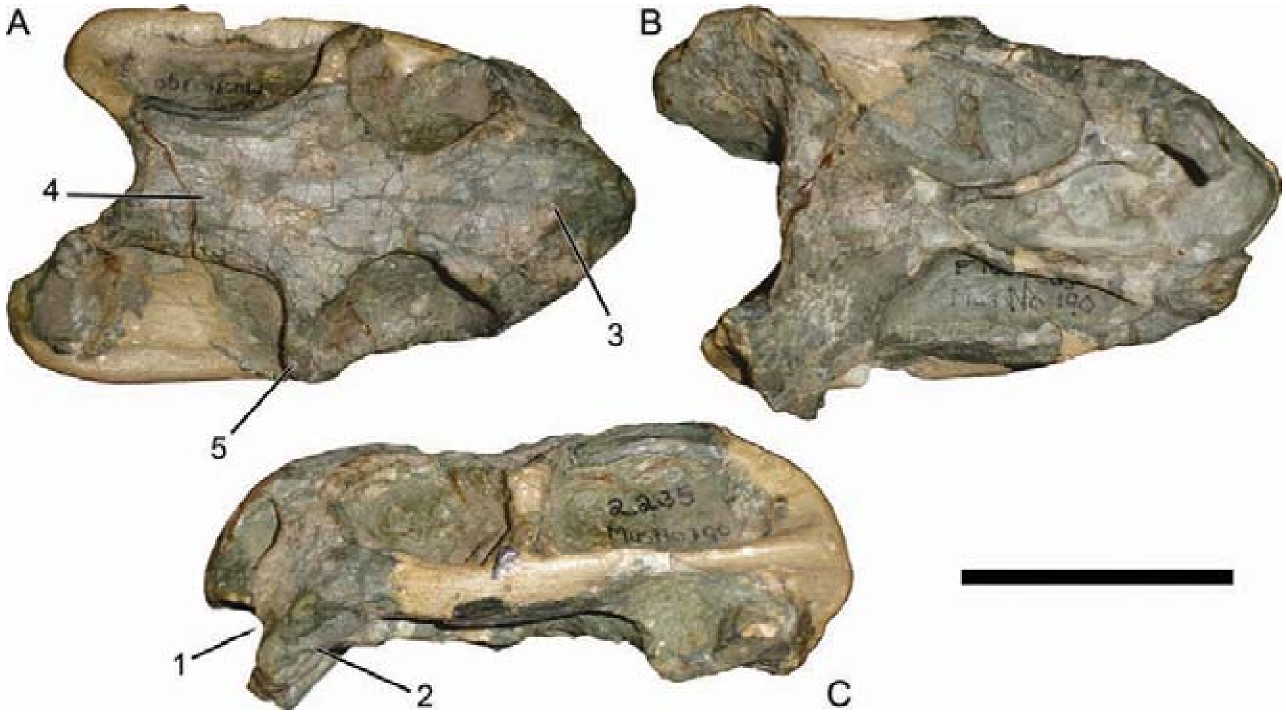

FIGURE 120. BP/1/2235, the holotype of *Dicynodon schroederi* (= *Robertia broomiana*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch, (2) ventral margin of the caniniform process at the level of the anterior margin of the orbit, and (3) median snout boss. This specimen can be identified as *Robertia* based on the combination of a (4) very wide intertemporal bar with broad exposure of the parietals and a (5) anteroposteriorly narrow postorbital bar. Scale bar equals 5 cm.

Locus Typicus—Harrismith, Free State, South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Nomen dubium (*Lystrosaurus* sp.).

Remarks—Broom (1913b) described *Dicynodon strigops* on the basis of a small, unusually flat skull with upwardly directed, anteriorly narrow orbits. He argued that these features are not the result of crushing, as they are present in several specimens referred to *D. strigops* from the type locality. Haughton (1917) transferred *D. strigops* to his new genus, *Prolystrosaurus*. The type species of *Prolystrosaurus*, *P. natalensis*, is based on a juvenile specimen of *Lystrosaurus murrayi* (SAM-PK-3715; see Grine et al., 2006), and the same could be true of *D. strigops* (as argued by Cluver, 1971), although the extremely poor state of the holotype makes this synonymy uncertain. Contra Broom's (1913b) original description, the unusual proportions of this specimen are almost certainly the result of taphonomic deformation.

Dicynodon sunanensis Li, Cheng, and Li, 2000

Holotype—IGCAGS V296, a well-preserved skull missing the right caniniform process and zygomatic arch.

Locus Typicus—Sunan, Xinjiang, China.

Horizon—Guodikeng Formation (Upper Permian).

Status—Junior subjective synonym of *Turfanodon bogdaensis* Sun, 1973.

Remarks—Li et al. (2000) considered *Dicynodon sunanensis* to be most similar to the fellow Chinese dicynodontoid *Dicynodon* (= *Turfanodon*) *bogdaensis*, sharing with it contact between the premaxilla and frontals, but distinguishable by snout proportions. IGCAGS V296 is a well-preserved, well-prepared skull showing very close similarity to the holotype of *Turfanodon bogdaensis* (IVPP V3241). In addition to the converging processes of the premaxilla and frontals, these two skulls share a steeply sloping, mediolaterally broad snout, anteroposteriorly wide squamosal with broadly rounded dorsal margin in lateral view, and a depression anterior to the pineal foramen. Proportional distinctions between these two specimens are minor and probably related to deformation by lateral compression in the holotype of *T. bogdaensis*, and we consider them synonymous.

Dicynodon swierstrai Broom, 1940b

Holotype—RC 43, a small skull and lower jaws, now lost.

Locus Typicus—Klipfontein, 12 miles north of Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Pristerodon mackayi* Huxley, 1868.

Remarks—In describing *Dicynodon swierstrai*, Broom (1940b) considered this species so distinct from other species in the genus as to probably warrant a new genus. He retained it in *Dicynodon* merely out of convenience. He diagnosed this new species based on its very broad intertemporal region (wider than the interorbital region), large pineal foramen, elongate posterior processes of the frontals, and single median boss above the nares. The holotype of *D. swierstrai* (RC 43) was one of several described by Broom (1940b) and apparently lost shortly after its description, as it was not listed by Haughton and Brink (1954). King (1988) listed *D. swierstrai* as a valid species of *Dicynodon*, but Brink (1986) considered it a nomen dubium due to the loss of the type. Although definitive identification of *D. swierstrai* is hindered by the loss of the type, Broom's (1940b) figure of RC 43 indicates that this specimen was probably an individual of *Pristerodon mackayi*. The intertemporal morphology in particular is characteristic of *P.*

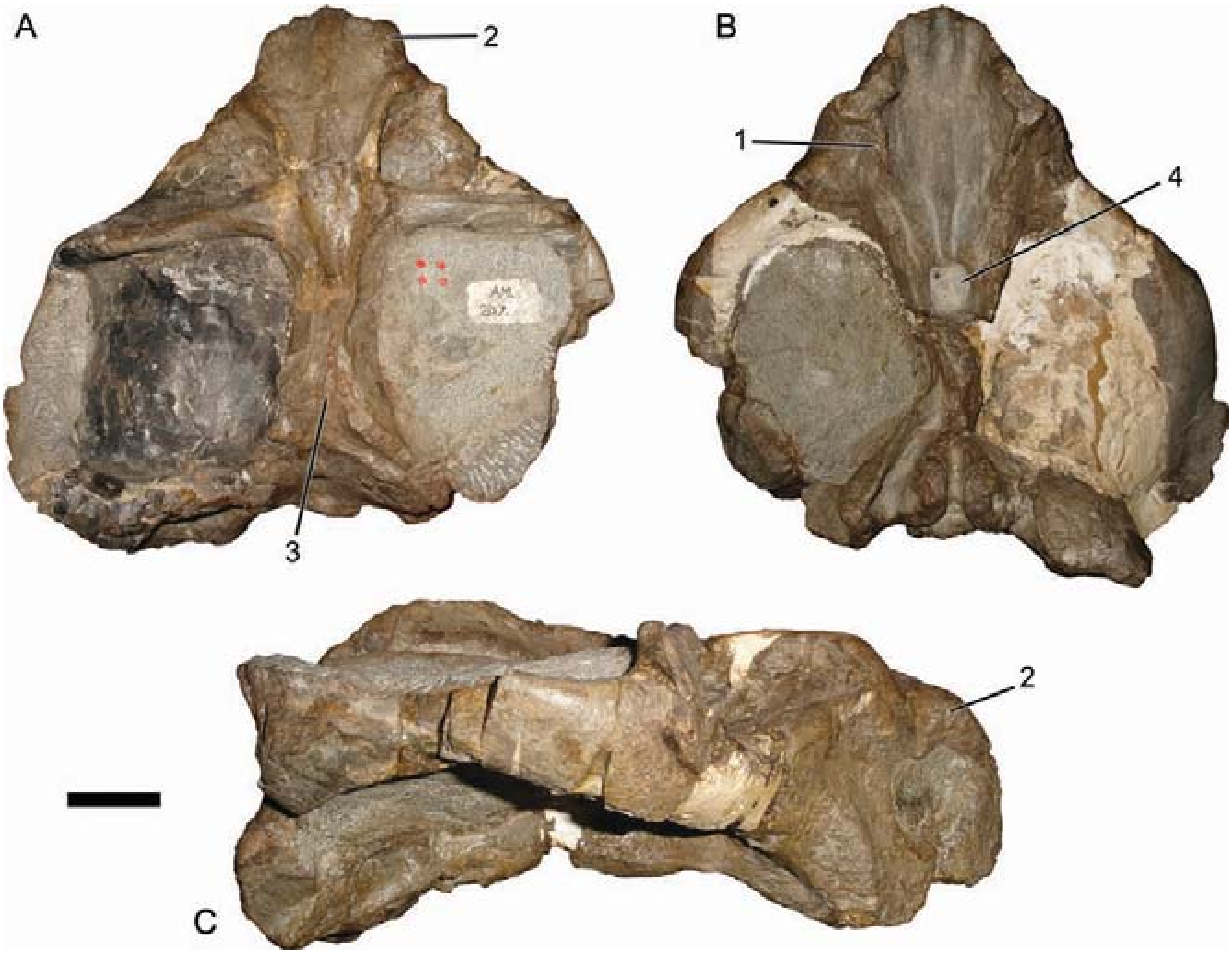

FIGURE 121. AMG 2817, the holotype of *Dicynodon schwarzi* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views (anterior is up in **A** and **B**). This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

mackayi, with long, broad posterior processes of the frontals and broad exposure of the parietals throughout, but with constriction in width of the bar at midlength and greater overlap by the postorbitals, unlike the relatively and more uniformly broader condition in *Emydops*.

Dicynodon taoshuyuanensis (Sun, 1973)

Syntypes—IVPP V3420.1, a nearly complete skull (missing the right temporal arcade and edge of occiput) and associated postcranial elements; V3420.2, the anterior half of a poorly preserved skull (Fig. 128); and V3420.3, a partial skull.

Locus Typicus—Taoshuyuanzi, Turpan Basin, Xinkiang, China.

Horizon—Guodikeng Formation (Upper Permian).

Status—Junior subjective synonym of *Jimusaria sinkianensis* (Yuan and Young, 1934).

Remarks—Sun (1973) described *Jimusaria taoshuyuanensis* based on a block containing the remains of three individuals, including partial postcrania. King (1988) synonymized this species with *Dicynodon sinkianensis*, but Lucas (1998a, 2001) retained it as valid (albeit in *Dicynodon*). We agree with King's (1988) synonymy; refer to the entry on *D. sinkianensis* for details.

Dicynodon taylori Broom, 1932

Holotype—ELM unnumbered, now lost.

Locus Typicus—Bashee River, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodon lacerticeps* Owen, 1845.

Remarks—Broom (1932) described *Dicynodon taylori* on the basis of a complete skull with tusks and a relatively short, narrow intertemporal region. The holotype was lost following description, and this species has received little subsequent attention, although King (1988) listed it as valid. Broom's (1932) figure indicates a skull consistent with the *Dicynodon lacerticeps* morphotype. The intertemporal bar is very narrow with nearly complete postorbital-parietal overlap and relatively short (compared to the condition typical of *Daptocephalus leoniceps*) and the premaxillary tip is distinctly squared-off.

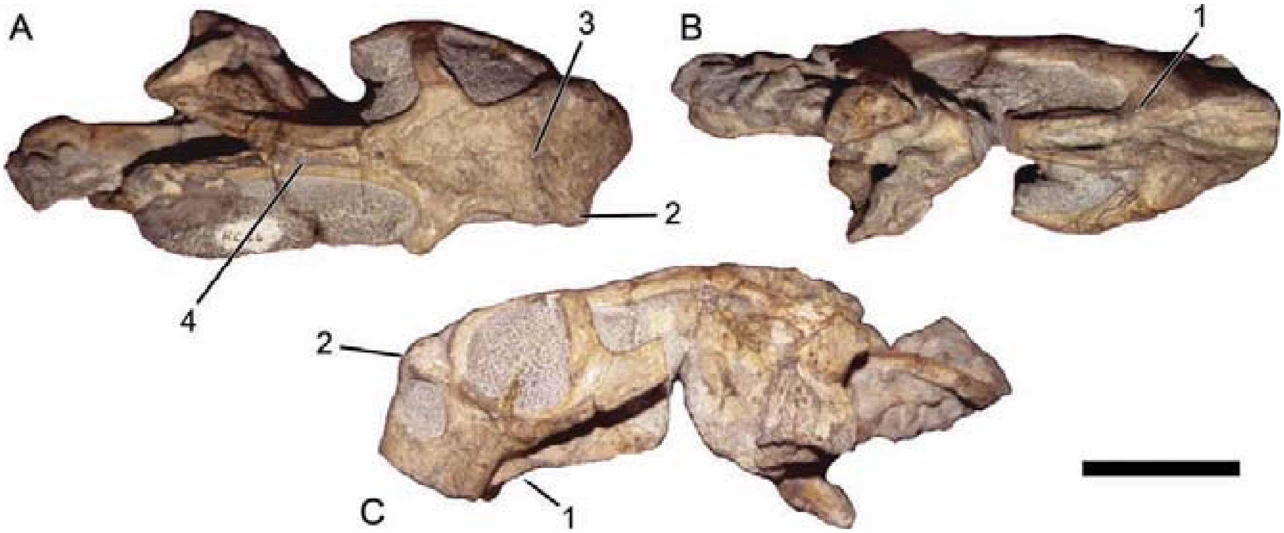

FIGURE 122. RC 44, the holotype of *Dicynodon sidneyi* (= ?*Pelanomodon moschops*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares and as a geikiine on the basis of the (3) transverse ridge running between the prefrontals. As a tuskless geikiine in the *Dicynodon* AZ of the Karoo Basin, this specimen is probably a juvenile *Pelanomodon*. However, the (4) extremely narrow intertemporal bar is not typical of geikiines, and juvenile dicynodonts usually have broader intertemporal regions than adults, making this identification somewhat suspect. Scale bar equals 5 cm.

Dicynodon tealei Haughton, 1932

Holotype—SAM-PK-10631, a fragment of skull roof surrounding the pineal foramen (Fig. 129).

Locus Typicus—Locality B32, Ruhuhu Valley, Tanzania.

Horizon—Usili Formation (Upper Permian).

Status—Nomen dubium (Rhachiocephalidae indet.).

Remarks—Haughton (1932) described *Dicynodon tealei* on the basis of a skull roof fragment (comprising the fronto-parietal region). He noted similarity in sutural positions to the South African species *Dicynodon cyclops* (= *Oudenodon bainii*), but considered this fragment sufficiently distinct to represent a new species. The isolated left maxilla and lower jaw tip from the type locality referred to this species by Haughton (1932) can be identified as *Dicynodon huenei*, but the thickened region surrounding the pineal foramen indicates that the type fragment is a rhachiocephalid cryptodont, not a dicynodontoid. This specimen is too fragmentary to identify as either *Rhachiocephalus* or *Kitchinganomodon*.

Dicynodon tener von Huene, 1935

Lectotype—GPIT unnumbered, a skull fragment consisting of the frontals and preparietal.

Locus Typicus—'Grabung 39' on the Sanga of Theotonio Belés Xavier near Chiniquà, Rio Grande do Sul, Brazil.

Horizon—Santa Maria Formation (Middle-Upper Triassic).

Status—Nomen dubium (Kannemeyeriiformes indet.).

Remarks—Von Huene (1935) described *Dicynodon tener* based on a series of disarticulated cranial and postcranial fragments collected at a locality near Chiniquà, Brazil. Cox (1965) transferred this species to *Dinodontosaurus* but retained it as

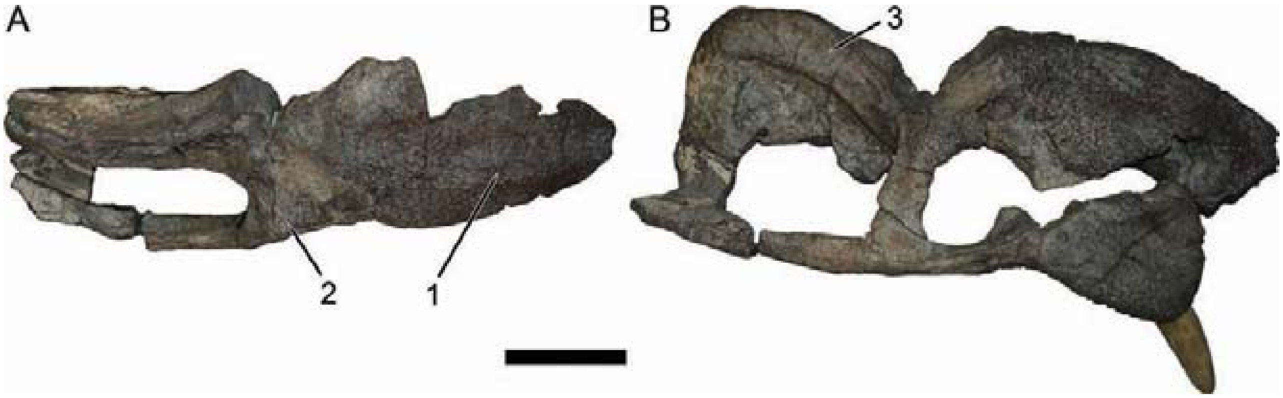

FIGURE 123. NMW 8178, the holotype of *Dicynodon simocephalus* (= *Kannemeyeria simocephala*), in dorsal (**A**) and right lateral (**B**) views. This specimen can be identified as a kannemeyeriiform on the basis of the (1) nasals swollen with a midline ridge and (2) absence of the postfrontal. *Kannemeyeria simocephala* has traditionally been distinguished from other kannemeyeriiforms by the (3) sagittal crest curving upwards to a plane above the level of the snout, a narrow intertemporal bar with no exposure of the postparietal dorsally, parallel temporal arches in dorsal view, a triangular palatal tip of the premaxilla, and a very well-developed midnasal ridge. Scale bar equals 10 cm.

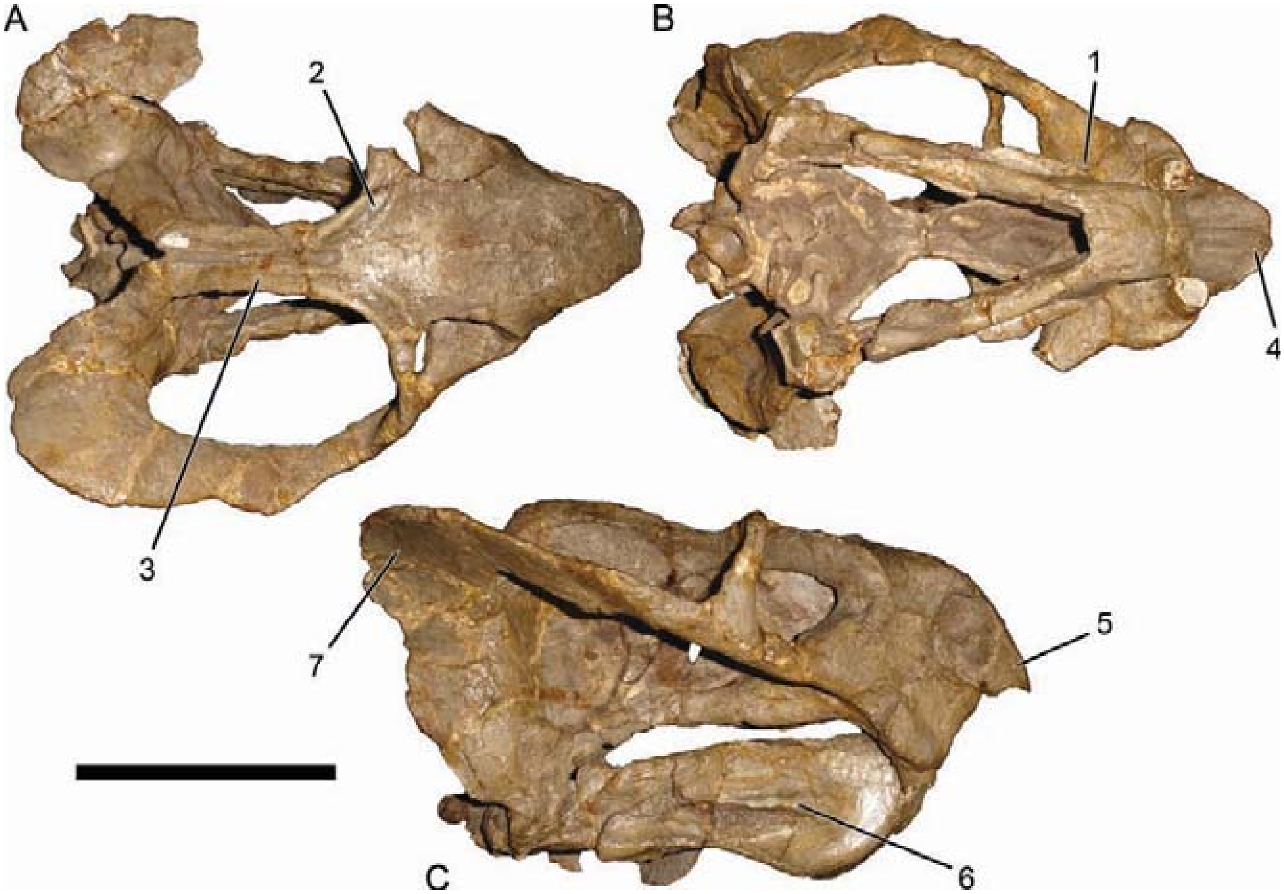

FIGURE 124. IVPP 341407, the holotype of *Dicynodon sinkianensis* (= *Jimusaria sinkianensis*), in dorsal (**A**), ventral (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. *Jimusaria sinkianensis* can be distinguished from other dicynodontoids based on the combination of (2) arcuate grooves on the postorbitals at the anteromedial margin of the temporal fenestrae, (3) a short but very narrow intertemporal bar, with complete postorbital-parietal overlap, (4) a relatively short, pointed premaxilla in palatal view with a (5) distinctly hooked tip, (6) a sharp lateral dentary shelf immediately dorsal to the mandibular fenestra, expanding slightly at its anterior terminus, and (7) acutely angled squamosal rami in lateral view. Scale bar equals 10 cm.

valid, a referral followed by King (1988). Lucas and Harris (1996) designated an undiagnostic fragment of skull roof as the lectotype of *D. tener* and accordingly considered this taxon a nomen dubium.

Dicynodon testudiceps Owen, 1845

Holotype—NHMUK 47054, a dorsoventrally crushed anterior half of a skull (Fig. 130).

Locus Typicus—Near Fort Beaufort, South Africa.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontoidea indet.).

Remarks—Owen (1845) described *Dicynodon testudiceps* based on an isolated snout with a strongly arched profile. Subsequent studies have generally retained this species as valid (e.g., Cluver and Hotton, 1981; King, 1988) despite the poor quality of the holotype. NHMUK 47054 is poorly prepared and badly distorted, rendering interpretation of its morphology difficult. No snout ridges or sculpturing can be observed on the dorsal surface of the skull, because the external layer of bone has been prepared off. A prefrontal boss appears to have been present on the left side of the skull but is badly worn; the right side is broken off. The nares are extremely large, but their size has been exaggerated by overpreparation at their anterior and posterior edges. In palatal view, the premaxilla is not squared-off but has an evenly rounded profile; however, because the ventral margin of the premaxilla is broken, this shape may not represent the true palatal profile of this individual. Similarly, although the paired anterior lateral premaxillary ridges are remarkably short, terminating anterior to the caniniform processes, their apparent brevity may be an artifact of the broken premaxillary margin and generally poor preparation of the palate. The separation of these ridges from the caniniform processes is likely heightened by the fact that those processes have been ground down to their bases, exposing the tusk roots in a more posterior position relative to where they would be visible in an intact skull. No original bone surface is exposed on the palate (this region is covered in chisel marks, either into the bone itself or remaining matrix), making it impossible to determine rugosity of the maxilla and palatine. NHMUK 47054 is a bidentalian, as indicated by the large tusks, lack of postcanines, and paired anterior palatal ridges that do not converge posteriorly on the premaxilla. Although poorly preserved, a labial fossa appears to be present on the left side of the skull (the suborbital region is not preserved on the right), indicating that this specimen is a dicynodontoid. Among Permian Karoo dicynodontoids,

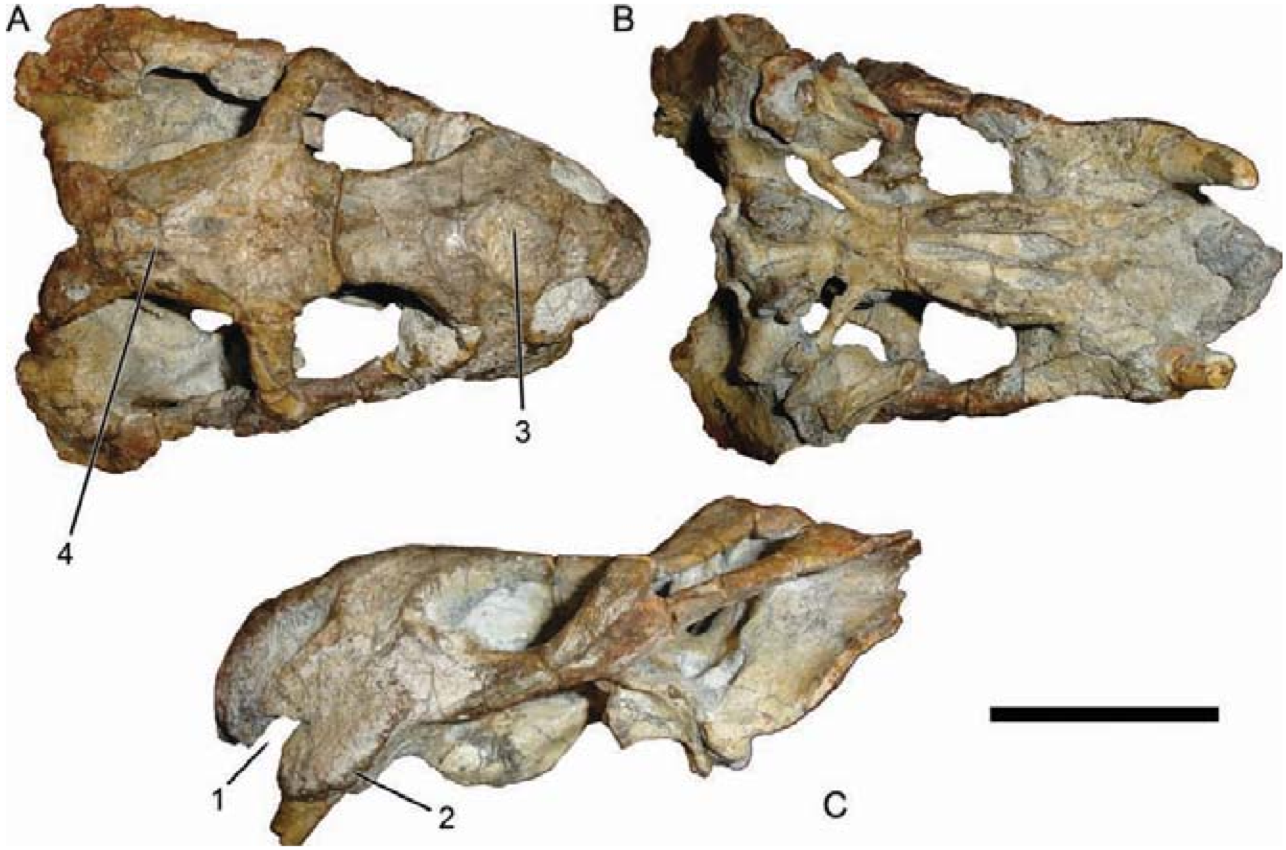

FIGURE 125. SAM-PK-7420, the holotype of *Dicynodon sollasi* (= *Diictodon feliceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch, (2) ventral margin of the caniniform process at the level of the anterior margin of the orbit, and (3) median snout boss and as *D. feliceps* on the basis of the (4) relatively narrow intertemporal bar, with extensive postorbital-parietal overlap, and the absence of postcanines. Scale bar equals 5 cm.

the general morphology of NHMUK 47054 is consistent with either *Dicynodon lacerticeps* or *Daptocephalus leoniceps*. Unfortunately, all of the cranial regions exhibiting characters that can distinguish these two taxa (caniniform process, intertemporal bar, squamosal) are not preserved in this specimen. Additionally, because this specimen is badly crushed, the preserved snout profile (somewhat closer to the steeper curvature of *D. leoniceps*) should not be taken as indicative of the undistorted condition. *Dicynodon testudiceps* should be considered a nomen dubium, identifiable only as Dicynodontoidea indet.

Dicynodon testudirostris Broom and Haughton, 1913

Holotype—SAM-PK-2354, a dorsoventrally crushed complete skull (Fig. 131).

Locus Typicus—Dunedin, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Broom and Haughton (1913) considered the tuskless holotype of *Dicynodon testudirostris* to be a female representative of a new *Dicynodon* species. In particular, they considered the relatively small lacrimal and prefrontal bones of SAM-PK-2354 to be distinct from the condition in other species of *Dicynodon* and more similar to that of *Cistecephalus*. Van Hoepen (1934) included this species in *Pylaecephalus*, and Cluver and Hotton (1981) transferred it to *Diictodon*. Brink (1986) and Sullivan and Reisz (2005) considered *D. testudirostris* to be synonymous with *Diictodon feliceps*, and this approach is followed here.

Dicynodon tienshanensis Sun, 1973

Holotype—IVPP V3260, a dorsoventrally crushed skull (missing the right postorbital bar) and lower jaws (Fig. 132).

Locus Typicus—Tienshan, Xinjiang, China.

Horizon—Guodikeng Formation (Upper Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Sun (1973) described *Dicynodon tienshanensis* based on a small, tuskless skull that Cluver and Hotton (1981) recognized was referable to *Diictodon*. Subsequent studies (King, 1988; Lucas, 1998a, 2001) have retained *Diictodon tienshanensis* as a valid species, but Angielczyk and Sullivan (2008) demonstrated that the holotype is indistinguishable from *Diictodon feliceps*, and considered the two species synonymous.

Dicynodon tigriceps Owen, 1855

Holotype—NHMUK 36235, a well-preserved, complete skull (Fig. 133) and associated skeleton.

Locus Typicus—Fort Beaufort, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Aulacephalodon bainii* (Owen, 1845).

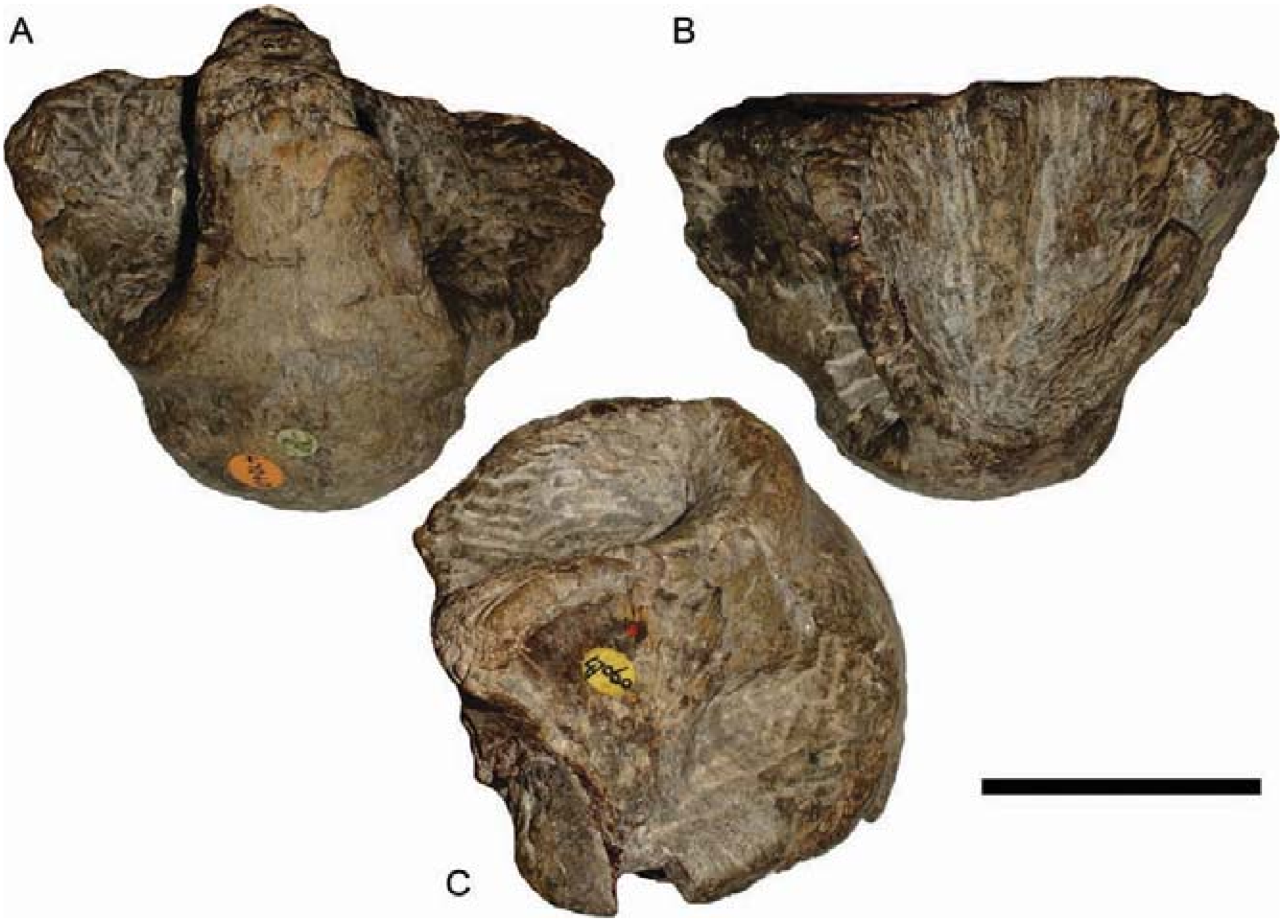

FIGURE 126. NHMUK 47060, the holotype of *Dicynodon strigiceps*, in dorsal (**A**), palatal (**B**), and right lateral (**C**) views (anterior is down in **A** and **B** and right in **C**). This specimen is too incomplete, poorly preserved, and poorly prepared to identify beyond Dicynodontia indet. Tusks appear to be absent (although this is uncertain) and combined with the shape of the snout this suggests that this may be a specimen of *Oudenodon bainii*, but this referral is far from certain. Scale bar equals 5 cm.

Remarks—Owen (1855) described *Dicynodon tigriceps* based on a well-preserved, extremely broad skull with prominent nasal bosses, and for most of the late 19th and early 20th centuries this species was the best-known member of the *Aulacephalodon* morphotype. Broom (1921) made this the type species of a new genus, *Bainia*, distinguished by the very broad parietal region and tuskedness in males and females, but later (Broom, 1932) he recognized the priority of Seeley's (1898) *Aulacephalodon* (misspelled as *Aulacocephalodon*) to house this species. Keyser (1972) and Tollman et al. (1980) recognized only a single species of *Aulacephalodon*, considering *A. tigriceps* to be a junior synonym of *A. bainii*, and this approach is followed here.

Dicynodon traquairi (Newton, 1893)

Holotype—BGS GSE11703, a slab containing the natural mold of a skull, lower jaw, and partial skeleton.

Locus Typicus—Cutties Hillock Quarry, Elgin, Scotland.

Horizon—Cutties Hillock Sandstone Formation (Upper Permian).

Status—Valid as *Gordonia traquairi* Newton, 1893.

Remarks—Newton (1893) described the new dicynodont genus *Gordonia* with four species (*G. traquairi*, the type, *G. duffiana*, *G. huxleyana*, and *G. juddiana*) based on skulls and postcranial elements preserved as natural sandstone molds, found in the same quarry as the geikiine dicynodont *Geikia elginensis* and the dwarf parieasaur *Elginia mirabilis*. Amalitzky (1922) described two new species of *Gordonia* from Russia (*G. annae* and *G. rossica*), but these species are not referable to *Gordonia* and instead represent synonyms of "*Dicynodon*" *trautscholdi* (see entry on *Dicynodon annae* for further information). Von Huene (1940) synonymized *Gordonia* with *Dicynodon*, but retained all four species as valid in new combinations. Independently, King (1988) also synonymized *Gordonia* with *Dicynodon*, but went further and synonymized all four nominal Scottish species, recognizing only *Dicynodon traquairi* as valid. Cruickshank et al. (2005) described a new specimen of *D. traquairi* and provided the first information on the palate of this taxon based on magnetic resonance images of a natural sandstone mold. We concur with King (1988) that the four species of *Gordonia* described by Newton (1893) are synonymous. Based on examination of casts of the holotype (AMNH FARB 4995; Fig. 134) and referred material (NHMUK R2107, R2108, and R2109) and information from Cruickshank et al. (2005), these specimens all share the same suite of characters: proportionally short snout, large orbits, and very long, narrow intertemporal bar (unusually so given the small size of these skulls compared to South African taxa of similar relative intertemporal length), prominent sagittal crest, anteriorly

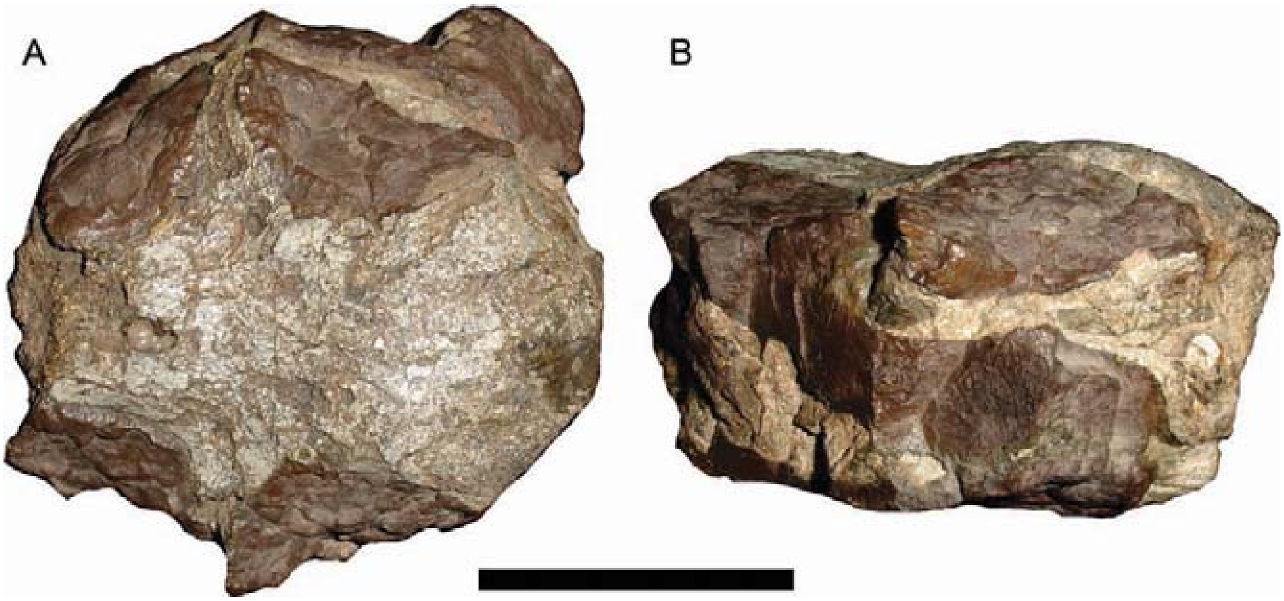

FIGURE 127. AMNH FARB 5581, the holotype of *Dicynodon strigops* (= *Lystrosaurus* sp.), in dorsal (**A**) and right lateral (**B**) views. The short, broad intertemporal bar of this Triassic dicynodont indicates that it is *Lystrosaurus*, but this specimen is too poorly preserved and poorly prepared to identify to species. Scale bar equals 5 cm.

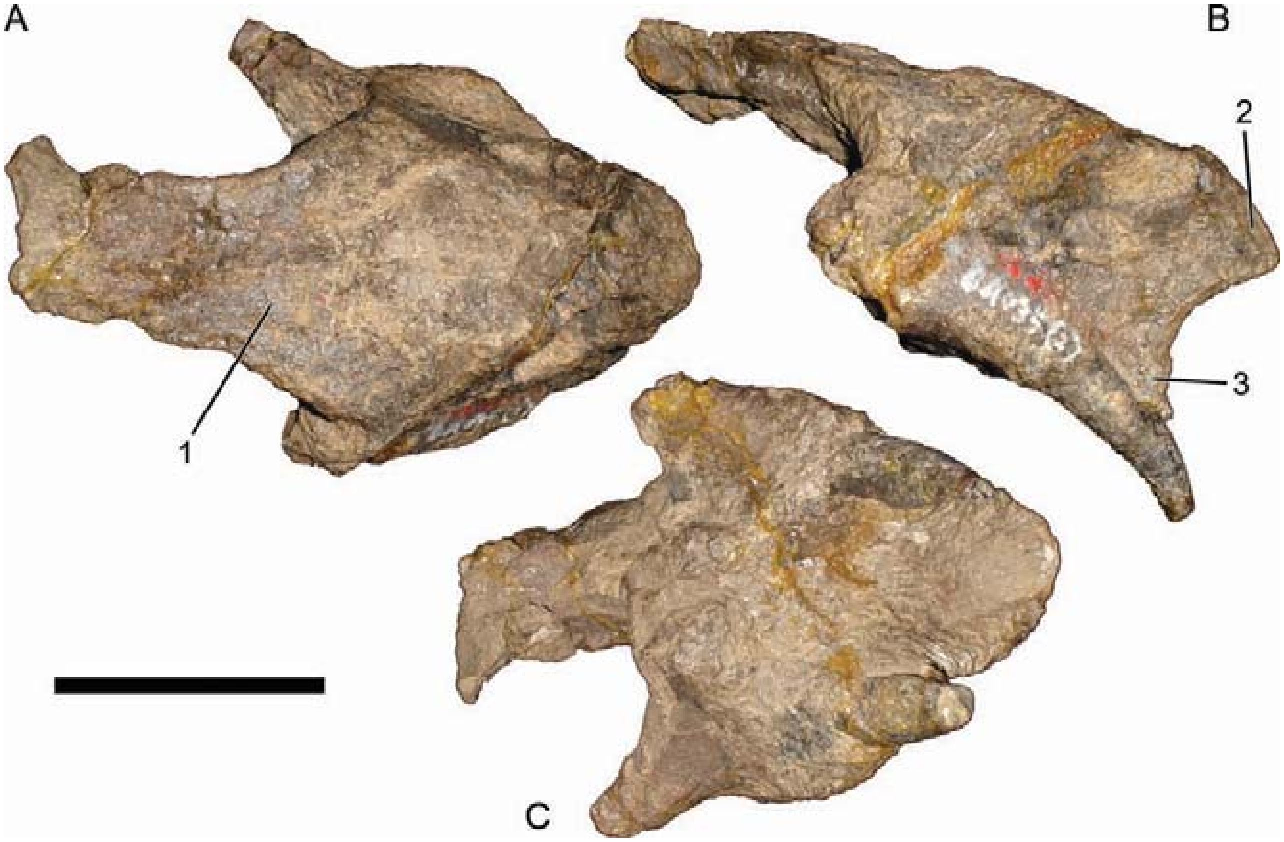

FIGURE 128. IVPP V3420.2, a syntype of *Dicynodon taoshuyuanensis* (= *Jimusaria sinkianensis*), in dorsal (**A**), right lateral (**B**), and palatal (**C**) views. This specimen can be identified as *J. sinkianensis* on the basis of the (1) narrow interorbital region, (2) 'hooked' premaxillary tip, and (3) anteriorly directed caniniform process. Scale bar equals 5 cm.

FIGURE 129. SAM-PK-10631, the holotype of *Dicynodon tealei*, in dorsal view. Anterior is up. Although the surface is eroded off, the base of the pineal boss indicates that it was massive and, combined with the convergence of the postorbitals immediately posterior to it, indicates that this specimen is a rhachiocephalid. Unfortunately this specimen is too fragmentary to identify at a lower taxonomic level. Scale bar equals 5 cm.

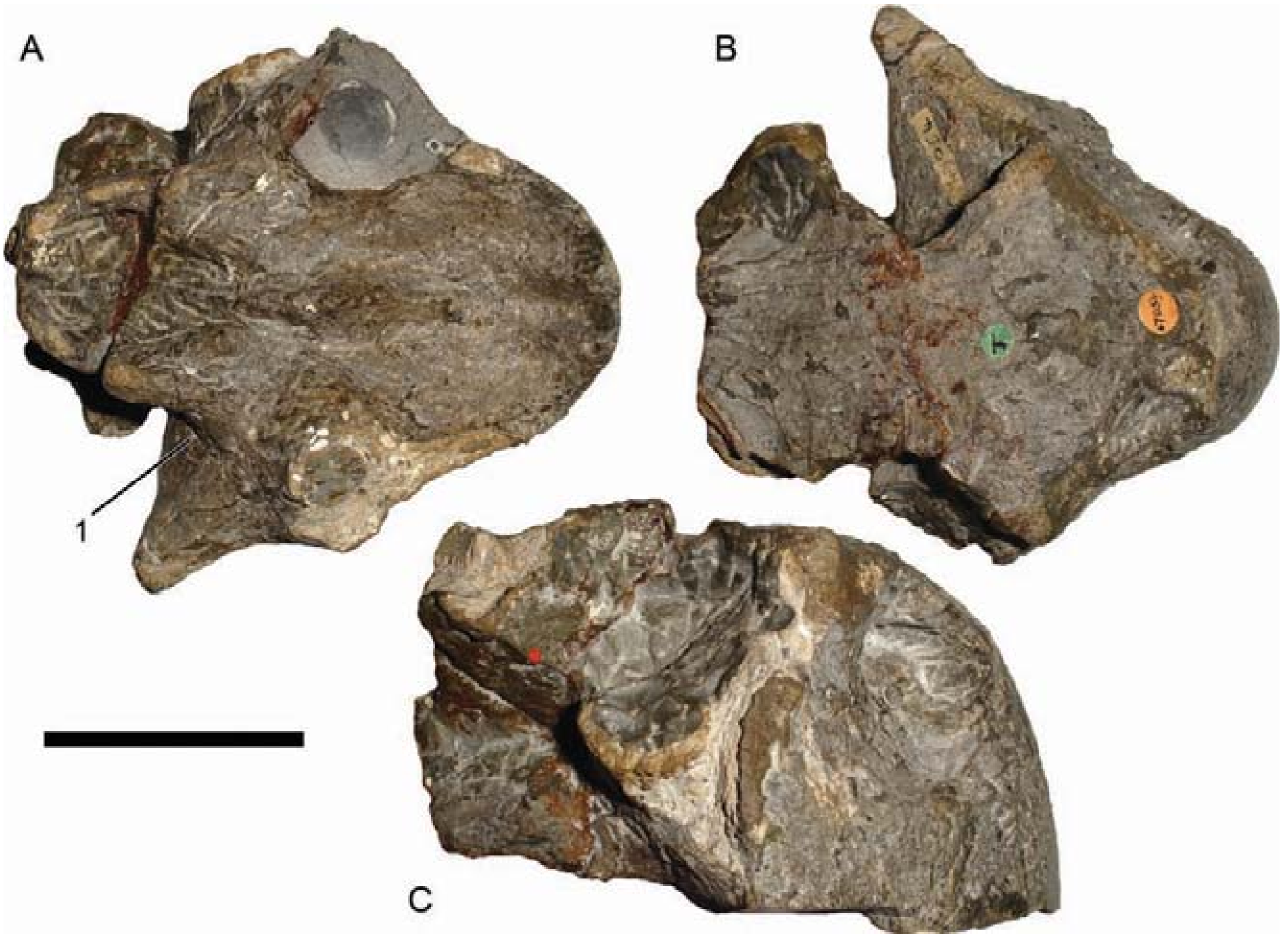

FIGURE 130. NHMUK 47054, the holotype of *Dicynodon testudiceps*, in palatal (**A**), dorsal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. The incompleteness and poor preparation of this specimen do not permit identification to lower taxonomic levels. Scale bar equals 5 cm.

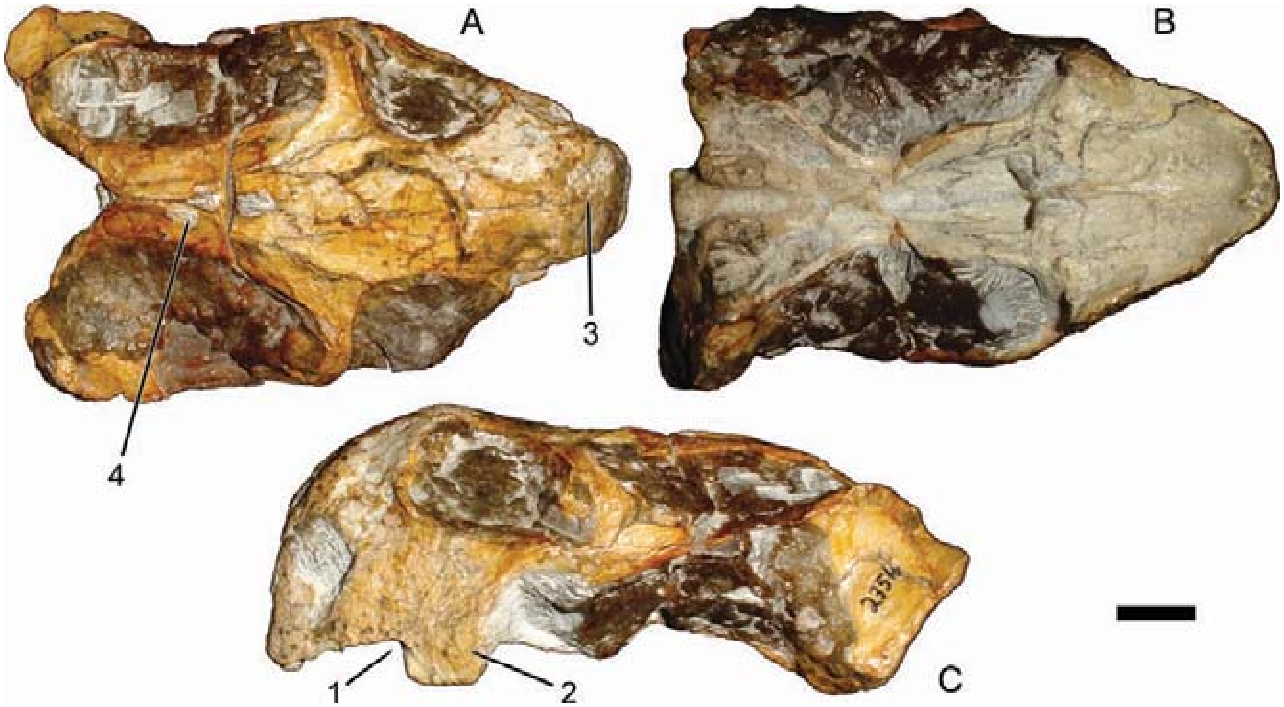

FIGURE 131. SAM-PK-2354, the holotype of *Dicynodon testudirostris* (= *Diictodon feliceps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch, (2) ventral margin of caniniform process at the level of the anterior edge of the orbit, and (3) median ridge on anterior surface of the snout, and as *D. feliceps* on the basis of the (4) narrow intertemporal bar with extensive postorbital-parietal overlap and lack of teeth. Scale bar equals 1 cm.

directed caniniform process, relatively tall, robust dentary, and slender, rod-like lateral dentary shelf angled anterodorsally immediately above the mandibular fenestra. Refer to the Phylogenetic Analysis for our rationale in recognizing *Gordonia* as a valid genus.

Dicynodon trautscholdi Amalitzky, 1922

Holotype—PIN 2005/1, a well-preserved, complete skull and lower jaws (Fig. 135).

Locus Typicus—Sokolki, Arkhangelsk Region, Kotlasskii District, Russia.

Horizon—Upper Vyatkian substage, Tatarian series (Upper Permian).

Status—Valid as *Vivaxosaurus trautscholdi* (Amalitzky, 1922), comb. nov.

Remarks—Amalitzky (1922) described four species of dicynodont from the North Dvina River excavations, of which *Dicynodon trautscholdi* was based on the best-preserved and most complete skull, associated with a complete set of lower jaws. Sushkin (1926) revised the North Dvina dicynodonts and synonymized *Gordonia rossica* with *Dicynodon trautscholdi*. Efremov (1940) regarded all North Dvina dicynodonts (*D. trautscholdi*, *Dicynodon amalitzkii*, *Gordonia rossica*, *Gordonia annae*, and *Oudenodon venyukovi*) as conspecific, giving priority to *D. trautscholdi*. The synonymy of *D. amalitzkii* and *D. trautscholdi* has subsequently been called into question (see Angielczyk and Kurkin [2003a, 2003b] and the entry for *D. amalitzkii*), but the conspecificity of the other North Dvina specimens has not been debated and is upheld here. Recently, Kalandadze and Kurkin (2000) described a new taxon of Russian Permian dicynodontoid, *Vivaxosaurus permirus*, based on a complete skull that they argued represented a Permian stem-member of Kannemeyerioidea. Lucas (2005a) argued that the nominal Late Permian Russian dicynodont taxa *Vivaxosaurus permirus*, *Delectosaurus arefjevi*, and *Elph borealis* are all synonymous with *D. trautscholdi*, the former as a large adult and the latter two as juveniles. Numerous discrete characters and phylogenetic evidence support the distinction of *Delectosaurus* and *Elph* (see Angielczyk and Kurkin, 2003a, 2003b), but the validity of *Vivaxosaurus permirus* is less secure. The holotype of *V. permirus* (PIN 1536/1) is very similar to that of *Dicynodon trautscholdi*, sharing the relatively thin, anteroventrally directed snout morphology, unique caniniform process morphology (narrow and anteroventrally directed with a rounded lobe anterior to the tusk), and a near contact between the dorsal process of the premaxilla and anterior process of the frontals. As this combination of characters is unique among dicynodontoids, and the differences between *V. permirus* and *D. trautscholdi* are minor proportional differences that may be attributable to taphonomic distortion or individual variation, we regard these species as synonyms, in the new combination *Vivaxosaurus trautscholdi* (refer to the Phylogenetic Analysis for maintenance of *Vivaxosaurus* rather than *Dicynodon* for this species).

Dicynodon trigoniceps (Broom, 1904a)

Holotype—AMG 2825, a slightly dorsoventrally crushed skull and lower jaws (Fig. 136).

Locus Typicus—Pearston, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Pristerodon mackayi* Huxley, 1868.

Remarks—Broom (1904a) described *Oudenodon trigoniceps* based on a small, poorly preserved skull lacking tusks (thus the referral to *Oudenodon*) and distinguished from other members of the genus by its small size and broadly triangular skull. Broom

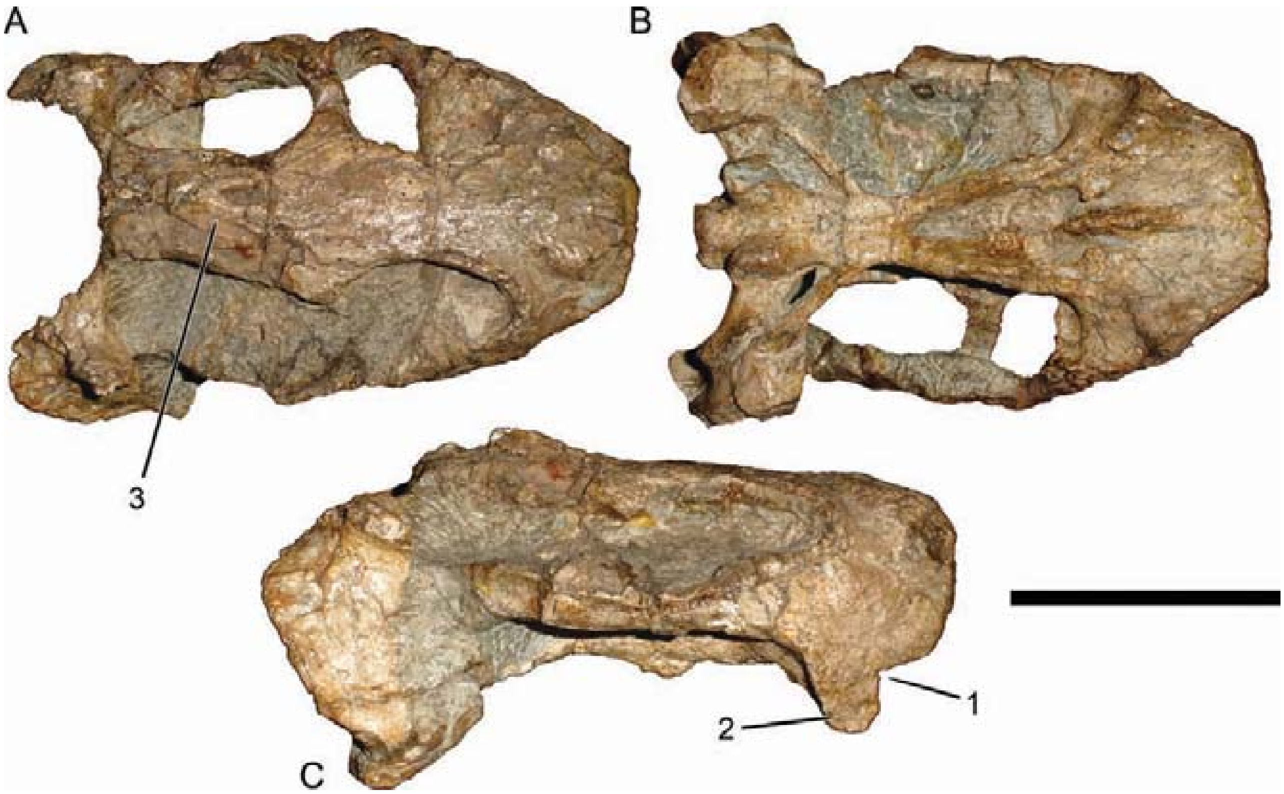

FIGURE 132. IVPP V3260, the holotype of *Dicynodon tienshanensis* (= *Diictodon feliceps*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) precaniniform notch and (2) ventral margin of caniniform process at level of anterior margin of orbit and as *D. feliceps* on the basis of the (3) narrow intertemporal bar with extensive postorbital-parietal overlap and lack of teeth. Scale bar equals 5 cm.

(1913a) transferred this species to *Dicynodon* along with all other nominal species of *Oudenodon*, but later (1921) made it the type species of the genus *Emydopsis*. Toerien (1953) transferred this species to *Emydops*, a referral upheld by King (1988), but Keyser (1993) considered the holotype indeterminate and considered *D. trigoniceps* a nomen dubium. Most recently, Fröbisch and Reisz (2008) reexamined AMG 2825 and concluded that it represents an individual of *Pristerodon mackayi*.

Dicynodon trigonocephalus Broom, 1940b

Holotype—RC 38, a nearly complete, anteroposteriorly crushed skull (Fig. 137).

Locus Typicus—Klipfontein, 12 miles north of Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Dicynodon lacerticeps* Owen, 1845.

Remarks—Broom (1940b) named *Dicynodon trigonocephalus* because of its unusual skull shape, forming an equilateral triangle in dorsal view, and particularly noted the distinctive shape of the squamosals, which flare laterally rather than posteriorly as in other broad-headed dicynodonts (e.g., *Dicynodon corstorphinei*, *Dicynodon halli*, and *Dicynodon planus*). King (1981) referred a nearly complete skeleton from Zambia to *D. trigonocephalus*, and later (King, 1988) maintained that the species was valid. The unusually short, broad skull of RC 38 can be attributed to anteroposterior compression. The presence of a labial fossa and the narrow intertemporal bar with complete postorbital-parietal overlap indicate that this specimen is a dicynodontoid, and the acutely angled squamosal and shortness of the intertemporal bar place it in the *Dicynodon lacerticeps* morphotype. The Zambian '*D. trigonocephalus*' is here considered to represent a specimen of *Dicynodon huenei*, because it displays the diagnostic postorbital morphology of that species, with a flattened plate at the posteroventral edge of the orbital margin.

Dicynodon truncatus (Broom, 1899)

Holotype—PEM unnumbered, a very poorly preserved partial skull preserving part of the snout and palate, now lost.

Locus Typicus—Probably the Hanover District, South Africa.

Horizon—*Cistecephalus* or *Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1899:455) described *Oudenodon truncatus* on the basis of a weathered palate of uncertain provenance (although he noted that "there is some reason to believe that it came from Hanover" without further explanation). He distinguished it from previously described species of *Oudenodon* based on the squared-off snout and palatal ridges (one median posterior and two lateral anterior). Broom (1913a) transferred this and all other species of *Oudenodon* to *Dicynodon*. Keyser (1975) could not locate the holotype in the Port Elizabeth Museum and considered it lost. He noted that based on Broom's (1899:pl. 10, fig. 4) original figure, it is consistent with *Oudenodon* albeit devoid of specific characters. As such, Keyser (1975:45) considered the

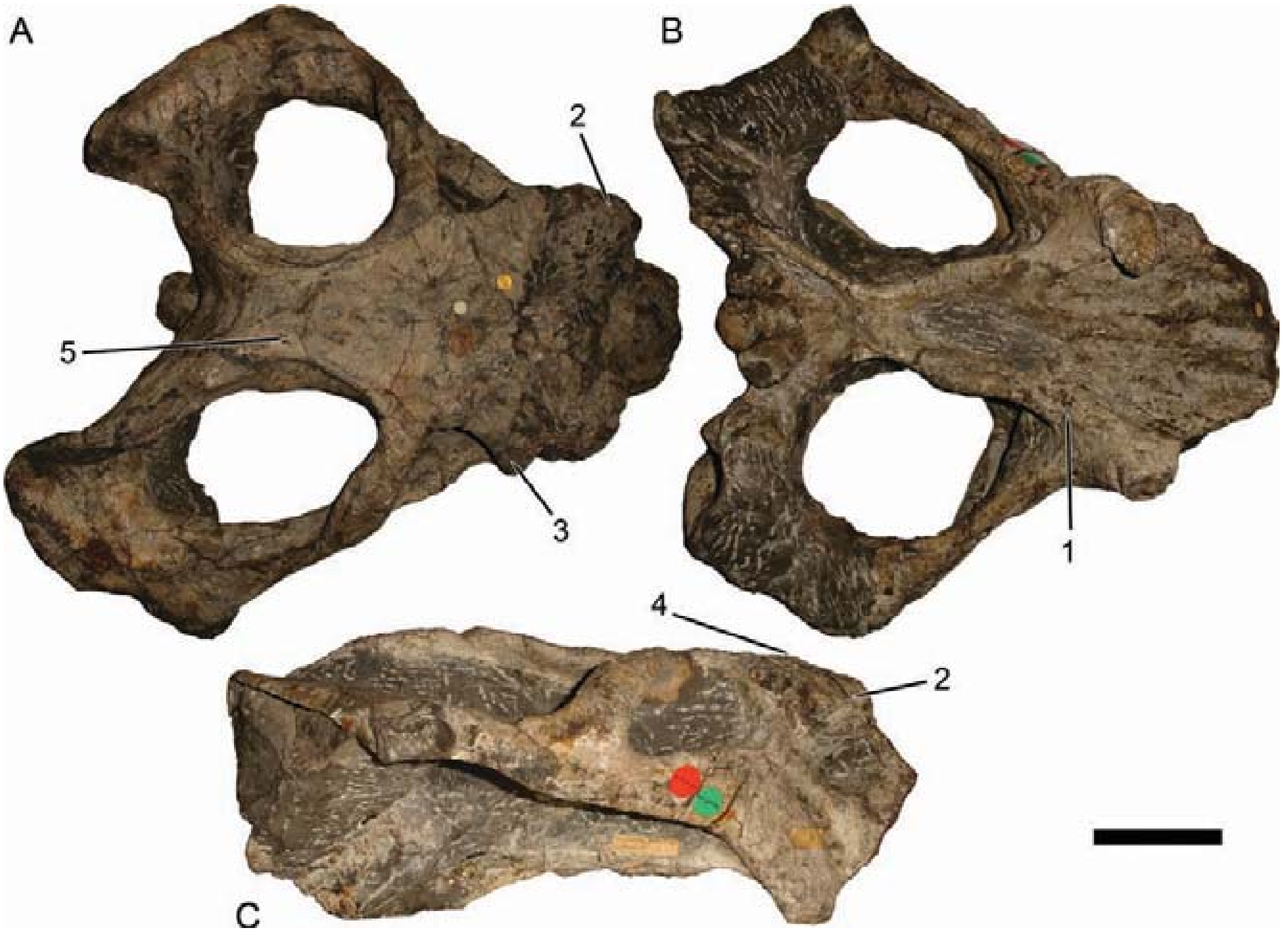

FIGURE 133. NHMUK 36235, the holotype of *Dicynodon tigriceps* (= *Aulacephalodon bainii*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as a geikiine on the basis of the (2) massive nasal and (3) prefrontal bosses, (4) transverse ridge running between the prefrontals, and (5) broad intertemporal bar, and as *Aulacephalodon* on the basis of the massive tusks. Scale bar equals 10 cm.

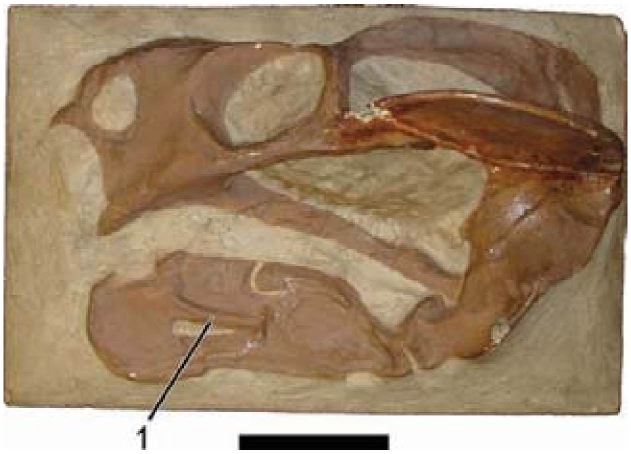

FIGURE 134. AMNH FARB 4995, a cast made from the holotype of *Dicynodon traquairi* (= *Gordonia traquairi*) (a natural sandstone mold), in left lateral view. The (1) narrow, rod-like lateral dentary shelf is characteristic of this species. Scale bar equals 5 cm.

species "best ignored or considered a nomen-dubium of historical interest only." King (1988) listed *O. truncatus* in the synonymy of *Oudenodon bainii*. We consider this to be the preferred treatment of *O. truncatus*. Although this species is based on an extremely poor, lost holotype, Broom's (1899) description provides sufficient indication that it represents a specimen of *O. bainii*. Of the characters originally used to diagnose this species, the squared-off snout relative to other *Oudenodon* specimens is an artifact of weathering, and the palatal ridges are now known to be commonplace in dicynodonts and typically present in *Oudenodon*.

Dicynodon turpior von Huene, 1935

Lectotype—GPIT unnumbered, a right humerus.

Locus Typicus—'Grabung 42,' near Chiniquà, Brazil.

Horizon—Santa Maria Formation (Upper Triassic).

Status—Nomen dubium (Kannemeyeriiformes indet.).

Remarks—Von Huene (1935) named *Dicynodon turpior* and *Dicynodon tener* based on fragmentary, disarticulated material from the Santa Maria Formation of Brazil. The two species were separated mostly on size, with *D. turpior* as the larger

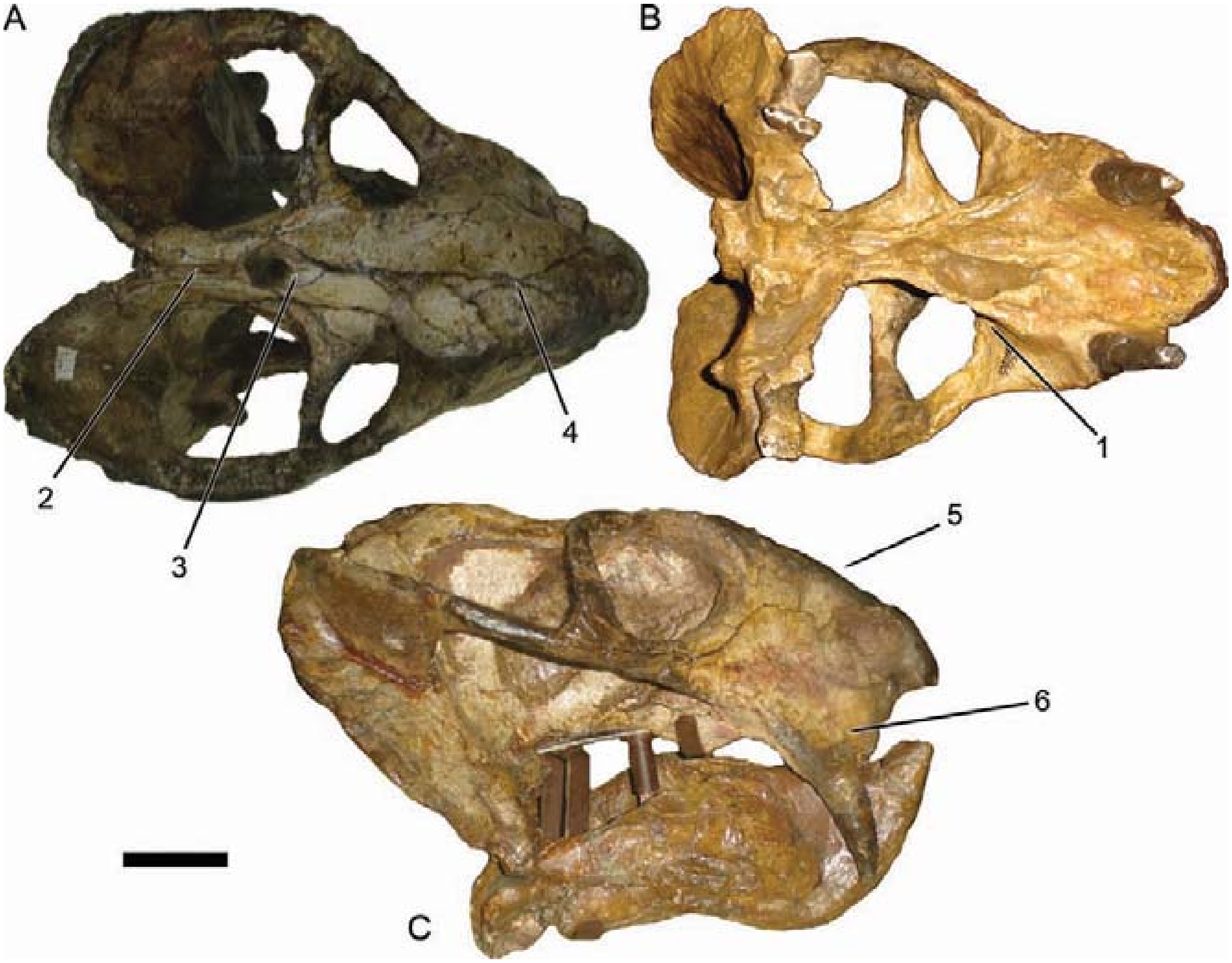

FIGURE 135. PIN 2005/1, the holotype of *Dicynodon trautscholdi* (= *Vivaxosaurus trautscholdi*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views (the specimen in **B** is a cast). This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. *Vivaxosaurus trautscholdi* can be distinguished from other dicynodontoids by the combination of (2) a short intertemporal bar with narrow but consistent exposure of the parietals, (3) a depression on the preparietal at the anterior edge of the pineal foramen, (4) an anterior process of the frontals nearing contact with an elongate ascending process of the premaxilla, (5) a gradually sloping, dorsoventrally narrow snout, and a (6) anteriorly directed caniniform process. Scale bar equals 5 cm.

species. Cox (1965) transferred this species to *Dinodontosaurus* and considered it to be the senior synonym of the type species *D. oliveirai*. Most subsequent authors have used the combination *D. turpior* to refer to *Dinodontosaurus* (e.g., King, 1988), but Lucas and Harris (1996) designated an isolated right humerus that they considered undiagnostic as the lectotype of *D. turpior*, rendering it a nomen dubium and reinstating *D. oliveirai*. However, as noted by Langer et al. (2007), the proposal to suppress the senior synonym *Diodontosaurus pedroanum* Tupí-Caldas, 1936, in favor of *Dinodontosaurus oliveirai* Romer, 1943 (Lucas, 1992), was only approved at the generic level, meaning that *Dinodontosaurus pedroanum* is the valid name for this species.

Dicynodon tylorhinus Broom, 1913c

Holotype—AMNH FARB 5511, a well-preserved snout (Fig. 138).

Locus Typicus—Wilgerbosch, New Bethesda, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Uncertain (see below).

Remarks—Broom (1913c) described *Dicynodon tylorhinus* on the basis of the anterior half of a skull from Wilgerbosch. He distinguished *D. tylorhinus* from other dicynodonts by its extremely short snout and massive, knob-like nasal bosses. The boss morphology of *D. tylorhinus* was unique among dicynodonts until Toerien's (1955) description of *Propelanomodon devilliersi*. Keyser (1975) recognized the similarity between these specimens and synonymized them in the new combination *Propelanomodon tylorhinus*, and this has been maintained by most subsequent authors (e.g., Brink, 1986; King, 1988). The massive nassal bosses of *P. tylorhinus* are very similar to those observed in specimens of the Tanzanian geikiine *Geikia locusticeps*, but the absence of such geikiine synapomorphies as a prominent ridge running across the snout at the level of the prefrontals or prefrontal bosses, combined with the unusually narrow intertemporal bar, makes it doubtful that *P. tylorhinus* represents a juvenile of one of the nominal geikiine species. More research on the ontogeny of this group is needed, but we tentatively concur with

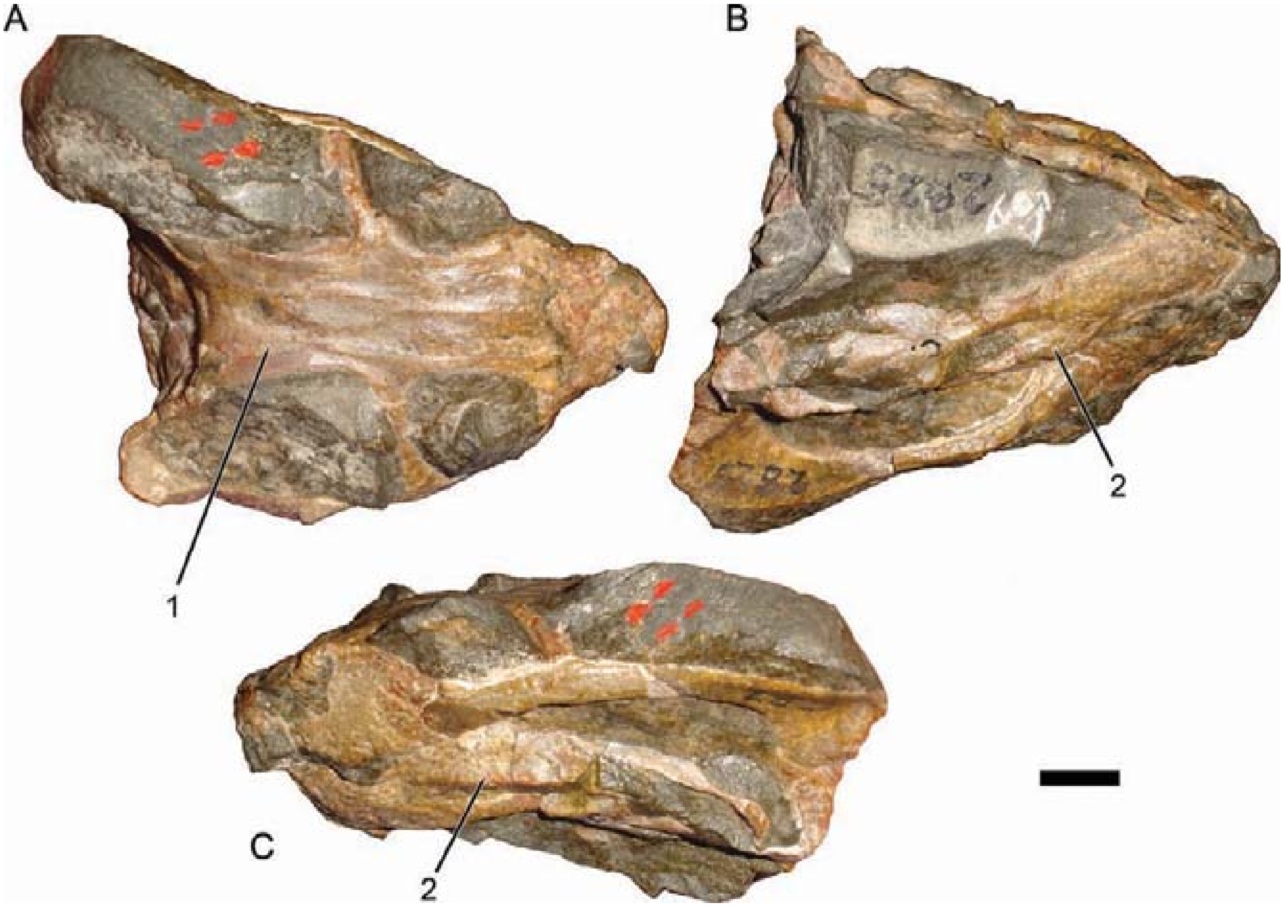

FIGURE 136. AMG 2825, the holotype of *Dicynodon trigoniceps* (= *Pristerodon mackayi*), in dorsal (**A**), ventral (**B**), and left lateral (**C**) views. This specimen can be identified as *Pristerodon* on the basis of the (1) broad intertemporal bar with nearly equal postorbital and parietal contributions to its width and (2) sharp lateral dentary shelf angled over the mandibular fenestra. Scale bar equals 1 cm.

previous authors in considering *P. tylorhinus* a valid species of cryptodont.

Dicynodon validus Broom, 1935

Holotype—TM 252, a distorted snout and anterior portion of the lower jaws (Fig. 139).

Locus Typicus—Leeukloof, Beaufort West, South Africa.

Horizon—*Tropidostoma* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Tropidostoma dubium* (Owen, 1876).

Remarks—Broom (1935) described *Dicynodon validus* based on a partial skull from the large collection of dicynodonts at Leeukloof (also incuding *Dicynodon acutirostris* [= *Tropidostoma dubium*] and *Dicynodon sollasi* [= *Diictodon feliceps*]). Keyser (1973) synonymized *D. validus* with *Tropidostoma microtrema*, and King (1988) listed these species as synonyms, even though she doubted this referral. Botha and Angielczyk (2007) demonstrated that TM 252 is identifiable as *Tropidostoma* on geometric morphometric grounds, and this synonymy is upheld here.

Dicynodon vanderbyli Broom, 1928

Holotype—MMK 4042, a very poorly preserved skull missing the temporal arches and much of the pterygoid and occipital regions (Fig. 140).

Locus Typicus—Bethesda Road, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1928) described *Dicynodon vanderbyli* as a new species of tuskless *Dicynodon* characterized by raised orbital rims. Keyser (1975) synonymized this species with *Oudenodon bainii*. Subsequent studies have supported this assessment (e.g., Kitching, 1977; Brink, 1986; King, 1988) and it is maintained here. MMK 4042 is extremely poorly preserved and much of its anatomy is still obscured by matrix and plaster. However, the small, ovoid nasal bosses overhanging the nares, postcaniniform crest, short, tall snout, and absence of tusks allow it to be identified as *O. bainii*.

Dicynodon vanderhorsti Toerien, 1953

Holotype—BP/1/175, a complete skull (Fig. 141).

Locus Typicus—Antjiesfontein, Prince Albert, South Africa.

Horizon—*Tapinocephalus* Assemblage Zone (middle Permian).

Status—Junior subjective synonym of *Diictodon feliceps* (Owen, 1876).

Remarks—Toerien (1953) described *D. vanderhorsti* on the basis of a good skull from the *Tapinocephalus* AZ with an unusual bony ring around the pineal foramen. Cluver and Hotton (1981) transferred this species to *Diictodon*, and King (1988)

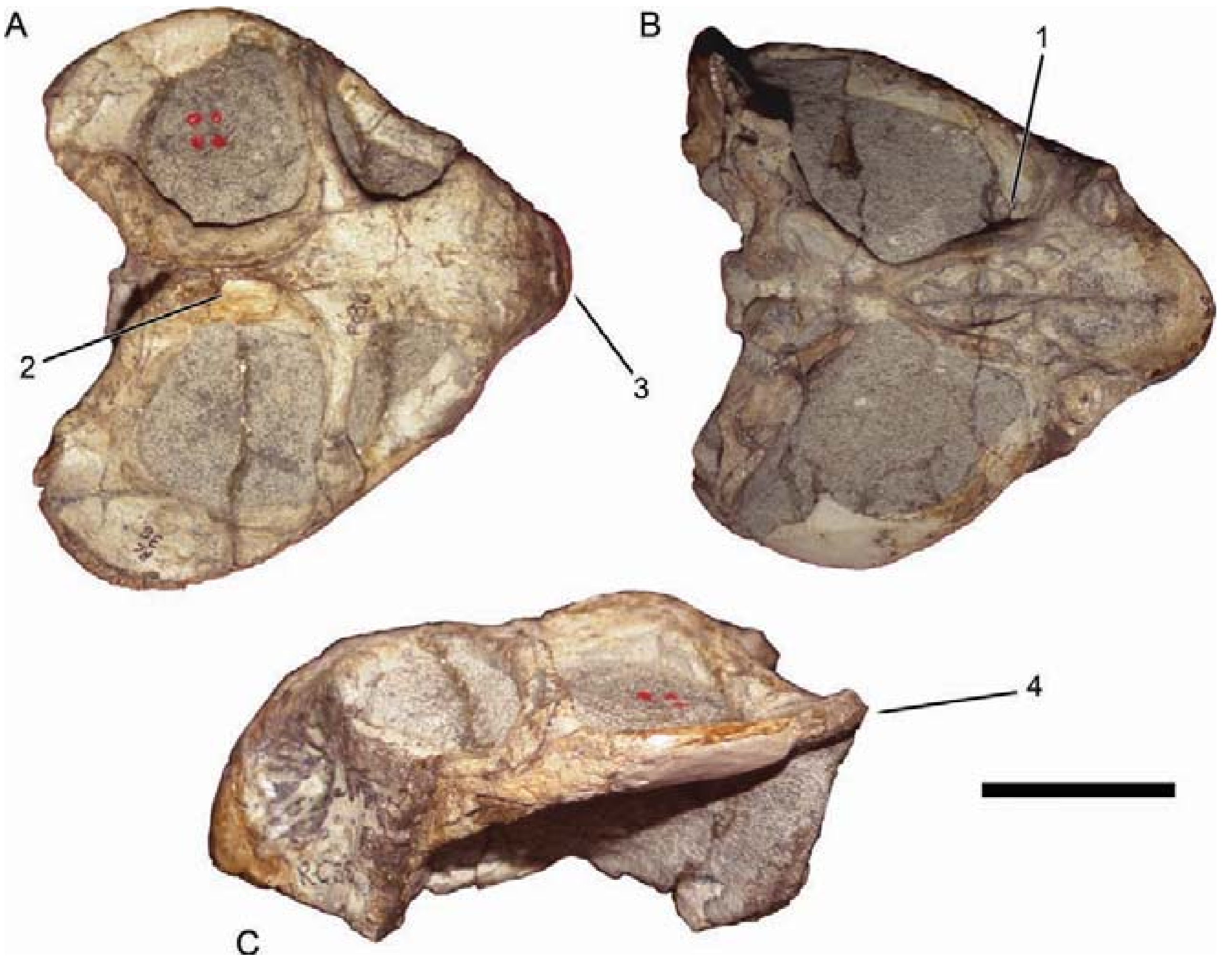

FIGURE 137. RC 38, the holotype of *Dicynodon trigonocephalus* (= *Dicynodon lacerticeps*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa and as *D. lacerticeps* on the basis of the (2) short intertemporal bar with nearly complete postorbital-parietal overlap, (3) blunt premaxillary tip, and (4) acutely angled squamosal rami in lateral view. Scale bar equals 5 cm.

maintained *Diictodon vanderhorsti* as valid and added *D. antjiesfonteinensis* as its junior synonym, noting that the holotypes of these species are from the same locality and nothing in Toerien's (1953) original description separates them. Brink (1986) and Sullivan and Reisz (2005) considered *D. vanderhorsti* to represent a junior synonym of *D. feliceps*, and this approach is followed here.

Dicynodon vanhoepeni Boonstra, 1938

Holotype—SAM-PK-11311, a snout and anterior portion of the lower jaws (Fig. 142).

Locus Typicus—Luangwa Valley, Zambia.

Horizon—Upper Madumabisa Mudstone (Upper Permian).

Status—Valid as *Syops vanhoepeni* (Boonstra, 1938), comb. nov.

Remarks—Boonstra (1938) named *Dicynodon vanhoepeni* as one of several species in the genus from the Luangwa Valley, the others being *D. luangwanensis*, *D. euryceps*, *D. helenae*, *D. parabreviceps*, and *D. roberti*. Of these species, the first four are clearly referable to *Oudenodon*, and here are all considered junior synonyms of *Oudenodon bainii*. Brink (1986) also listed *D. vanhoepeni* as a junior synonym of *Oudenodon luangwanensis*, but SAM-PK-11311 is not referable to *Oudenodon*. This specimen exhibits an unusual combination of features that allow it to be diagnosed as a valid species: it is tusked, with strongly anteriorly canted caniniform processes, paired dorsal grooves on the premaxilla, and a long, low premaxillary region characterized by a distinct break between the premaxillary and nasal planes. These features are also observed in the type material of *Dicynodon roberti*, and these species are here considered synonymous (see entry on *D. roberti*). For the creation of a new genus *Syops* for this species, refer to the Phylogenetic Analysis.

Dicynodon venteri Broom, 1935

Holotype—TM 199, a complete, dorsoventrally crushed skull (Fig. 143).

Locus Typicus—New Bethesda, Graaff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Nomen dubium (Dicynodontoidea indet.).

Remarks—Broom (1935) described *Dicynodon venteri* based on a complete but badly dorsoventrally compressed skull.

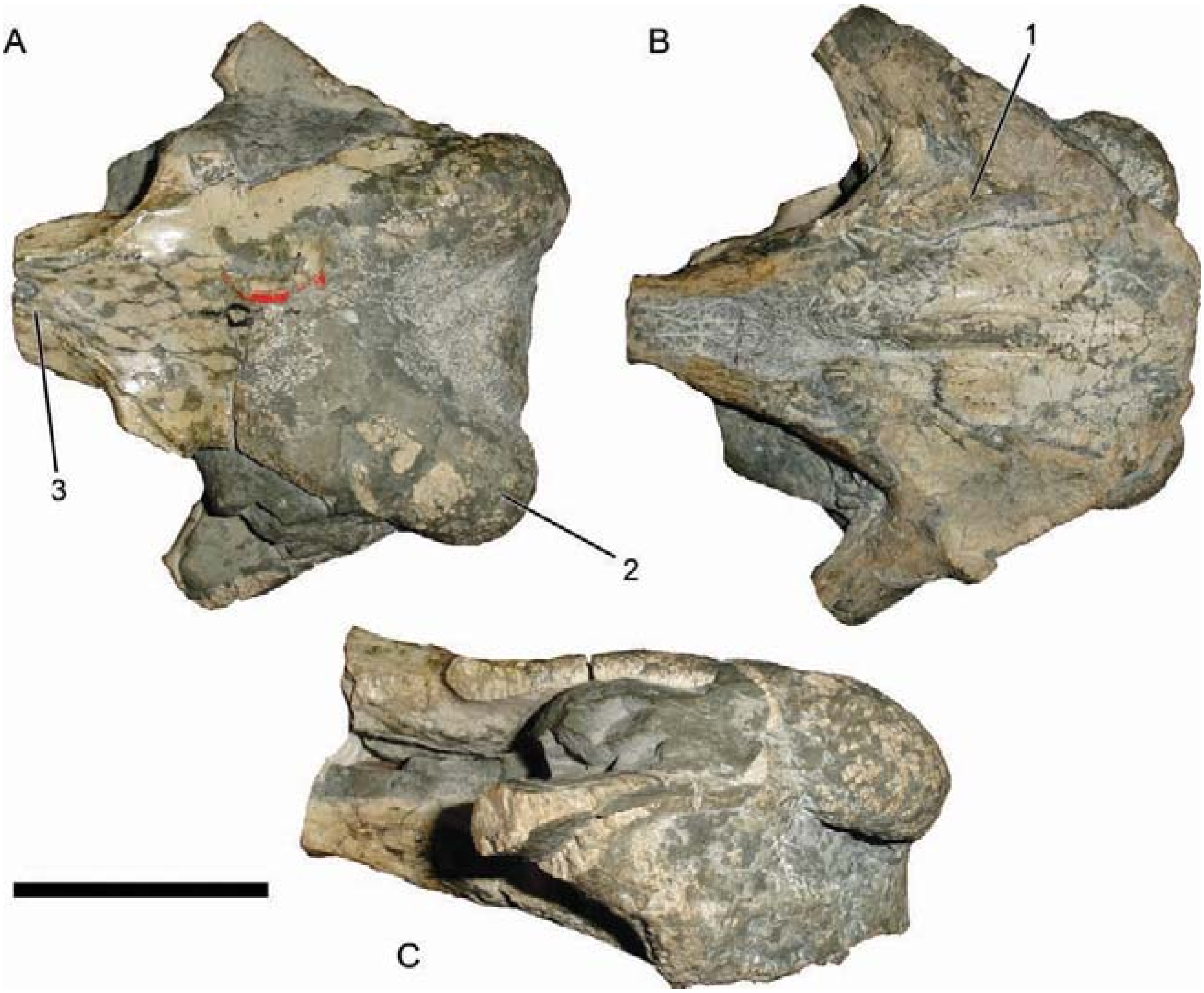

FIGURE 138. AMNH FARB 5511, the holotype of *Dicynodon tylorhinus*, in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and the (2) paired nasal bosses overhanging the external nares, and the position and massive size of these bosses are similar to those of geikiines. However, the (3) narrow intertemporal region is atypical of geikiines (with *Dicynodon sidneyi* being another exception). This species is sometimes included within *Propelanomodon*, whose relationships to other geikiids remain obscure. Scale bar equals 5 cm.

Haughton and Brink (1954), Cluver and Hotton (1981), and King (1988) listed *D. venteri* as a valid species, but Brink (1986) considered it a junior synonym of *Diictodon feliceps*. Although this specimen is too poorly preserved to tell whether a precaniniform notch is present, the palatine morphology of TM 199 is more similar to that of bidentalians (broad and flush with the palate) than *Diictodon*. Unfortunately the intense dorsoventral compression and probable juvenile nature of this specimen renders specific identification difficult, and we consider it Dicynodontoidea indet. at present.

Dicynodon venyukovi (Amalitzky, 1922)

Holotype—PIN 2005/6, a poorly preserved, laterally crushed skull (Fig. 144).

Locus Typicus—Sokolki, Arkhangelsk Region, Kotlasskii District, Russia.

Horizon—Upper Vyatkian substage, Tatarian series (Upper Permian).

Status—Junior subjective synonym of *Vivaxosaurus trautscholdi* (Amalitzky, 1922).

Remarks—Amalitzky (1922) described *Oudenodon venyukovi* as the first Russian *Oudenodon* species known from a complete skull (*Oudenodon rugosus* Trautschold, 1884, was named for an isolated angular boss that actually belongs to an *Anteosaurus*-like dinocephalian [Kammerer, 2011]). Sushkin (1926) argued that *O. venyukovi* was not referable to *Oudenodon*, and instead should be considered a junior synonym of *Dicynodon* (originally *Gordonia*) *annae* from the same North Dvina locality. Von Huene (1940) retained both species as valid within *Dicynodon*. Efremov (1940) argued that *Gordonia annae*, *Gordonia rossica*, and *Oudenodon venyukovi* were all synonymous with *Dicynodon trautscholdi*, a position followed by subsequent studies (e.g., King, 1988; Ivakhnenko et al., 1997; Angielczyk and Kurkin, 2003a; Ivakhnenko, 2003) and upheld here.

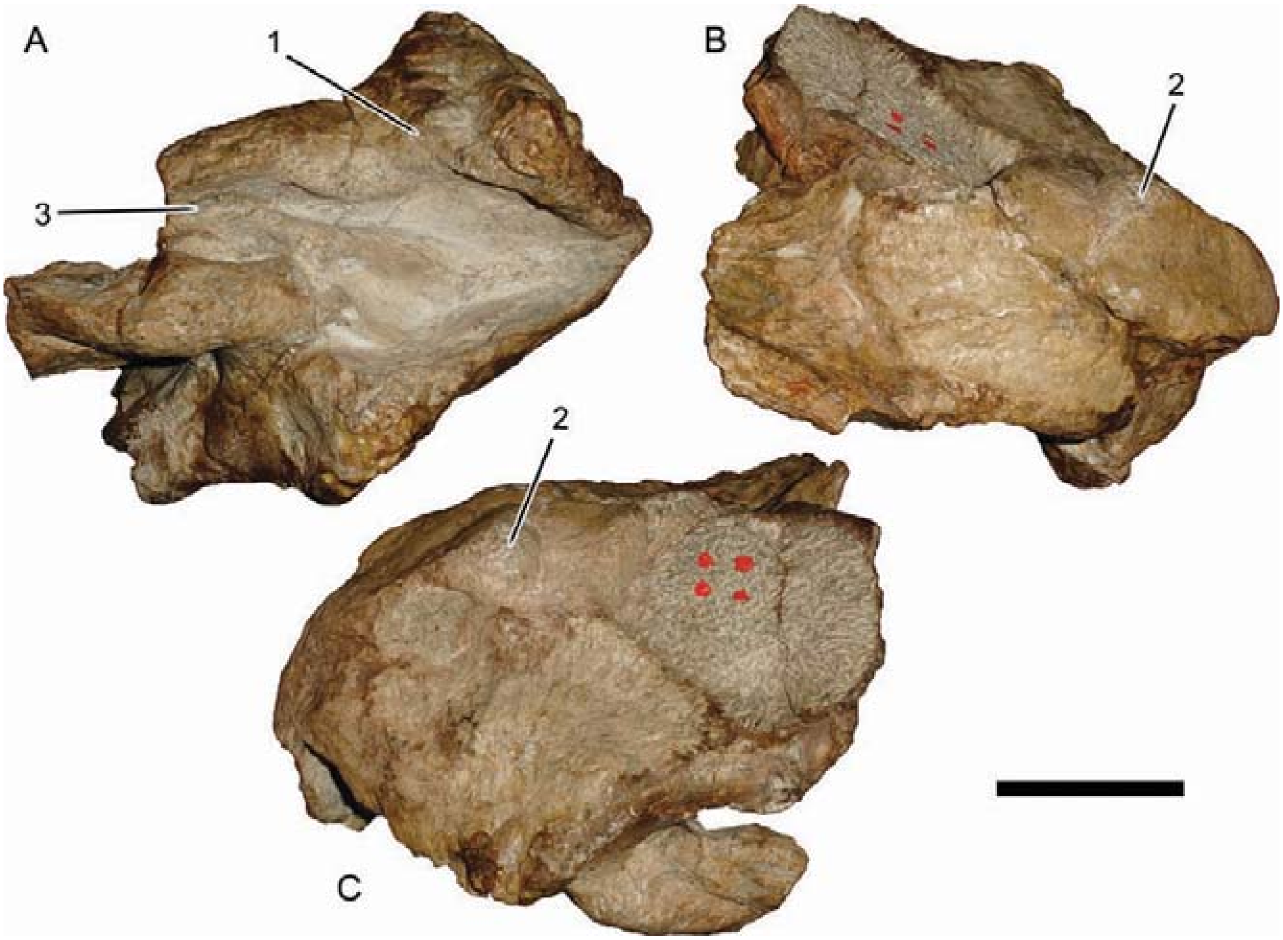

FIGURE 139. TM 252, the holotype of *Dicynodon validus* (= *Tropidostoma dubium*), in palatal (**A**), dorsal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) lengthy interpterygoid vacuity, and as *Tropidostoma* on the basis of tusks and snout proportions. Scale bar equals 5 cm.

Dicynodon verticalis Owen, 1860b

Holotype—NHMUK 36224, a poorly preserved skull missing the left zygomatic arch (Fig. 145).

Locus Typicus—Rhenosterberg, South Africa.

Horizon—*Lystrosaurus* Assemblage Zone (Lower Triassic).

Status—Junior subjective synonym of *Lystrosaurus murrayi* (Huxley, 1859).

Remarks—As for *Dicynodon declivis* and *Dicynodon latirostris*, we include an entry for *Dicynodon verticalis* because it was named when Owen (1860b) included *Ptychognathus* (= *Lystrosaurus*) as a subgenus of *Dicynodon*. Owen (1860b) distinguished this species from other *Ptychognathus* by its proportionally larger orbits and more vertically oriented snout and occiput. Cluver (1971) considered this species to be synonymous with *Lystrosaurus murrayi*, and this synonymy has been followed by all subsequent authors (e.g., Colbert, 1974; King, 1988; Grine et al., 2006).

Dicynodon watsoni Broom, 1921

Holotype—SAM-PK-7849, a skull roof fragment preserving the interorbital and intertemporal regions (Fig. 146).

Locus Typicus—East of New Bethesda, 800 feet above the village horizon, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Daptocephalus leoniceps* (Owen, 1876).

Remarks—Broom (1921) believed SAM-PK-7849 to be from the *Lystrosaurus* Assemblage Zone, and to differ from the other nominal species of large *Lystrosaurus* AZ *Dicynodon* (*D. osborni*) by the lack of supraorbital bosses. Van Hoepen (1934) included this species in *Daptocephalus* with *D. leoniceps*. Despite the fragmentary nature of the holotype, Haughton and Brink (1954), Cluver and Hotton (1981), and King (1988) considered *D. watsoni* to represent a valid species of *Dicynodon*. The morphology of the intertemporal bar in SAM-PK-7849 indicates that this specimen is a dicynodontoid, and its extreme length and narrowness, combined with broad interorbital region and narrow, strap-like dorsal exposure of the postfrontals, indicates that this is a specimen of *Daptocephalus leoniceps*.

Dicynodon weatherbyi Broom, 1941

Holotype—MMK 5264, a crushed skull missing much of the right zygomatic arch (Fig. 147).

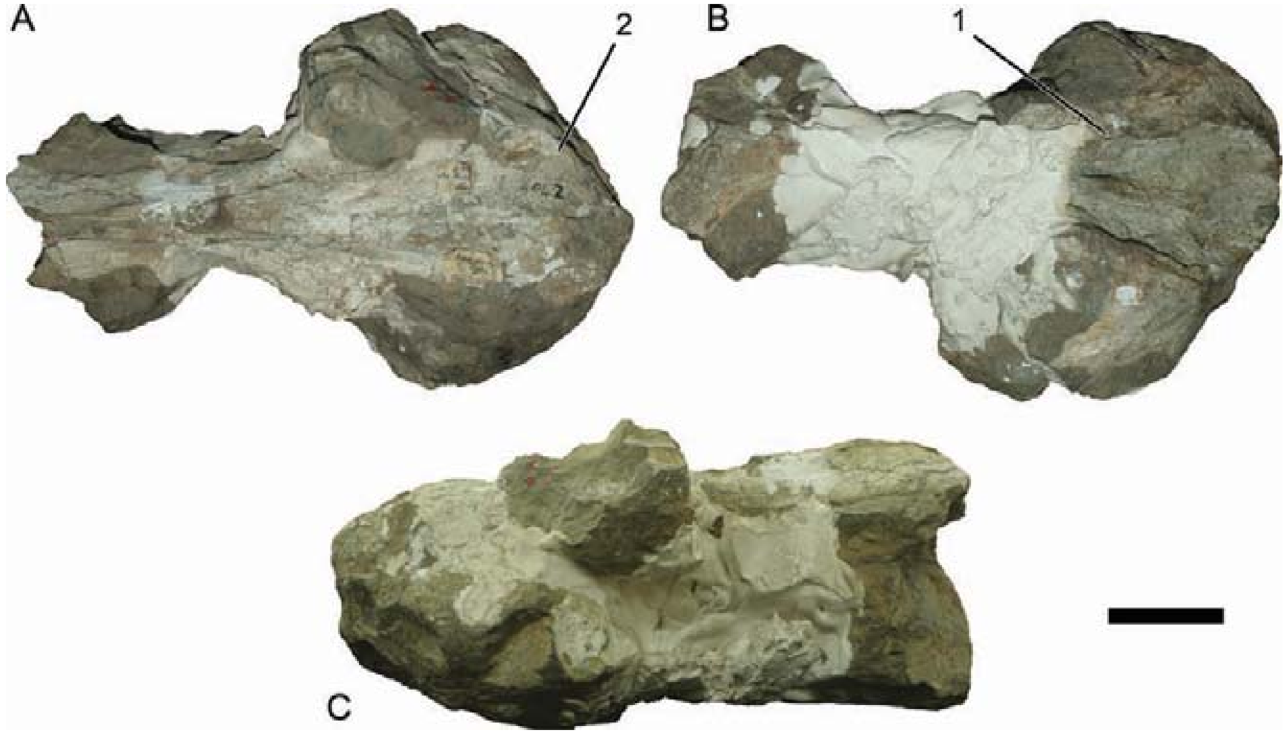

FIGURE 140. MMK 4042, the holotype of *Dicynodon vanderbyli* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

Locus Typicus—Houdconstant, Graaff-Reinet, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Basilodon woodwardi* (Broom, 1921).

Remarks—Broom (1941) considered *Dicynodon weatherbyi* to be very similar to *Dicynodon alticeps*, but distinguished the new species by its shorter intertemporal region and narrower snout. Haughton and Brink (1954), Kitching (1977), and King (1988) listed *D. weatherbyi* as a valid species, but Brink (1986) listed it as a synonym of *Tropidostoma microtrema*. The stratigraphic position of this specimen (from the *Dicynodon* AZ) makes such a referral unlikely, and MMK 5264 lacks the lengthy interpterygoid vacuity, nasal bosses overhanging the nares, and characteristic snout morphology of *Tropidostoma*. The presence of a labial fossa indicates that this specimen is a dicynodontoid, although the broad intertemporal bar with exposure of the parietals throughout is unusual for that group. Only two taxa of South African Permian dicynodontoids have an intertemporal region similar

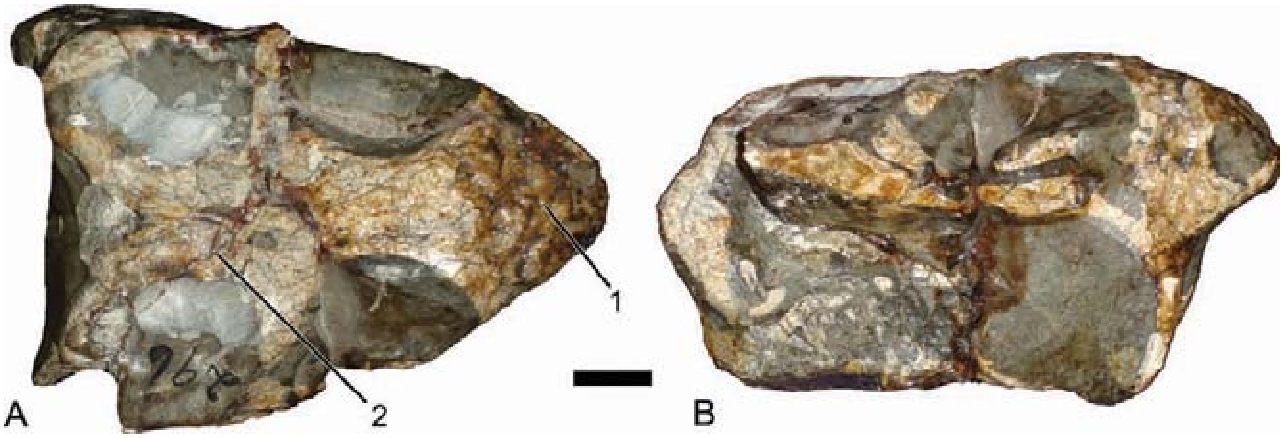

FIGURE 141. BP/1/185, the holotype of *Dicynodon vanderhorsti* (= *Diictodon feliceps*), in dorsal (**A**) and right lateral (**B**) views. This specimen can be identified as a pylaecephalid on the basis of the (1) median snout ridge and as *D. feliceps* on the basis of the (2) narrow intertemporal bar with extensive postorbital-parietal overlap. Scale bar equals 1 cm.

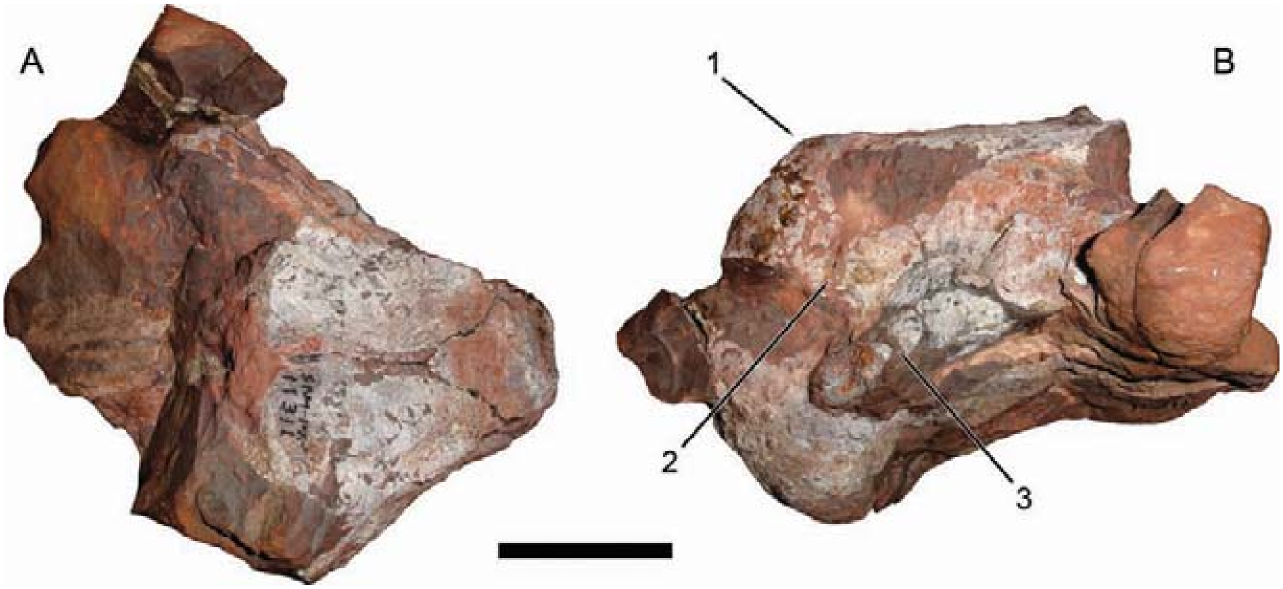

FIGURE 142. SAM-PK-11311, the holotype of *Dicynodon vanhoepeni* (= *Syops vanhoepeni*), in dorsal (**A**) and left lateral (**B**) views. *Syops vanhoepeni* can be distinguished from other dicynodonts by the combination of a (1) distinctly biplanar snout, with the break in slope above the anterodorsal edge of the external nares, (2) a ridge on the premaxillary-maxillary suture, and (3) a strongly anteriorly directed, massive tusk. Scale bar equals 5 cm.

to MMK 5264: *Basilodon woodwardi* and *Sintocephalus alticeps*. MMK 5264 lacks steeply but evenly sloping snout of *S. alticeps*, but displays all the characteristic features of *B. woodwardi* (distinctly biplanar snout with break in slope above external naris, triangular depressions on the dorsal surface of the postorbital contribution to the postorbital bar, and an elongate premaxillary portion of the palate with a distinctly squared-off tip), and here we consider *D. weatherbyi* a junior synonym of *B. woodwardi*.

Dicynodon wellwoodensis Broom, 1936

Holotype—TM 262, a well-preserved skull missing the left temporal arch and edge of the occiput (Fig. 148).

Locus Typicus—Wellwood, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1936) described *Dicynodon wellwoodensis* based on a good skull, but did not explicitly distinguish this taxon from other members of the genus. Keyser (1975) argued that TM 262 falls within the range of variation for *Oudenodon bainii*, and synonymized *D. wellwoodensis* with that taxon. Subsequent studies have supported this assessment (e.g., Kitching, 1977; Brink, 1986; King, 1988) and it is maintained here.

Dicynodon whaitsi Broom, 1913c

Holotype—AMNH FARB 5566, a laterally crushed skull (missing most of the posterior portion of the skull) and the anterior portion of the lower jaws (Fig. 149).

Locus Typicus—Nieuwveld, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Valid as *Odontocyclops whaitsi* (Broom, 1913c).

Remarks—Broom (1913c) described *Dicynodon whaitsi* on the basis of a partial mandible and a large, laterally crushed skull missing most of the occiput and temporal arches from the Nieuwveld. Broom considered *D. whaitsi* to be most similar to *Dicynodon leoniceps* in general proportions, but considered it most closely related to *Dicynodon prognathus* (= *Oudenodon bainii*). He distinguished *D. whaitsi* from other species on the basis of its broad intertemporal region and well-developed posterior portion of the postorbitals. Van Hoepen (1934) included this species in *Oudenodon* in the subgenus *Mastocephalus*. Haughton and Brink (1954), Kitching (1977), and King (1988) listed *D. whaitsi* as a valid species, but Brink (1986) considered it synonymous with *Dicynodon lacerticeps*. Angielczyk (2002a) reexamined this species and demonstrated that it is referable to the cryptodont genus *Odontocyclops* and has priority over the other nominal species of that taxon.

Dicynodon whitsonae Toerien, 1954

Holotype—RC 42, a dorsoventrally crushed skull with a poorly preserved ventral surface.

Locus Typicus—Wellwood, Graaff-Reinet, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Unnecessary replacement name for *Dicynodon anneae* Broom, 1940 (not preoccupied by *Dicynodon annae* [Amalitzky, 1922]); junior subjective synonym of *Dinanomodon gilli* (Broom, 1932).

Remarks—See entry on *Dicynodon anneae* Broom, 1940.

Dicynodon wilmanae Broom, 1928

Holotype—MMK 4167, a well-preserved skull missing the right zygomatic arch (Fig. 150).

Locus Typicus—$2^1/_2$ miles east of Biesjiespoort Station, Victoria West, South Africa.

Horizon—*Cistecephalus* Assemblage Zone (Upper Permian).

Status—Junior subjective synonym of *Oudenodon bainii* Owen, 1860b.

Remarks—Broom (1928) considerd *Dicynodon wilmanae* to be very similar to *Dicynodon mustoi* (= *Oudenodon bainii*), but from a higher stratigraphic horizon and thus necessitating a new species name. Van Hoepen (1934) transferred this species to *Oudenodon*. Keyser (1975) argued that this species represents

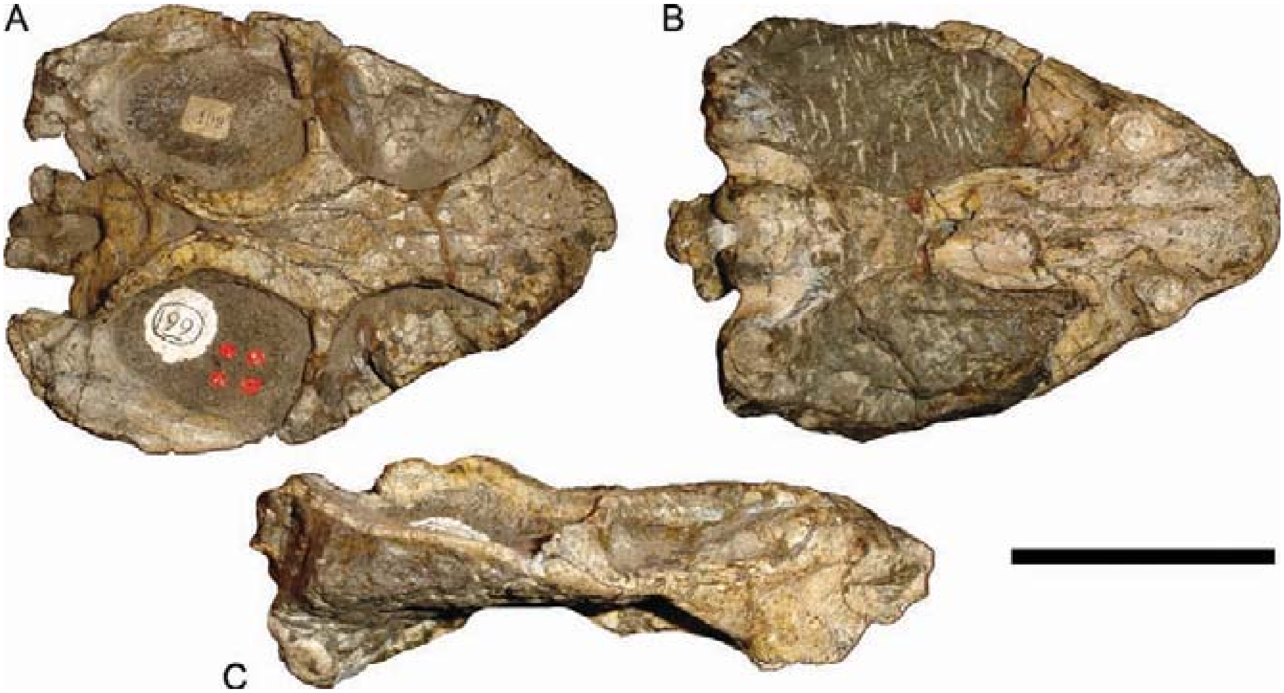

FIGURE 143. TM 199, the holotype of *Dicynodon venteri*, in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen appears to represent a juvenile dicynodontoid, but cannot be identified to species. Scale bare equals 5 cm.

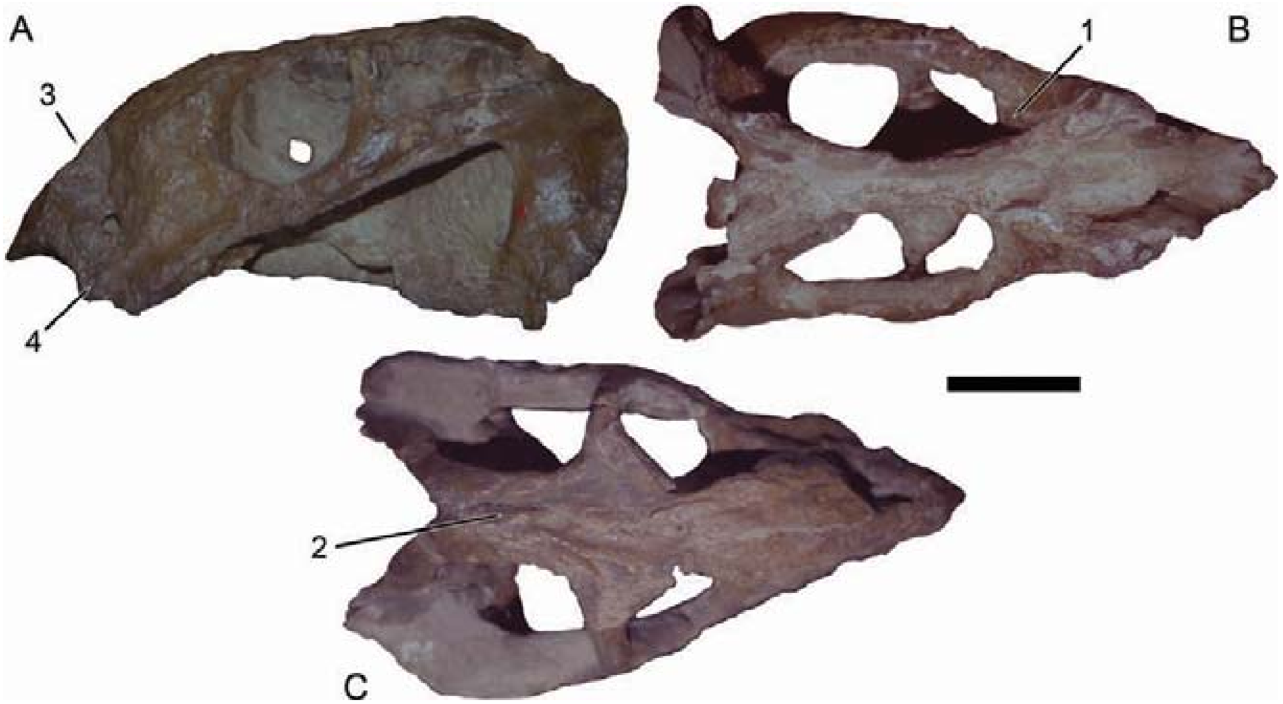

FIGURE 144. PIN 2005/6, the holotype of *Dicynodon venyukovi* (= *Vivaxosaurus trautscholdi*), in left lateral (**A**), palatal (**B**), and dorsal (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa, and as *V. trautscholdi* on the basis of the (2) short intertemporal bar with narrow but consistent exposure of the parietals, (3) gradually sloping, dorsoventrally narrow snout, and (4) anteriorly directed caniniform process with rounded anterior lobe. Scale bar equals 5 cm.

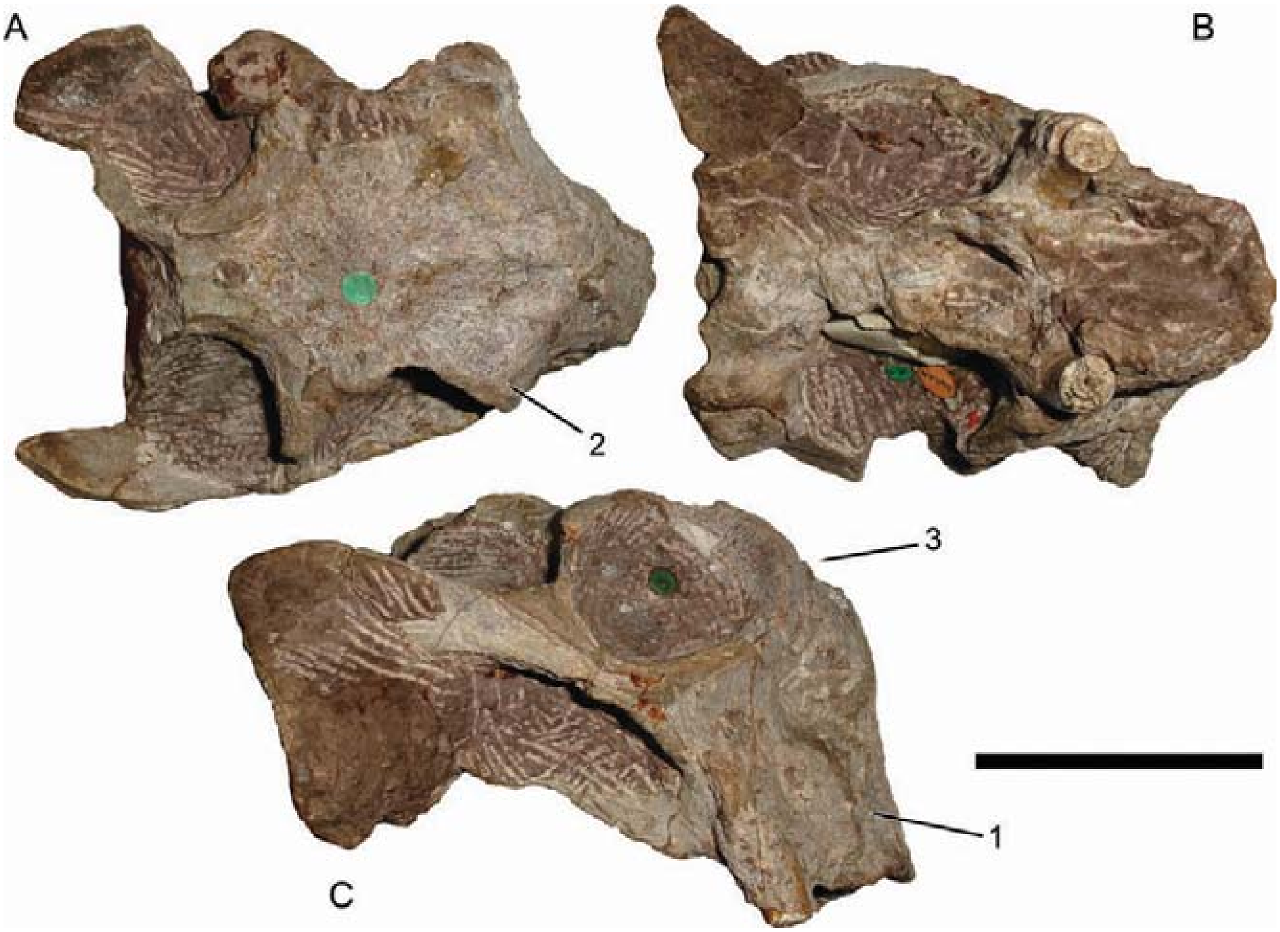

FIGURE 145. NHMUK 36224, the holotype of *Dicynodon verticalis* (= *Lystrosaurus murrayi*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a lystrosaurid on the basis of the (1) tall, strongly deflected snout and (2) well-developed prefrontal bosses, and as *L. murrayi* on the basis of the (3) triplanar snout profile, with distinct breaks in slope between the naso-premaxillary, naso-frontal, and fronto-parietal planes. Scale bar equals 5 cm.

a junior synonym of *Oudenodon bainii*, an approach followed by subsequent authors (e.g., Brink, 1986; King, 1988) and maintained here. MMK 4167 is only partially prepared and has had much of the bone surface on the dorsal side of the skull ground off, but still clearly exhibits the lengthy interpterygoid vacuity, postparietal contribution to the skull roof, and lack of tusks diagnostic for *O. bainii*.

Dicynodon woodwardi Broom, 1921

Holotype—MMK 4166, a badly weathered partial skull missing the temporal arches and much of the palate and occiput (Fig. 151).

Locus Typicus—Near New Bethesda, South Africa.

Horizon—*Dicynodon* Assemblage Zone (Upper Permian).

Status—Valid as *Basilodon woodwardi* (Broom, 1921), comb. nov.

Remarks—Broom (1921) diagnosed *Dicynodon woodwardi* by its remarkably broad preparietal. Van Hoepen (1934) included this species in *Sintocephalus* with *Dicynodon alticeps*. Haughton and Brink (1954) and King (1988) considered *D. woodwardi* to be valid, whereas Brink (1986) listed it in the synonymy of *Dicynodon lacerticeps*. The absence of nasal bosses and postcaniniform crest coupled with the apparent presence of a labial fossa indicate that this specimen represents a dicynodontoid. The intertemporal bar of MMK 4166 is poorly preserved and incomplete, but it appears to be broad at the level of the pineal foramen. The broad intertemporal region and ventrally directed caniniform processes are at odds with identification as *D. lacerticeps*, but are similar to the condition in *Sintocephalus alticeps*. However, MMK 4166 differs from *S. alticeps* in having a distinctly biplanar snout profile (with the break in profile between the nasals and premaxilla above the external naris), a relatively wider median pterygoid plate, a depression on the dorsal portion of the postorbital contributing to the postorbital bar, and an elongate premaxillary portion of the palate with a distinctly squared-off tip. This unique set of characters is also observed in several other "*Dicynodon*" holotypes, such as *D. calverleyi* and *D. microdon*, and we recognize this morphotype as a distinct species, for which the name *D. woodwardi* has priority. For placement of this species in the new genus *Basilodon*, refer to the Phylogenetic Analysis.

MORPHOMETRIC ANALYSIS

Background and Methods

In the first line of his description of *Dicynodon leoniceps*, Owen (1876:32) stated that the holotype of this species (NHMUK

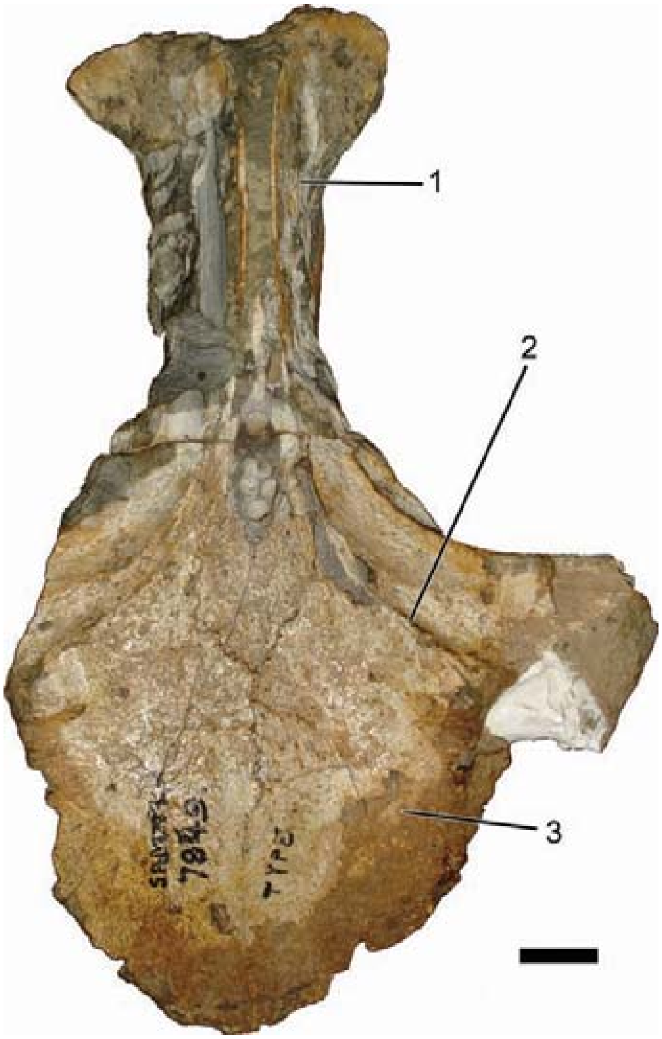

FIGURE 146. SAM-PK-7849, the holotype of *Dicynodon watsoni* (= *Daptocephalus leoniceps*), in dorsal view. Although this specimen is only a partial skull roof, it can confidently be referred to *D. leoniceps* based on the combination of a (1) long, extremely narrow intertemporal bar with vertically oriented postorbitals, (2) thin, strap-like postfrontal, and (3) very broad interorbital region. Scale bar equals 1 cm.

47047) is "not an old individual or large variety of *Dicynodon lacerticeps*." That said, the possibility of synonymy between these species has loomed large in all subsequent studies, beginning with Lydekker (1890) and persisting to the present day. The holotype of *D. leoniceps* is much larger than that of *D. lacerticeps*, and subsequent referrals to these species have usually been made based on size: in Karoo fossil vertebrate collections, large "*Dicynodon*" skulls are generally referred to *D. leoniceps* and small- to medium-sized "*Dicynodon*" skulls are generally referred to *D. lacerticeps*.

In our broadly inclusive approach to the taxonomic binning of South African Permian dicynodontoids, we have recognized large presumed adults and small presumed juveniles of both the *D. lacerticeps* and *D. leoniceps* morphotypes. In large specimens, there are consistent differences in the length and width of the intertemporal bar separating them, but because these characters are strongly ontogenetically variable in dicynodontoids (with very small specimens of different species having relatively short, broad intertemporal bars), we wanted to test whether these species could be distinguished across sizes. To accomplish this, we analyzed two additional shape characters observed to vary between large adult *D. lacerticeps* and *D. leoniceps*: snout profile and squamosal morphology. Large, presumed adult specimens of *D. lacerticeps* exhibit gradually sloping snout profiles and acutely angled rami of the squamosal in lateral view, whereas *D. leoniceps* specimens exhibit steeply sloping snout profiles and broadly rounded rami of the squamosal in lateral view.

We undertook an outline-based geometric morphometric analysis based on photographs of representatives of these species in lateral view (refer to Appendix 1 for list of specimens used). Using the program tpsDig2 (Rohlf, 2008), we manually fitted curves to the snout profile (dorsal edge of the snout, covering the area running from a vertical plane through the anterior margin of the orbits to the anterior-most tip of the premaxilla) and dorsal margin of the squamosal (covering the area from the upper edge of the contact between the postorbital and squamosal to the posterior contact between the squamosal-quadratojugal-quadrate) of *Dicynodon lacerticeps* and *D. leoniceps* skulls. We resampled these curves to evenly space 10 semi-landmarks along each of them and converted these semi-landmark positions into coordinate data (Fig. 152). We excluded specimens in which the pertinent portions of the skull were broken off (unfortunately, the temporal arches are broken in many dicynodont specimens, limiting the sample size for the squamosal analysis) but included specimens that had been subjected to taphonomic deformation, because one of the aims of this analysis was to determine whether

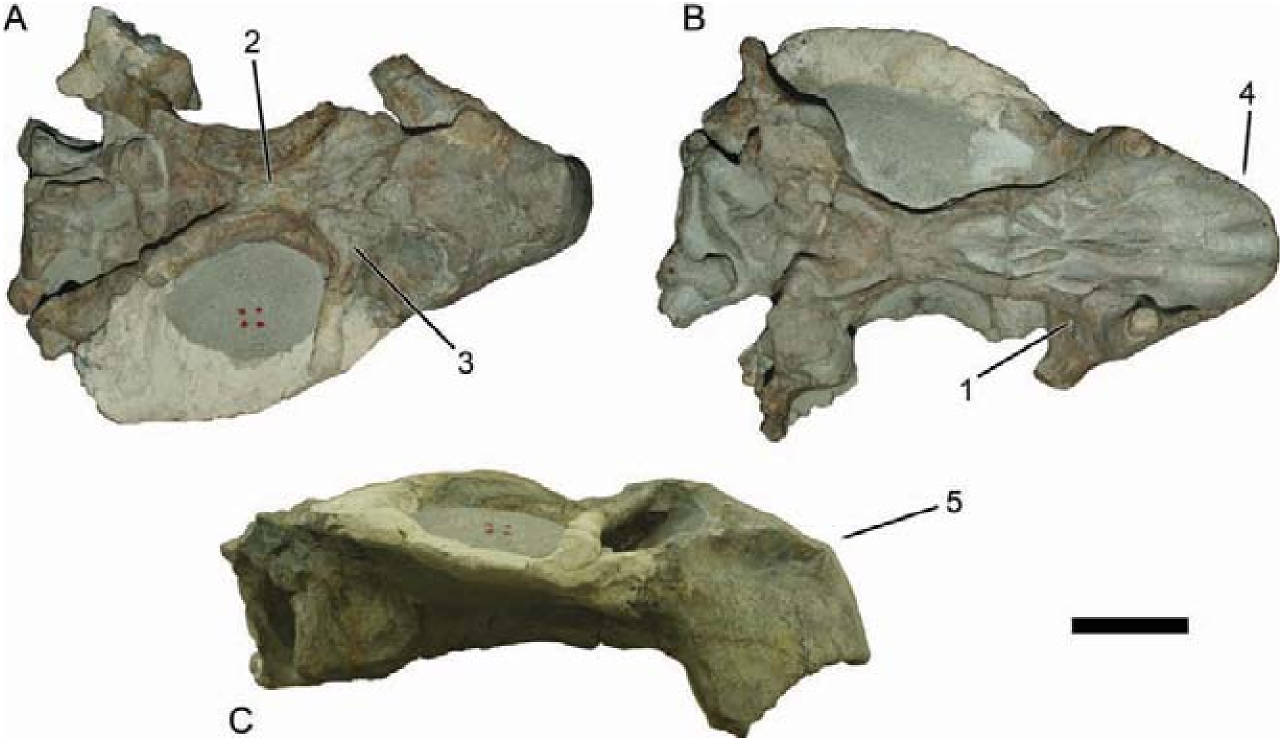

FIGURE 147. MMK 5264, the holotype of *Dicynodon weatherbyi* (= *Basilodon woodwardi*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid by the (1) labial fossa and as *B. woodwardi* by the (2) broad exposure of the parietals in the intertemporal bar, (3) triangular depressions on the dorsal surface of the postorbital contribution to the postorbital bar, (4) elongate premaxillary portion of the palate ending in a distinctly squared-off tip, and a (5) distinct break in slope in the snout profile between the nasals and premaxilla, above the external nares. Scale bar equals 5 cm.

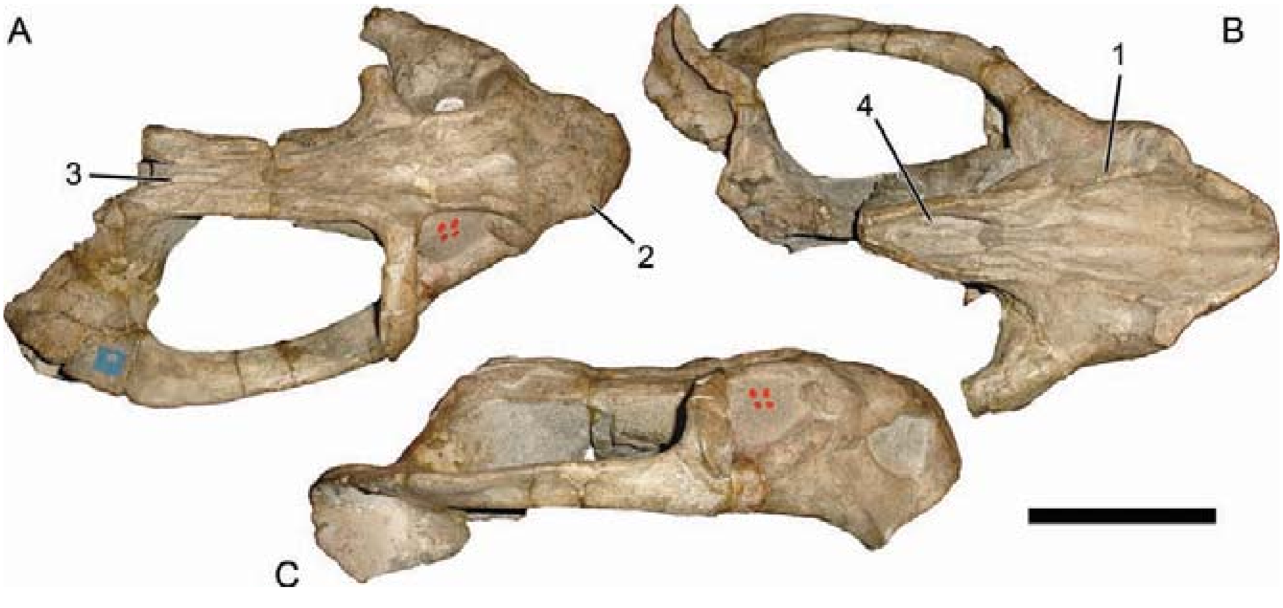

FIGURE 148. TM 262, the holotype of *Dicynodon wellwoodensis* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 10 cm.

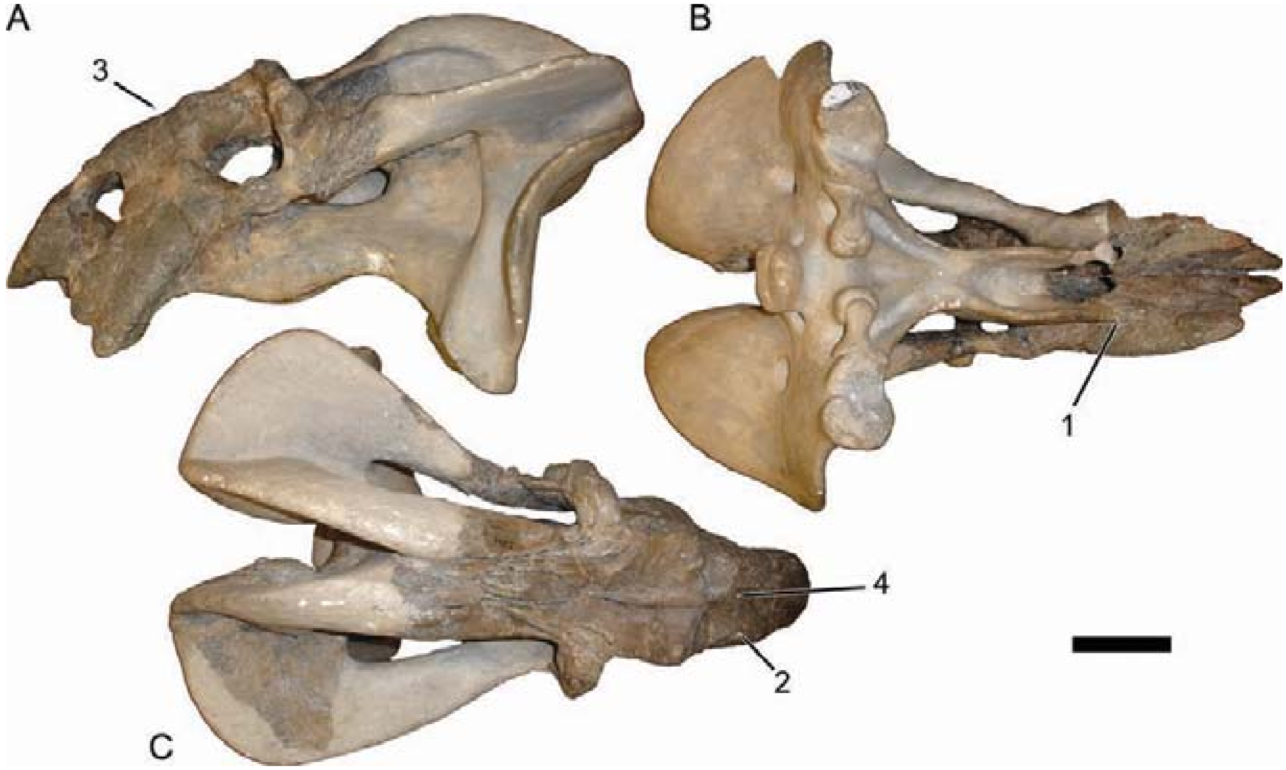

FIGURE 149. AMNH FARB 5566, the holotype of *Dicynodon whaitsi* (= *Odontocyclops whaitsi*), in left lateral (**A**), palatal (**B**), and dorsal (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares. *Odontocyclops whaitsi* can be identified by (2) elongate nasal bosses (3) extending from the posterodorsal end of the external nares to the prefrontal, with a (4) concavity between them. Scale bar equals 10 cm.

the shape characters we use to distinguish *D. lacerticeps* and *D. leoniceps* are robust to size-based and deformational variation among specimens. In the snout curve analysis we included 50 specimens (23 of *D. lacerticeps* and 27 of *D. leoniceps*) and in the squamosal curve analysis we included 25 specimens (a subset of the sample used in the prior analysis, with 11 of *D. lacerticeps* and 14 of *D. leoniceps*). We binned specimens a priori—this test was not to determine, agnostic of referral, the attribution of juvenile specimens, but rather to see whether proportional characters utilized in diagnosing these species were quantitatively discrete. We used the program TwoGroup in the IMP software package (Sheets, 2004) to test for statistically significant separation between the species groups using a Goodall's *F*-test (100 bootstrap replicates). This test compares the Procrustes distance between sample means (with means determined through generalized least squares Procrustes analysis) and sample variance. We used the program MorphoJ (Klingenberg, 2008) to explore distribution of the specimens in morphospace, using PC1 and 2 from a principal component analysis (PCA) of shape as the morphospace axes.

Results and Discussion

We found the *Dicynodon lacerticeps* and *D. leoniceps* samples to have statistically significant shape differences for both snout profile and squamosal shape (Goodall's *F*-test $P = 0.0100$, *F*-score 10.73 for snout profile and $P = 0.0100$, *F*-score 31.39 for squamosal shape). The PCA produced two significant axes for both the snout and the squamosal analyses, with PC1 accounting for 70.156% of snout variance and 67.432% of squamosal variance and PC2 accounting for 21.866% of snout variance and 21.181% of squamosal variance. Variation in shape along PC1 (Fig. 153) closely matches the distinction in snout profile we have described for *D. lacerticeps* and *D. leoniceps*, with specimens with a high positive value for PC1 having a sharply sloping snout profile (*D. leoniceps*; Fig. 153B) and specimens with a high negative value for PC1 having a gradually sloping snout profile (*D. lacerticeps*; Fig. 153C). Similarly, for variation along PC1 for squamosal shape, specimens with a high negative value for PC1 have a broadly rounded dorsal profile of the squamosal in lateral view (*D. leoniceps*; Fig. 153E) and specimens with a high positive value for PC1 have an acutely angled dorsal profile of the squamosal in lateral view (*D. lacerticeps*; Fig. 153F). For snout profile, PC2 is associated with degree of curvature along the dorsal surface of the snout (with positive values of PC2 having a more convex naso-frontal region and more concave naso-premaxillary region). For squamosal shape, PC2 is associated with separation between the endpoints of the curve (with positive values of PC2 having curve endpoints nearer to each other).

Examining the position of individual specimens used in these analyses in morphospace reveals that there is overlap between the *Dicynodon lacerticeps* and *D. leoniceps* clusters for snout profile (Fig. 154A) but nearly complete separation for squamosal shape (Fig. 154B). Only a single specimen (RC 38, the holotype of *Dicynodon trigonocephalus*) occupies an intermediate position between the *D. leoniceps* and *D. lacerticeps* clusters for the squamosal shape plot. The region of overlap in the snout profile plot is occupied by *D. leoniceps* specimens that have suffered from dorsoventral compression (e.g., CGP GHG36a, RC 96, SAM-PK-6044), resulting in a more flattened, less steeply sloping snout than would have been present in life.

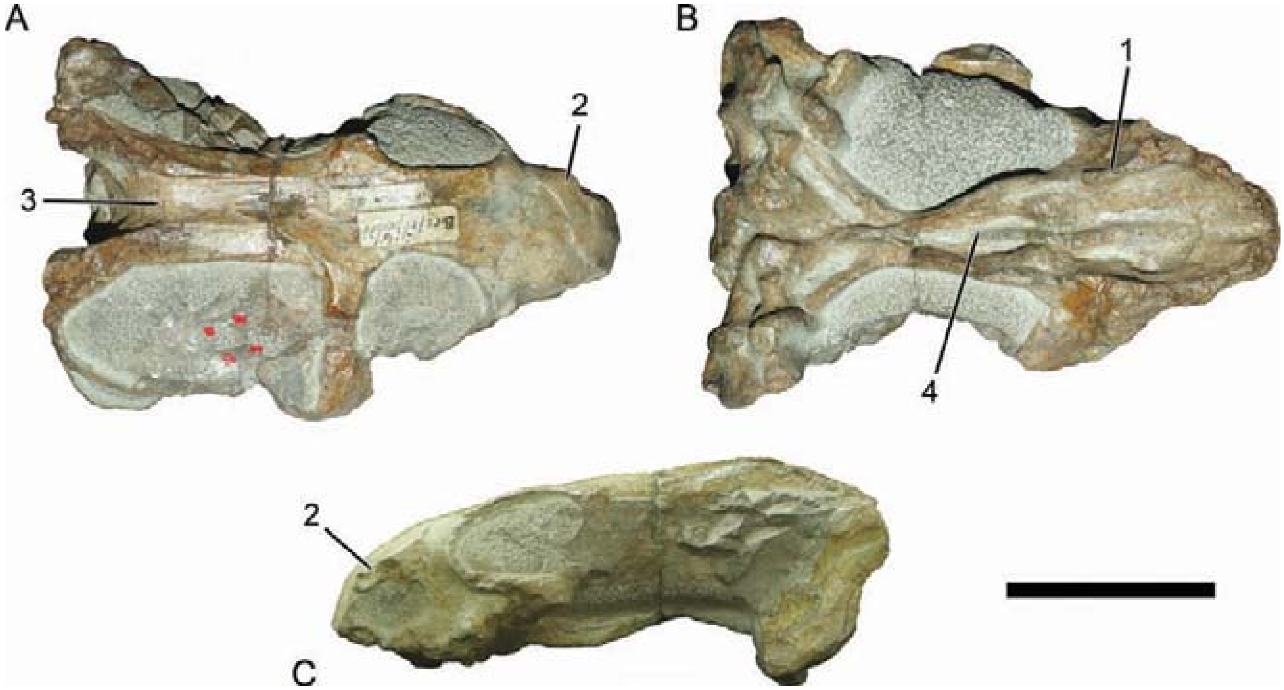

FIGURE 150. MMK 4167, the holotype of *Dicynodon wilmanae* (= *Oudenodon bainii*), in dorsal (**A**), palatal (**B**), and left lateral (**C**) views. This specimen can be identified as a cryptodont on the basis of the (1) postcaniniform crest and (2) paired nasal bosses overhanging the external nares, as an oudenodontid on the basis of the (3) dorsal skull roof exposure of the postparietal and (4) lengthy interpterygoid vacuity, and as *O. bainii* on the basis of the lack of tusks and snout proportions. Scale bar equals 5 cm.

The results of the morphometric analysis indicate that *Dicynodon lacerticeps* and *D. leoniceps* differ significantly in snout profile and squamosal shape. Furthermore, squamosal shape appears to be a robust character for referral to these species, because these taxa cluster by squamosal shape regardless of skull size (and thus presumed ontogenetic state) and degree of taphonomic deformation. Regarding snout profile, undistorted skulls of *D. lacerticeps* and *D. leoniceps* occupy different regions of morphospace, but specimens of *D. leoniceps* that have suffered dorsoventral compression overlap with *D. lacerticeps*. As such, this character by itself cannot be used to identify a skull to species, especially if deformation has occurred. However, in combination with squamosal shape and intertemporal bar length (or in undistorted skulls), this is a useful character for specific identification.

PHYLOGENETIC ANALYSIS

Background and Methods

The roots of our current understanding of anomodont phylogeny can be traced back to the pioneering work of Cluver and King (1983) and King (1988, 1990). Since then, and particularly in the last decade, numerous phylogenetic analyses of anomodonts have been undertaken (summarized in Fig. 155) (Rubidge and Hopson, 1990; Cox, 1998; Modesto et al., 1999, 2002, 2003; Modesto and Rubidge, 2000; Modesto and Rybczynski, 2000; Rybczynski, 2000; Angielczyk, 2001, 2002a, 2002b, 2004, 2007; Maisch, 2001, 2002a; Liu et al., 2002, 2010; Angielczyk and Kurkin, 2003a, 2003b; Liu and Li, 2003; Surkov and Benton, 2004; Vega-Dias et al., 2004; Maisch and Gebauer, 2005; Surkov et al., 2005; Ray, 2006; Damiani et al., 2007; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Surkov and Benton, 2008; Govender and Yates, 2009; Angielczyk and Rubidge, 2010, in press; Fröbisch et al., 2010; Cisneros et al., 2011). None of these analyses provide a comprehensive picture of anomodont phylogeny, however, because taxon sampling has tended to focus on either Permian or Triassic taxa. For example, Maisch (2001) and Fröbisch et al. (2010) are the most comprehensive analyses of Triassic and Permian anomodonts, respectively, but the former analysis includes only one Permian taxon and the latter includes only five Triassic taxa. Similarly, analyses with more balanced samples of Permian and Triassic taxa (e.g., Damiani et al., 2007; Surkov and Benton, 2008) have not included the full diversity of anomodonts known from either period. As a result, studies focusing on large-scale trends in anomodont evolution and diversity in a phylogenetic framework (e.g., Angielczyk and Walsh, 2008; Botha-Brink and Angielczyk, 2010) have relied on composite trees grafted together from various sources, and a complete, phylogenetically informed higher-level taxonomy of anomodonts has yet to be undertaken (Kammerer and Angielczyk, 2009).

Given its apparent position at the base of the dicynodontoid radiation, *Dicynodon* sensu lato has the potential to provide a critical link between the Permian and Triassic histories of anomodonts. Two particular questions arise in this context: (1) Is *Dicynodon* sensu lato monophyletic and, if so, where does this clade fall relative to other Permian and Triassic dicynodonts? (2) If *Dicynodon* is not monophyletic, do the valid species currently included in the genus form a paraphyletic assemblage at the base of the dicynodontoid radiation or do they represent Permian members of lineages that otherwise make their first appearances in the Middle Triassic (e.g., kannemeyeriiforms)? Previous analyses that included multiple species of *Dicynodon* (Angielczyk and Kurkin, 2003a, 2003b; Angielczyk, 2007; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Angielczyk and Rubidge 2010, in press; Fröbisch et al., 2010) found that *Dicynodon* is not monophyletic and that it forms a paraphyletic assemblage at the base of the Triassic dicynodontoid radiation, but these results should be

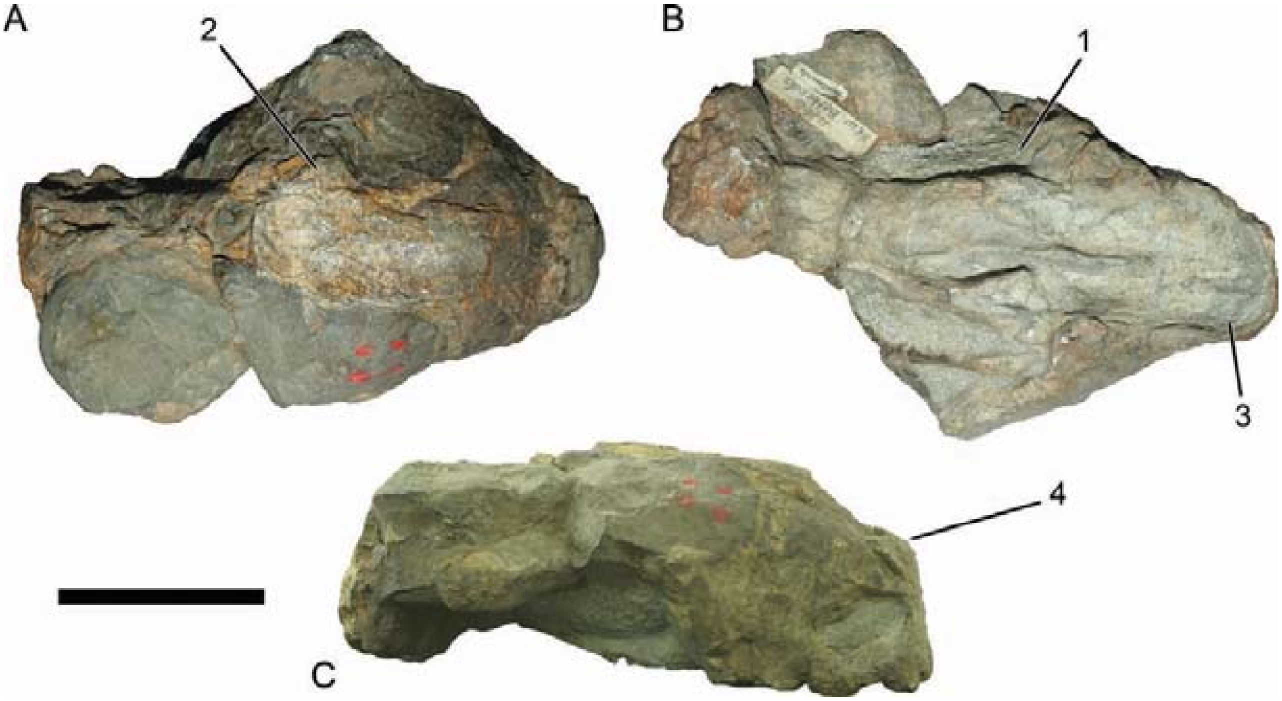

FIGURE 151. MMK 4166, the holotype of *Dicynodon woodwardi* (= *Basilodon woodwardi*), in dorsal (**A**), palatal (**B**), and right lateral (**C**) views. This specimen can be identified as a dicynodontoid on the basis of the (1) labial fossa. *Basilodon woodwardi* can be distinguished from other dicynodontoids by the combination of (2) triangular depressions on the dorsal surface of the portion of the postorbital contributing to the postorbital bar (only part of this depression is observed in this specimen, but it is in the same location as in better-preserved specimens of this species, e.g., RC 39 and TM 267), (3) elongate premaxillary portion of the palate with a distinctly squared-off tip, and a (4) distinct break in slope in the snout profile between the nasals and premaxilla, above the external nares. Scale bar equals 5 cm.

considered tentative because they did not include all (valid) species of *Dicynodon* or a large sample of Triassic taxa.

To investigate the phylogenetic relationships of the valid species of *Dicynodon* recognized herein, and to answer the two questions above, we undertook a new phylogenetic analysis that samples known anomodont diversity as comprehensively as possible. Our data set includes a total of 87 operational taxonomic units (OTUs). The majority of OTUs are genera, but we used individual species in cases where genera include distinctive, well-characterized species (e.g., species of *Lystrosaurus*), as well as when a genus included problematic species (e.g., we coded *Oudenodon bainii* specifically because of the problematic status of *O. grandis*; see Botha and Angielczyk [2007] and this study). Most of the genera included in this analysis are monotypic. A polytypic genus was treated as a single OTU only when its component species had identical codings in our data matrix (e.g., *Emydops*, *Dicynodontoides*, *Kombuisia*). We included the 15 valid species of *Dicynodon* sensu lato that we recognize as distinct OTUs to test the monophyly of the genus. One OTU (TSK 2) is an individual specimen that likely represents a new dicynodont species from Zambia (see Angielczyk et al., in press) Of the 87 OTUs, 10 are non-dicynodontian anomodonts, 49 are Permian dicynodonts, and 27 are Triassic dicynodonts. *Lystrosaurus curvatus* is the only OTU that is currently known from both the Permian and Triassic (Botha and Smith, 2007).

FIGURE 152. BP/1/2880, a specimen of *Dicynodon lacerticeps*, illustrating the semi-landmark positions used in the morphometric analysis. Ten semi-landmarks were distributed evenly over each of the resampled curves being compared among specimens. The semi-landmarks in the posterior portion of the skull represent the shape of the dorsal margin of squamosal, from the dorsal edge of the squamosal-postorbital contact to the posterior contact between the squamosal-quadratojugal-quadrate. The semi-landmarks on the snout represent the snout profile, from a vertical plane running through the anterior margin of the orbits to the anteriormost tip of the premaxilla.

The character set used in the phylogenetic analysis is new to this study. Our first step was to compile a list of characters from all previous cladistic analyses of anomodont therapsids. We then removed duplicate characters and modified others to better represent our perception of variation among OTUs and/or to accommodate morphologies present in taxa that were not included in the original analyses. We also discarded several characters that we were unable to code consistently for the full range of OTUs. The complete list of characters and information on their sources can be found in Appendix 2.

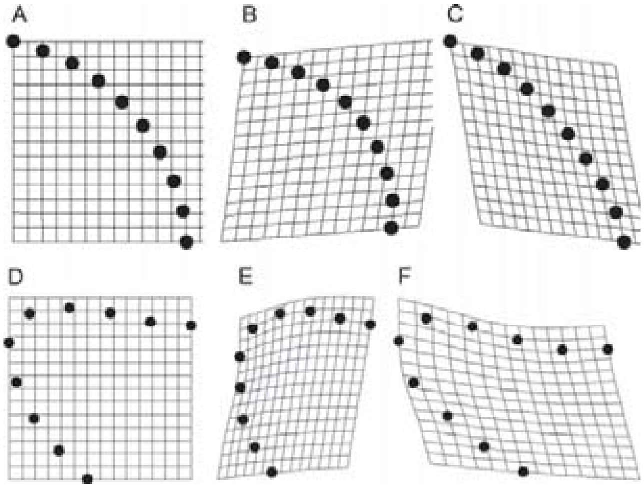

FIGURE 153. Deformation grids showing the maximal differences in shape along the primary axis of variation for specimens of *Dicynodon lacerticeps* and *D. leoniceps*. The top row illustrates differences in snout profile from the mean configuration (**A**) to a highly positive value for PC1 (**B**, the bulging, steeply sloping snout characteristic of *D. leoniceps*) and a highly negative value for PC1 (**C**, the flattened, weakly sloping snout characteristic of *D. lacerticeps*). The bottom row illustrates differences in shape of the dorsal margin of the squamosal from the mean configuration (**D**) to a highly negative value for PC1 (**E**, the broadly rounded shape characteristic of *D. leoniceps*) and a highly positive value for PC1 (**F**, in which the posterodorsal tip of the squamosal curves upwards and the two squamosal rami form an acute angle).

Our final data set includes 163 characters. One hundred forty-three of these characters are discrete binary or multistate characters, and we treated these characters as unordered and of equal weight. The remaining 20 characters are continuous. The use of continuous characters in cladistic analysis has been much discussed (e.g., Crisp and Weston, 1987; Pimentel and Riggins, 1987; Cranston and Humphries, 1988; Felsenstein, 1988, 2002, 2004; Farris, 1990; Stevens, 1991; Crowe, 1994; Disotell, 1994; Poe and Wiens, 2000; Goloboff et al., 2006; Hendrixson and Bond, 2009), and a number of methods for analyzing continuous characters have been proposed (e.g., Mickevich and Johnson, 1976; Colless, 1980; Almeida and Bisby, 1984; Thorpe, 1984; Archie, 1985; Baum, 1988; Felsenstein, 1988, 2002; Goldman, 1988; Chappill, 1989; Thiele, 1993; Miller and Coyle, 1996; Straight et al., 1996; Sosa and De Luna, 1998; Swiderski et al., 1998; Wiens, 2001; Guerrero et al., 2003; Garcia-Cruz and Sosa, 2006; Goloboff et al., 2006). Continuous characters have not played a major role in phylogenetic studies of anomodonts, although Angielczyk (2007) and Angielczyk and Rubidge (2010, in press) used continuous data that had been converted into discrete characters with Thiele's (1993) method in their analyses, and Cox and Li (1983) used measurement data as an important part of their classification of Triassic dicynodonts. However, many characters that have been discussed in the literature and/or used in phylogenetic analyses as discrete state characters are best described using measurements (e.g., relative length of the preorbital region, relative length of the temporal fenestra, relative length of the secondary palate), and our hope is that the inclusion of these characters in a continuous format will make them more informative. To code the continuous characters, we took measurements from photographs of specimens, and our final database includes 5357 individual measurements from over 960 specimens. Details of our measurement procedures and data processing for individual characters can be found in Appendix 2, and raw data can be found in the online supplementary material. We treated continuous characters as additive using the method of Goloboff et al. (2006), and used mean values (median) as the codings for the OTUs except where only a single measurement was available for an OTU. We coded unknown and inapplicable discrete state and continuous characters as '?' (Strong and Lipscomb, 2000).

We analyzed the data set using TNT v1.1 (October 2010 version) (Goloboff et al., 2008) and employed two search strategies. For the first search, we used the new technology methods, with default settings for sectorial searching, tree drifting, and parsimony ratchet, and a driven search with 5000 replicates in which the search level was checked every three hits (additional experiments in which we manually varied the search level produced identical results). In the second analysis, we used the traditional search method of TBR branch swapping with 5000 replicates, with 10 trees held per replicate. We used *Biseridens*, the most basal known anomodont (Liu et al., 2010; Cisneros et al., 2011), to root the most parsimonious cladograms from both analyses. To measure support for the most parsimonious cladograms, we utilized symmetric resampling (Goloboff et al., 2003) and decay analysis (Bremer, 1988, 1994). Our symmetric resampling results are based on 10,000 replicates, with 10 replicates of TBR branch swapping with two trees held per replicate for each resampling replicate. The decay analysis results are based on a sample of 95,000 suboptimal cladograms with lengths up to 12 steps longer than the most parsimonious cladograms. Following the recommendations of Goloboff et al. (2008), we generated them through a series of traditional searches in which we incrementally increased the length of suboptimal cladograms retained as well as the number of suboptimal cladograms.

Because the use of continuous characters is somewhat controversial (see above), and there is no guarantee that continuous characters will retain a phylogenetic signal comparable to other types of characters (Hendrixson and Bond, 2009), we conducted three additional manipulations of our data set to investigate the influence of these characters on our results. The first two manipulations consisted of the simple exclusion of characters: we excluded the 20 continuous characters in the first manipulation and we excluded the 143 discrete state characters in the second. For both of these manipulations, we conducted new technology searches using settings identical to those of our primary phylogenetic analysis. We also excluded three taxa (*Anomocephalus*, *Interpresosaurus*, *Moghreberia*) from the analysis based only on continuous characters because we were unable to code them for any of these characters. In the third manipulation, we examined the effects of transforming the continuous state characters into discrete state characters comparable to those used by Angielczyk (2007) and Angielczyk and Rubidge (2010, in press). We used Thiele's (1993) method with 31 possible states, as implemented for TNT by the script presented in Goloboff et al. (2006), to transform the characters. We then conducted a new technology search with settings identical to those of the primary phylogenetic analysis except that the metric characters were run as ordered with a weight of one and the discrete state characters were run as unordered with a weight of 31.

Finally, to gain insight into how the results of our primary phylogenetic analysis compared with the hypothesis of a monophyletic *Dicynodon*, we performed an analysis in which the search settings were the same as in our primary analysis but the 15 *Dicynodon* sensu lato OTUs were constrained to form a monophylum.

Results

Both the new technology search and the traditional search in the primary phylogenetic analysis resulted in the same two most parsimonious cladograms (885.399 steps, CI = 0.255, RI = 0.678), and the topological results are summarized in Figure 156. The

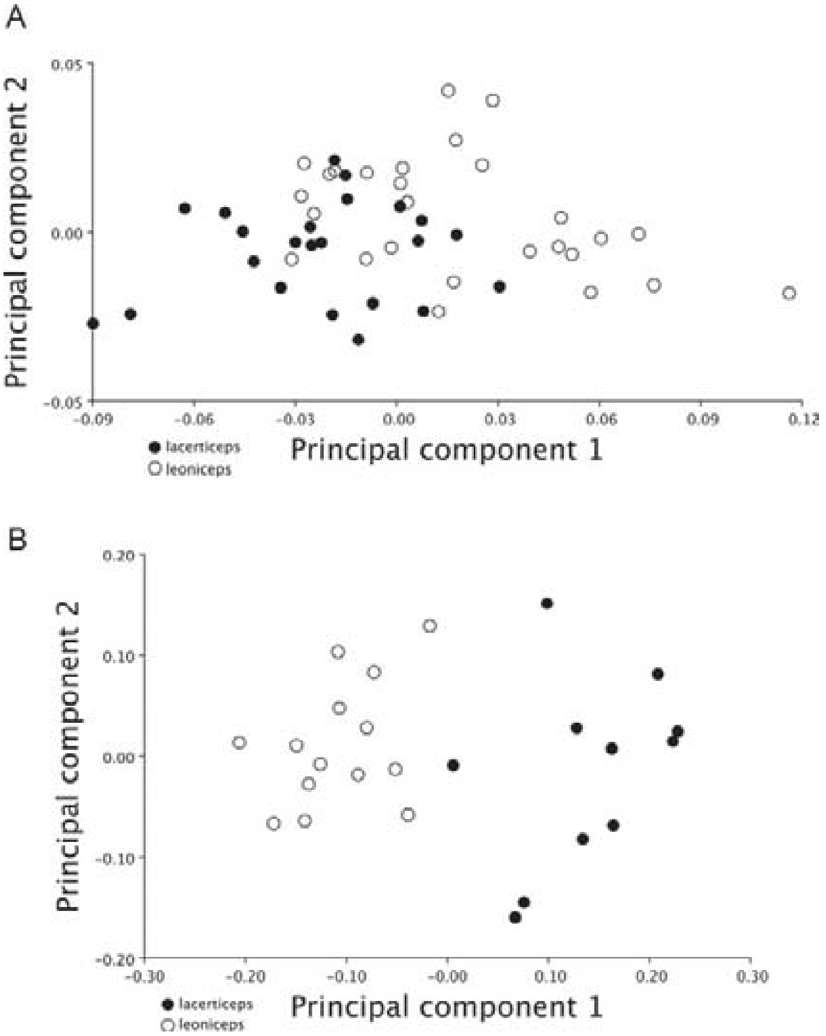

FIGURE 154. Morphospace plots showing results of morphometric analysis of snout profile (**A**) and squamosal shape (**B**).

cladograms show a mixture of similarities and differences to previous phylogenetic analyses of anomodonts. Of particular importance in the current context is the fact that the majority of the *Dicynodon* sensu lato OTUs form a paraphyletic assemblage at the base of the Triassic dicynodontoid radiation, with additional OTUs falling within Cryptodontia, Lystrosauridae, and at the base of Kannemeyeriiformes; not a single *Dicynodon* OTU is reconstructed as falling within a kannemeyeriiform subclade. However, decay analysis and symmetrical resampling show that the most parsimonious cladograms are not well supported. Many nodes decay in one step or less, and only eight nodes have resampling percentages higher than 50%.

Exclusion of the continuous characters results in 18 most parsimonious cladograms (702 steps, CI = 0.283, RI = 0.718) (Fig. 157). In general, the topology of the basal portions of these trees shows a high degree of similarity to the most parsimonious cladograms of the primary analysis. However, the poor resolution among the basal dicynodontoids and the lystrosaurids in these trees relative to those of the primary analysis stems from variation in the placement of *Delectosaurus*, "*Dicynodon*" (*Syops*) *vanhoepeni*, and *Kwazulusaurus*. There are also noteworthy differences between the kannemeyeriiform topologies present in the two sets of trees. We recovered a single most parsimonious cladogram (116.385 steps, CI = 0.228, RI = 0.660) when we excluded the discrete-state characters. The topology of this tree diverges strongly from any anomodont phylogeny that has been presented in the literature (Fig. 158), and the odd groupings of taxa on the tree (e.g., *Endothiodon* and *Prosictodon* closely related to Triassic taxa such as *Shansiodon* and *Stahleckeria*) make it unlikely to be accurate. The data set in which we transformed the continuous characters into discrete-state characters using Thiele's method produced two most parsimonious cladograms (25653.784 steps, CI = 0.264, RI = 0.690), and their topologies are summarized in Figure 159. As was the case when the continuous characters were excluded, the basal parts of these trees show a close correspondence to those from the primary analysis, but differ in their topologies for the basal dicynodontoids, lystrosaurids, and kannemeyeriiforms. Among basal dicynodontoids, TSK 2, "*Dicynodon*" (*Basilodon*) *woodwardi* and "*Dicynodon*" (*Sintocephalus*) *alticeps* have a more basal position than in the trees from the primary analysis, whereas "*Dicynodon*" (*Vivaxosaurus*) *trautscholdi* is more deeply nested. Similarly, *Kwazulusaurus* has a more basal position among lystrosaurids in the trees from the modified data set, and the relationships among *Lystrosaurus* species show a closer correspondence to their first appearances in the stratigraphic record. Differences are also apparent in the kannemeyeriiform topologies. Taken together, two important points emerge from the manipulated data sets. First, although the

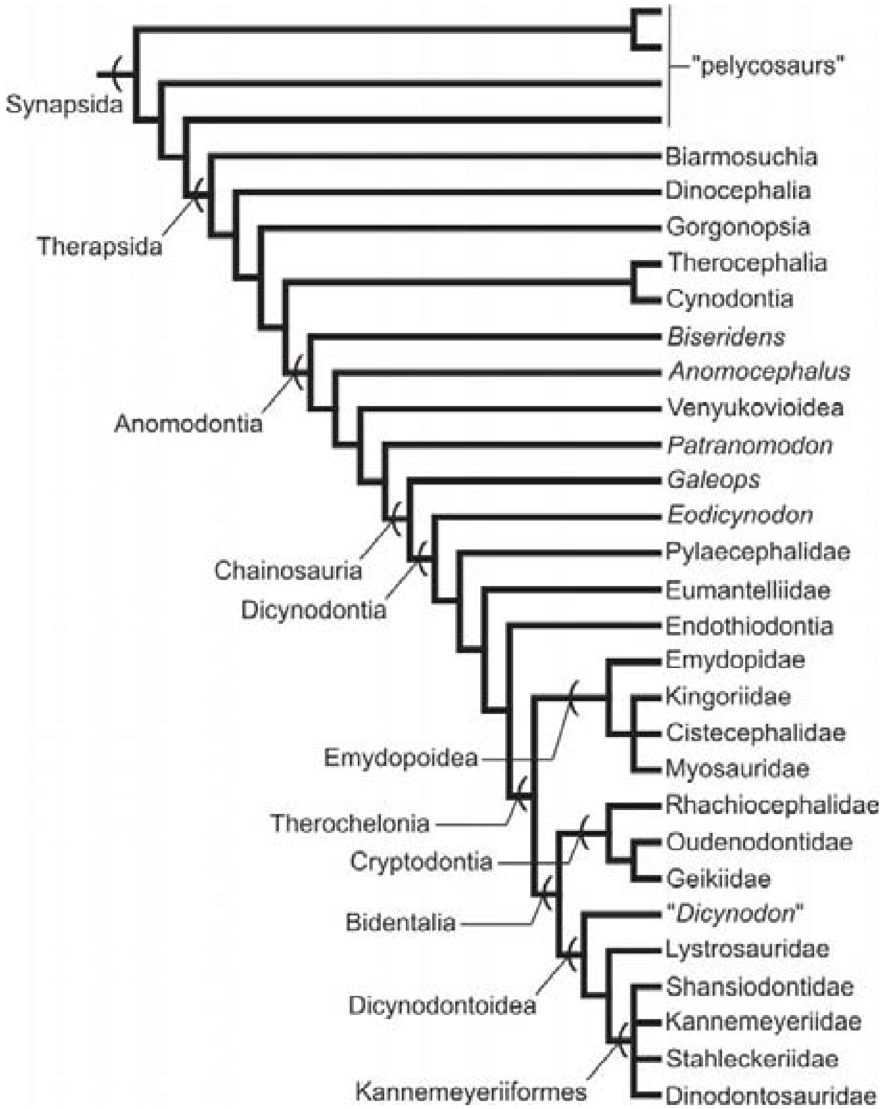

FIGURE 155. Summary of previous phylogenetic analyses of Anomodontia.

continuous characters do not appear to preserve enough information to provide an accurate picture of dicynodont phylogeny on their own, they do play an important role in resolving relationships among dicynodontoids when combined with other, discrete-state characters. Second, none of the manipulated data sets returned a monophyletic *Dicynodon* sensu lato, nor did they provide strong evidence for any *Dicynodon* species being a basal member of a kannemeyeriiform subclade, providing some corroboration of the results of the primary phylogenetic analysis.

Our constrained analysis produced two most parsimonious cladograms (897.925 steps, CI = 0.251, RI = 0.671) (Fig. 160). Adding this constraint caused relatively few changes to the topology for non-dicynodontoid anomodonts and within Lystrosauridae. The most notable changes in topology were within Kannemeyeriiformes, particularly Shansiodontidae becoming paraphyletic.

Discussion

The primary goal of the phylogenetic analysis was to provide insight on the relationships of the 15 species of *Dicynodon* sensu lato that we recognize as valid. However, because the phylogenetic positions of these species must be considered in the context of other anomodonts, and because our most parsimonious cladograms show a mixture of similarities to and differences from those of previous phylogenetic analyses, several aspects of our results require discussion. We generated the lists of synapomorphies described below using TNT v1.1 (October 2010 version) (Goloboff et al., 2008).

Basic Topology—Over the past decade a general consensus on the basic structure of anomodont phylogeny has emerged from a series of analyses (Modesto et al., 1999; Modesto and Rybczynski, 2000; Rybczynski, 2000; Angielczyk, 2001, 2002a, 2004, 2007; Angielczyk and Kurkin, 2003a; Maisch and Gebauer, 2005; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Angielczyk and Rubidge, 2010, in press; Liu et al., 2010, Cisneros et al., 2011; although see Surkov and Benton, 2004, 2008; Surkov et al., 2005; and Damiani et al., 2007, for divergent topologies). Kammerer and Angielczyk (2009) produced a higher-level taxonomy based on this consensus (Fig. 155) and our most parsimonious cladograms (Fig. 156) show considerable similarity to this topology. Both trees include a paraphyletic assemblage of

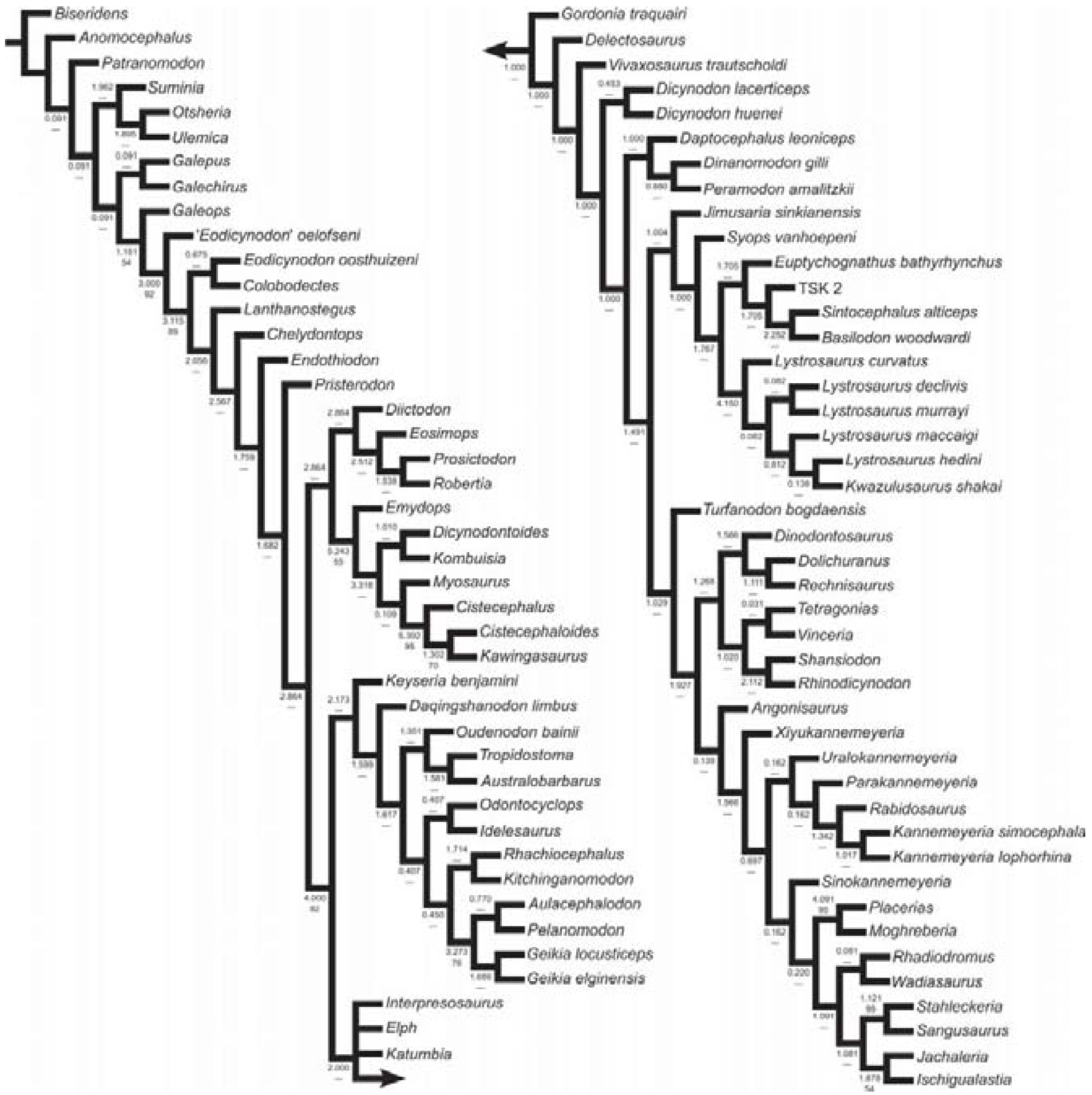

FIGURE 156. Consensus of the two most parsimonious cladograms (885.399 steps, CI = 0.255, RI = 0.678) derived from the phylogenetic analysis. Numbers at nodes represent decay indices (top) and symmetric resampling support (bottom).

non-dicynodontian anomodonts at the base of the tree as well as many shared major clades (e.g., Venyukovioidea, Dicynodontia, Emydopoidea, Bidentalia, Cryptodontia, Dicynodontoidea). One of the most noteworthy differences between our cladograms and the previous consensus is the placement of Pylaecephalidae as the sister taxon of Emydopoidea within Therochelonia, although a sister-group relationship between these clades was posited by Cluver and King (1983) and King (1988, 1990). Our topologies within Cryptodontia and Lystrosauridae also differ somewhat from previous analyses (e.g., Liu et al., 2002; Angielczyk, 2007; Angielczyk and Rubidge, 2010), and our topology within Kannemeyeriiformes diverges strongly from that of Maisch (2001), rendering his Kannemeyeriidae, Stahleckeriidae, and Dinodontosauridae polyphyletic.

Non-Dicynodontian Anomodonts—Several analyses have either focused on non-dicynodontian anomodont relationships (e.g., Rubidge and Hopson, 1990; Modesto et al., 1999; Modesto and Rubidge, 2000; Modesto and Rybczynski, 2000; Rybczynski, 2000; Angielczyk, 2004; Liu et al., 2010; Cisneros et al., 2011) or included a diverse sample of non-dicynodontian anomodonts in the context of dicynodont phylogeny (Modesto et al., 2003; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Fröbisch

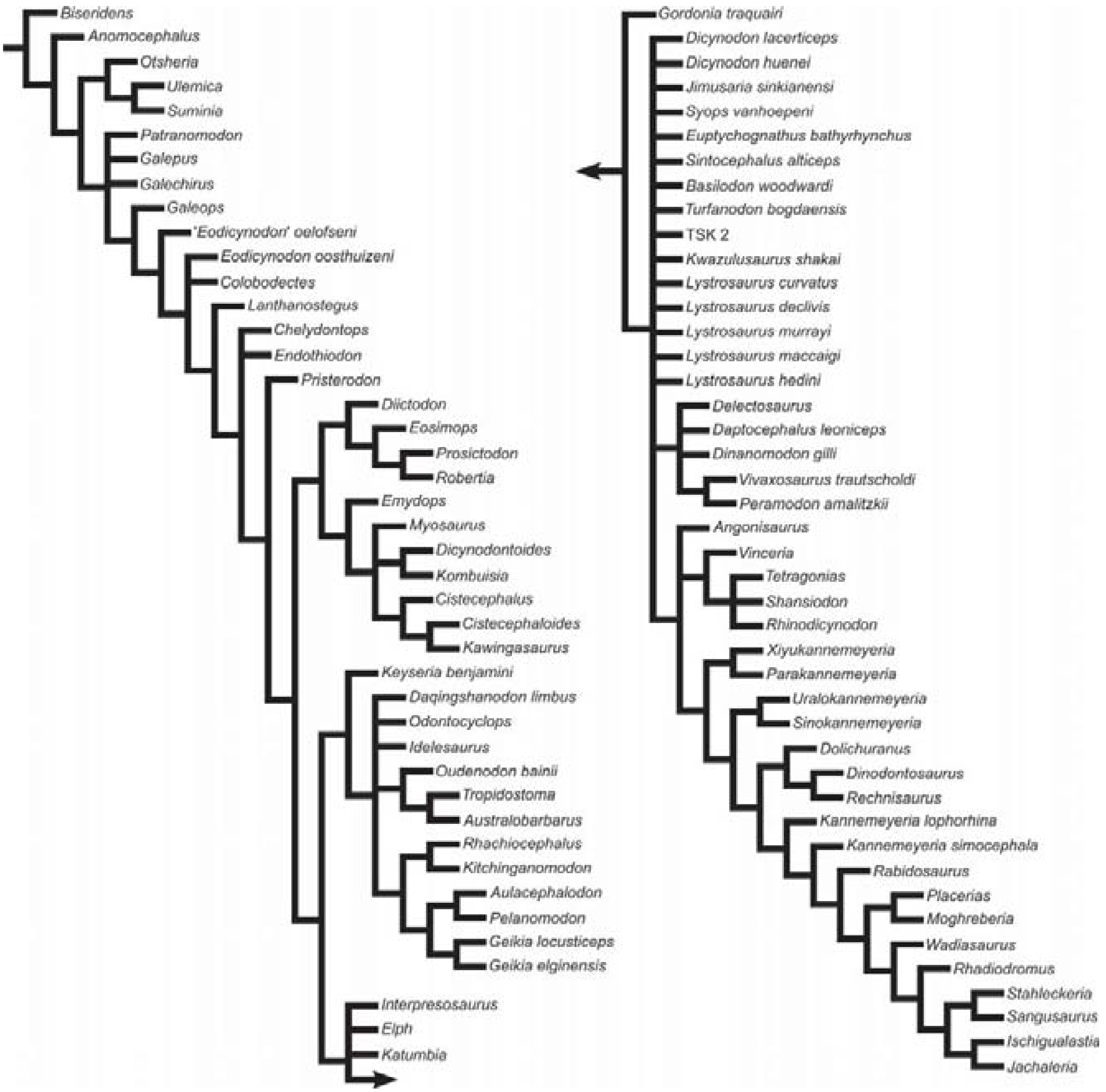

FIGURE 157. Consensus of the 18 most parsimonious cladograms (702 steps, CI = 0.283, RI = 0.718) derived from the phylogenetic analysis in which continuous characters were excluded.

et al., 2010). Our reconstruction of *Anomocephalus* near the base of Anomodontia, one node above *Biseridens*, is consistent with all analyses that have included this taxon, but the relatively basal placement of *Patranomodon* (outside the venyukovioid-chainosaur split) in our most parsimonious trees differs from some recent analyses (Liu et al., 2010; Cisneros et al., 2011; Fröbisch and Reisz, 2011). This result is based on five synapomorphies absent in *Biseridens*, *Anomocephalus*, and *Patranomodon* but present in more derived anomodonts (proportions of mandibular fenestra, squamosal with lateral fossa for the origin of the lateral slip of the M. adductor mandibulae externus, squamosal contacts supraoccipital, palatal surface of palatine with evidence of a keratinized covering, lateral dentary shelf present). However, symmetric resampling and decay support in this portion of the tree are low, and exclusion of the continuous characters or transforming the continuous characters using Thiele's method moves *Patranomodon* closer to Dicynodontia than Venyukovioidea, the same position found by Liu et al. (2010), Cisneros et al. (2011), and Fröbisch and Reisz (2011).

All previous cladistic analyses that included the venyukovioids *Otsheria*, *Ulemica*, and *Suminia* recovered the topology (*Otsheria* (*Ulemica* + *Suminia*)), an arrangement that also is logical from a functional standpoint (Angielczyk, 2004). The topology resulting from our primary phylogenetic analysis differs from

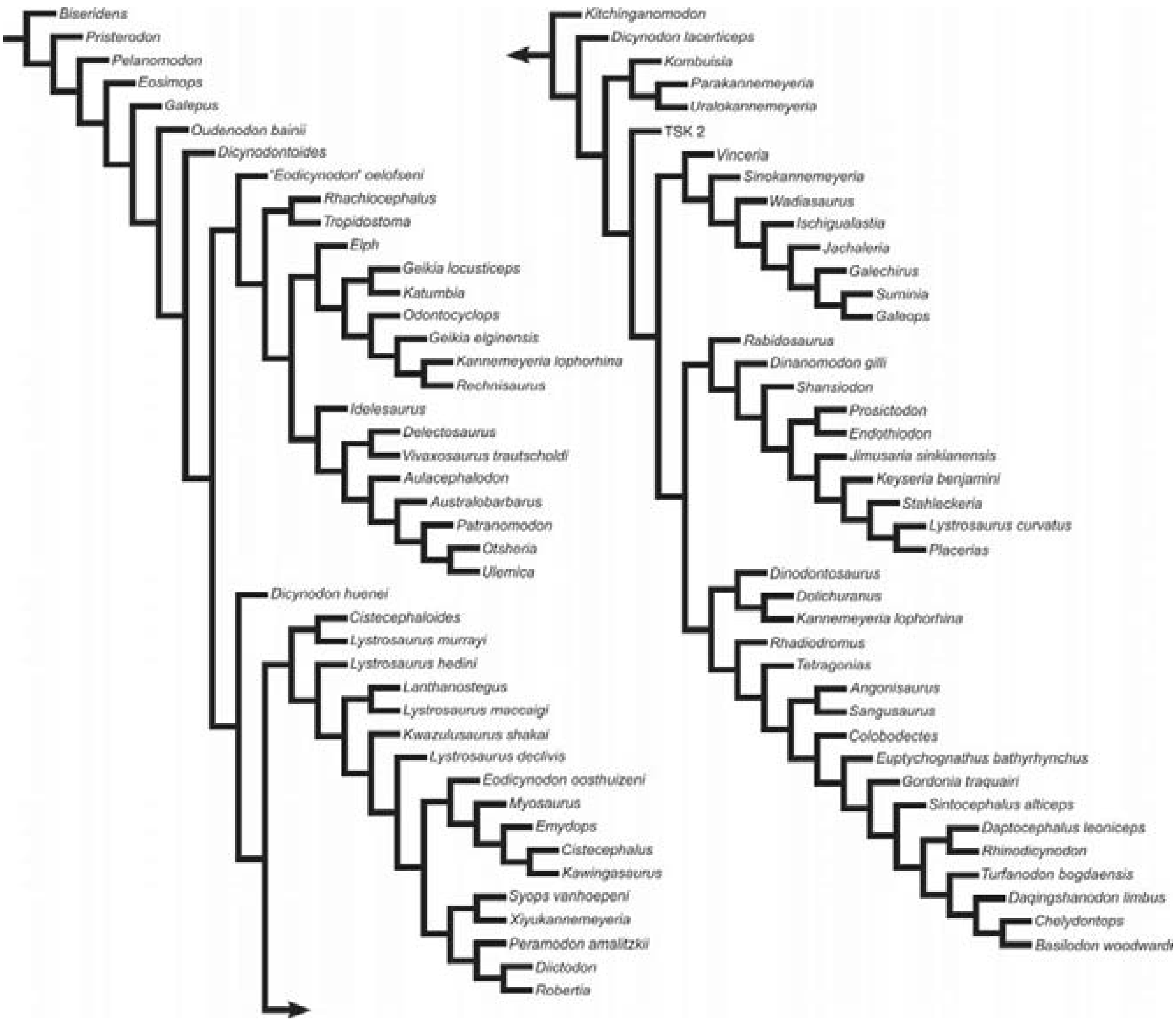

FIGURE 158. Most parsimonious cladogram (116.385 steps, CI = 0.228, RI = 0.660) derived from the phylogenetic analysis in which discrete-state characters were excluded.

this in reconstructing *Otsheria* and *Ulemica* as more closely related to each other than either is to *Suminia*. Five synapomorphies support the pairing of *Otsheria* and *Ulemica* in our most parsimonious cladograms (relative length of the preorbital region, relative length of the temporal fenestra, relative area of the internal nares, angle between the ascending and zygomatic processes of the squamosal, converging ventral keels on posterior portion of anterior pterygoid rami absent), and Bremer support within Venyukovioidea is slightly higher than average for branches among non-dicynodontian anomodonts. However, the more typical topology with *Otsheria* basal to *Ulemica* + *Suminia* is present in results from both the analysis based on only discrete-state characters and the analysis in which the continuous characters were recoded using Thiele's method. Because of this fact, and the ubiquity of this topology in previous analyses, we consider the alternate topology in the most parsimonious cladograms from our primary analysis and in the constrained analysis to be a tentative hypothesis at best.

Galeops has been included in most analyses that focus on non-dicynodont anomodonts, but *Galepus*, *Galechirus*, and "*Eodicynodon*" *oelofseni* have been included in many fewer studies (Modesto et al., 2003; Cisneros et al., 2011; Fröbisch and Reisz, 2011) and their relationships are consequently poorly known. The most parsimonious cladograms from our primary analysis corroborate the hypothesis that *Galeops* is more closely related to dicynodonts than to venyukovioids (i.e., Chainosauria of Kammerer and Angielczyk, 2009), and that "*Eodicynodon*" *oelofseni* is the sister taxon of Dicynodontia as suggested by Modesto et al. (2003). These branches receive relatively strong symmetric resampling and decay support, and are stable in the analyses excluding continuous characters and in which they are treated as discrete-state characters. Cisneros et al. (2011) reconstructed a relatively basal position for *Galechirus* (they did not include *Galepus*), but Fröbisch and Reisz (2011) placed them in a polytomy with *Patranomodon* at the base of Chainosauria. Our most parsimonious cladograms are more similar to the

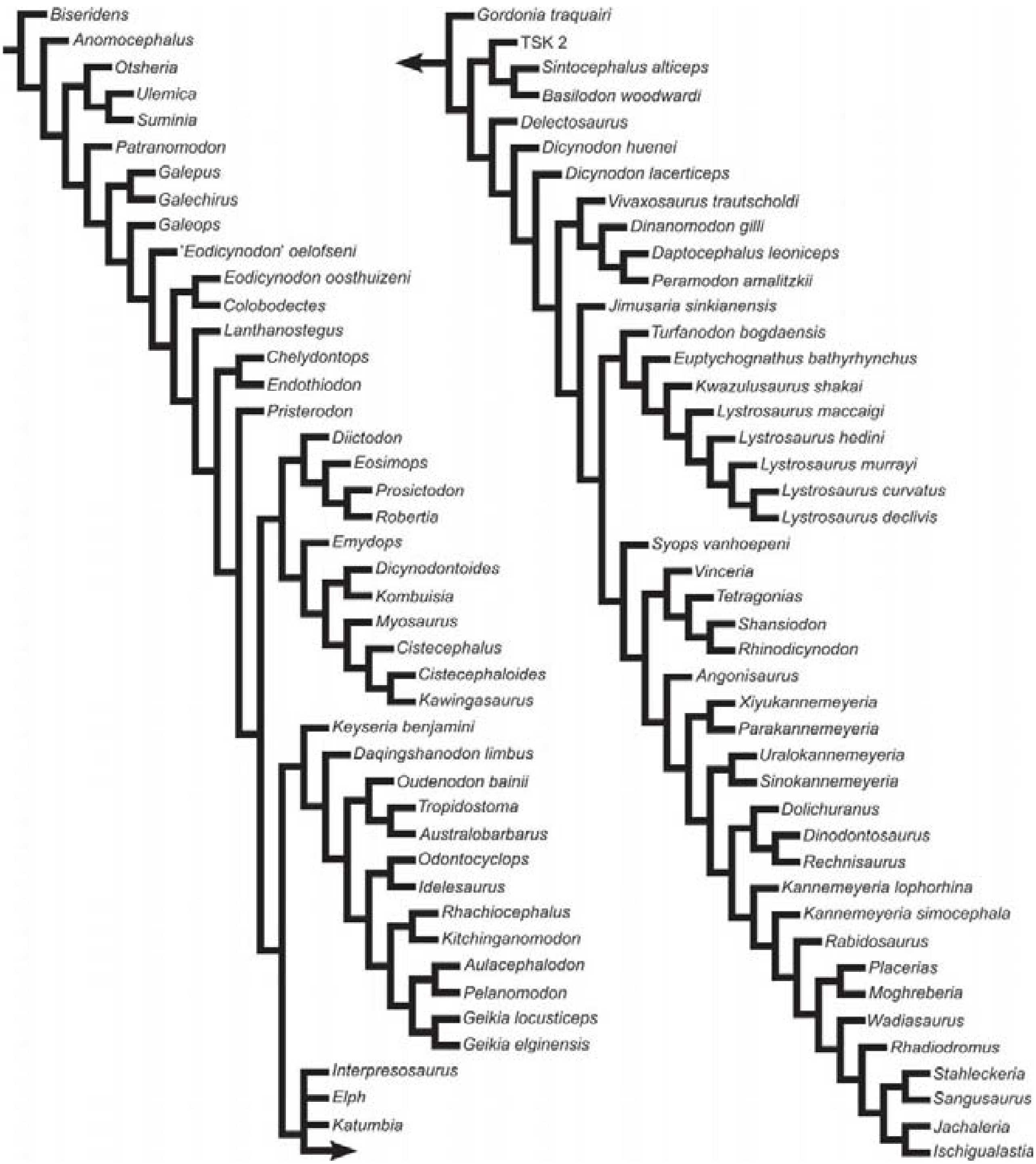

FIGURE 159. Consensus of the two most parsimonious cladograms (25653.784 steps, CI = 0.264, RI = 0.690) derived from the phylogenetic analysis in which continuous characters were transformed into discrete-state characters using Thiele's (1993) method.

hypothesis of Fröbisch and Reisz (2011), although we found *Galepus* and *Galechirus* to be sister taxa. Two characters (height of postdentary bones relative to height of dentary, nasal boss present as a single median swelling with a continuous posterior margin) support the position of *Galechirus* + *Galepus* as closer to Dicynodontia than Venyukovioidea, and one character supports *Galechirus* and *Galepus* as sister taxa (anterior and distal edges of deltopectoral crest very obtuse). Branch support in this region of the most parsimonious cladograms is low, but *Galechirus* and *Galepus* are consistently reconstructed closer to

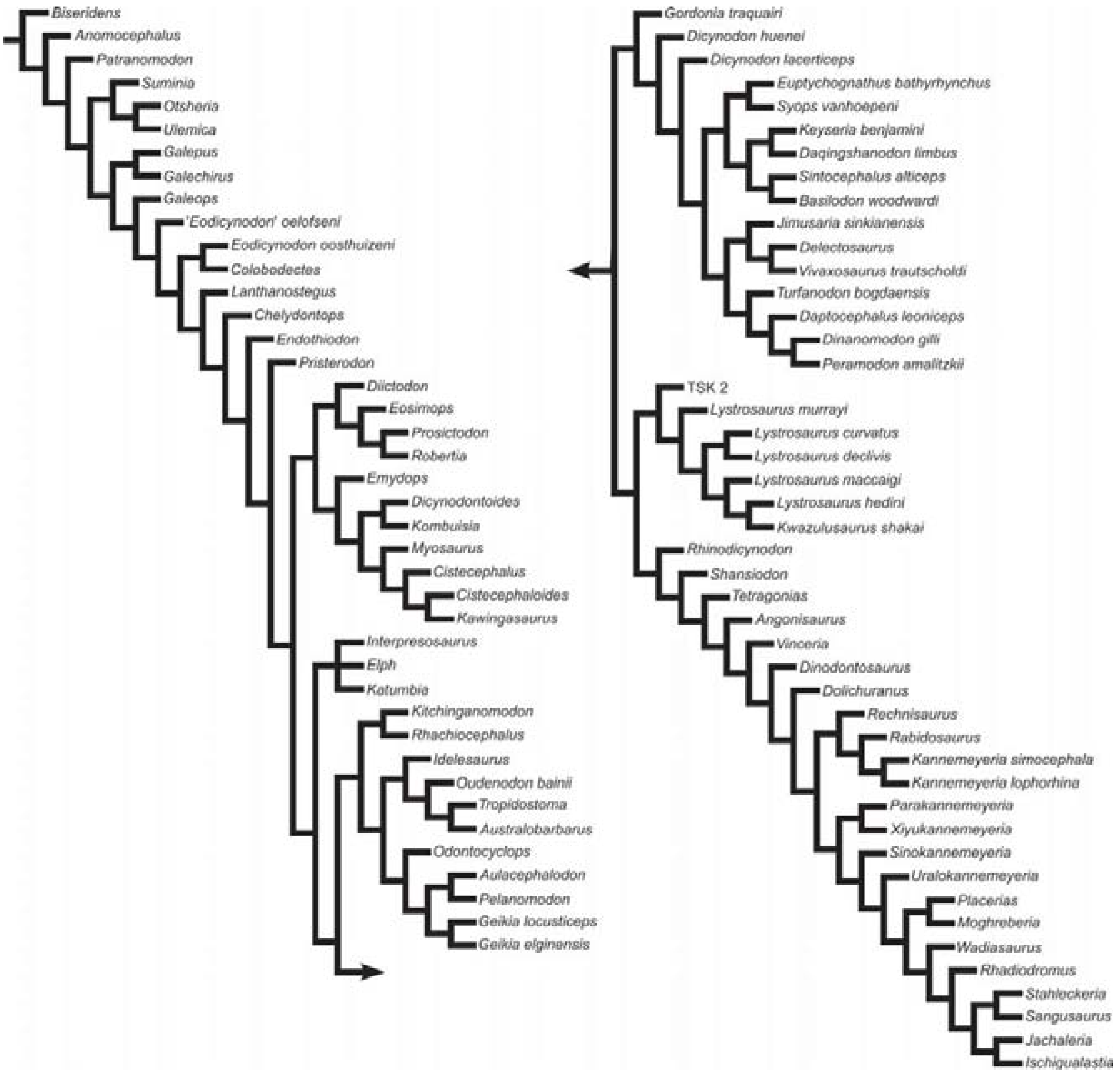

FIGURE 160. Consensus of the two most parsimonious cladograms (897.925 steps, CI = 0.251, RI = 0.671) in which *Dicynodon* sensu lato was constrained to be monophyletic.

Dicynodontia than Venyukovioidea in the analyses in which the continuous characters are excluded and treated as discrete-state characters, and when *Dicynodon* sensu lato is constrained to be monophyletic.

Pylaecephalidae, Eumantelliidae, Endothiodontia—Most recent analyses have reconstructed Pylaecephalidae as a relatively basal dicynodont clade, with Eumantelliidae (currently including only *Pristerodon mackayi*; Kammerer and Angielczyk, 2009) and Endothiodontia (variously consisting of *Endothiodon*, *Chelydontops*, and *Lanthanostegus*) in positions closer to Therochelonia (Angielczyk, 2001, 2002a, 2004, 2007; Angielczyk and Kurkin, 2003a; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Angielczyk and Rubidge, 2010, in press; Fröbisch et al., 2010). The cladograms resulting from our primary phylogenetic analysis, however, reconstruct *Lanthanostegus*, *Chelydontops*, *Endothiodon*, and *Pristerodon* as a paraphyletic assemblage of basal dicynodonts, and Pylaecephalidae as the sister taxon of Emydopoidea within Therochelonia, a topology somewhat similar to that of Cluver and King (1983) and King (1988, 1990). Surkov and Benton (2008) also favored a more basal position for *Endothiodon*, and Angielczyk (2002b) recovered it as the most basal dicynodont in some data set permutations he examined. On our most parsimonious trees, seven synapomorphies support Therochelonia (including Pylaecephalidae) to the exclusion of *Lanthanostegus*, *Chelydontops*, *Endothiodon*, and *Pristerodon* (relative length of the anterior iliac process, relative length of the posterior iliac process, absence of maxillary non-caniniform teeth, caniniform process at the same level as the anterior orbital margin, mid-ventral vomerine plate without an expanded area posterior to the junction with the premaxilla, blade-like mid-ventral vomerine plate, absence of a trough on the mid-ventral vomerine plate), and most of these branches receive moderate decay support. The sister-group relationship of Pylaecephalidae and Emydopoidea receives comparable decay support, and is based on four synapomorphies (relative length of the posterior iliac process, presence of lateral anterior palatal ridges, procoracoid foramen formed by contributions of the scapula and procoracoid in lateral view, ectepicondylar foramen present). These relationships also are stable when the continuous characters are excluded or run as discrete-state characters, and when *Dicynodon* sensu lato is constrained to be monophyletic. However, this topology is not without conflict. Several therochelonian synapomorphies are present only in *Diictodon*, whereas more basal states are found in *Eosimops*, *Prosictodon*, and *Robertia*. These basal states are reconstructed as reversals in our most parsimonious cladograms, but can also provide support for a basal position of Pylaecephalidae, as they have in many previous analyses. At the same time, pylaecephalids and emydopoids share certain characters, such as the presence of an ectepicondylar foramen, which are otherwise very rare among dicynodonts. Further evaluation of these alternative hypotheses will likely benefit from restudy of the poorly known species *Brachyprosopus broomi* and *Compsodon helmoedi*, both of which seem very likely to fall in this area of the tree (Angielczyk and Rubidge, in press; Angielczyk et al., in press), as well as new material of *Endothiodon* from Tanzania that is currently under study by C. B. Cox (also see Sidor et al., 2010). If future analyses continue to support a sister-group relationship between Pylaecephalidae and Emydopoidea, the taxon name Diictodontia Cluver and King, 1983, is available for this clade (technically, with this topology Pylaecephalidae would fall within Emydopoidea under the definitions of Kammerer and Angielczyk [2009], but in such a case we would recommend adding *Diictodon feliceps* to the external specifiers of Emydopoidea to maintain traditional usage.)

Cryptodontia—The position of Cryptodontia on our most parsimonious cladograms, and the topology within the clade, are quite similar to the results of most previous analyses (Angielczyk, 2001, 2002a, 2004, 2007; Angielczyk and Kurkin, 2003a; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Angielczyk and Rubidge, 2010, in press; Fröbisch et al., 2010; although see Maisch, 2002a; Surkov and Benton, 2004, 2008; Surkov et al., 2005), but two important differences are apparent. First, "*Dicynodon*" (*Keyseria*) *benjamini* and *Daqingshanodon limbus* are reconstructed as the most basal members of Cryptodontia. Five synapomorphies support their inclusion within Cryptodontia (angle formed by the posterior pterygoid rami, relative length of the interpterygoid vacuity, presence of a postcaniniform crest, presence of paired nasal bosses, raised circumorbital rim absent), and this hypothesis receives moderate decay support. The topology also is stable when the continuous characters are excluded or run as discrete-state characters. As noted above, "*D*." *benjamini* received little attention in the literature following its initial description by Broom (1948), and our identification of CGP S125b represents the first time a specimen other than the holotype has been referred to this species. Characters such as the relatively broad exposure of the parietals on the skull roof, moderate size, and the presence of tusks give "*D*." *benjamini* a very generalized appearance, and this fact, along with its possession of cryptodontian synapomorphies such as a postcaniniform crest and paired nasal bosses, make it an attractive model for the most basal members of the clade. *Daqingshanodon limbus* also has received little attention since Zhu's (1989) description, and he was the first to suggest that it was closely related to *Dicynodon* (also see Lucas 1998a, 2001, 2002; 2005a, 2005b, 2006, 2009; Li et al., 2000). However, the presence of cryptodontian synapomorphies such as paired nasal bosses and a postcaniniform crest, as well as characters such as the absence of a postfrontal, exposure of the parietals on the skull roof between the postorbitals, and a relatively long interpterygoid vacuity, belies its superficial resemblance to basal dicynodontoids. If our hypothesis that *Daqingshanodon* is a cryptodont is correct, the species is significant because it is the first member of this clade to have been found in China. Likewise, if the holotype of *Daqingshanodon limbus* is an adult, which seems likely given the strong development of the nasal bosses (see, e.g., Tollman et al., 1980), then it is the smallest known member of Cryptodontia.

Second, *Rhachiocephalus* + *Kitchinganomodon* (i.e., Rhachiocephalidae) is reconstructed as the sister taxon of Geikiidae instead of in the more basal position typical of past works. This topology is supported by only three synapomorphies (relative width of interorbital skull roof, maxillary canine absent, postorbital bar with thickenings and rugosities), and receives low symmetrical resampling and decay support, but it remains stable when the continuous characters are removed or run as discrete-state characters. This topology seems to be primarily driven by a reorganization of reconstructed character evolution within Cryptodontia by the inclusion of *Daqingshanodon* and "*Dicynodon*" (*Keyseria*) *benjamini* as basal members of the clade: when these taxa are constrained to be part of a monophyletic *Dicynodon*, Rhachiocephalidae falls at the base of Cryptodontia. Likewise, the three characters supporting the exclusion of Rhachiocephalidae from Oudenodontidae + Geikiidae on the constrained cladograms (relative width of dorsal end of scapula, relative width of the temporal bar, extent of overlap of the parietals by the postorbitals) have character-state changes on several branches within Cryptodontia on the cladograms from the primary phylogenetic analysis.

Basal Dicynodontoidea—Kammerer and Angielczyk (2009) defined Dicynodontoidea as all taxa more closely related to *Dicynodon lacerticeps* than to *Oudenodon bainii* or *Emydops arctatus*. When this definition is applied to the results of our primary phylogenetic analysis, basal dicynodontoids include *Elph*, *Interpresosaurus*, *Katumbia*, and the paraphyletic assemblage of former *Dicynodon* species leading up to the divergence of Lystrosauridae and Kannemeyeriiformes.

The hypothesized relationships of *Elph*, *Interpresosaurus*, and *Katumbia* have been somewhat variable in previous analyses. *Elph* and *Interpresosaurus* frequently have been reconstructed as sister taxa forming the clade Elphinae of Kurkin (2010), which in turn has been placed at the base of Dicynodontoidea (Angielczyk and Kurkin, 2003a; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011). The addition of *Katumbia* typically causes Elphinae to collapse into a polytomy with Cryptodontia and Dicynodontoidea or for one or more of the three taxa to be more closely related to Cryptodontia or Dicynodontoidea, whereas the others remain in a basal polytomy (Angielczyk, 2007; Angielczyk and Rubidge, 2010, in press). In the strict consensus of the two cladograms from our primary analysis, *Elph*, *Interpresosaurus*, and *Katumbia* are reconstructed in a polytomy at the base of Dicynodontoidea with five synapomorphies supporting their placement in the clade (relative width of the intertemporal bar, angle between ascending and zygomatic portions of the squamosal, angulation of the occiput, postorbitals overlap parietals extensively, anterior process of splenial absent). In one of the individual most parsimonious cladograms, the three taxa form a paraphyletic assemblage at the base on Dicynodontoidea (topology is (*Elph* (*Katumbia* (*Interpresosaurus* + remaining Dicynodontoidea)))), whereas in the other *Interpresosaurus* and *Elph* form a monophyletic Elphinae sensu Kurkin (2010) that is the sister taxon of *Katumbia* + the remaining dicynodontoids. The exact relationships of *Elph*, *Interpresosaurus*, and *Katumbia* also are not consistently resolved in the most parsimonious cladograms from the analyses in which the continuous characters were excluded or treated as discrete-state characters, or in the analysis in which *Dicynodon* sensu lato was constrained to be monophyletic, but in all cases they are placed as the most basal members of Dicynodontoidea.

The remaining basal dicynodontoids consist of the majority of the valid species that have been assigned to *Dicynodon* sensu lato in the past. Branch support for this area of the cladogram is weak and the detailed pattern of relationships differs among the various permutations of our data set that we examined, so we will not discuss all of the potential implications of the primary analysis topology in detail. However, two broader points deserve consideration. First, none of our unconstrained phylogenetic analyses returned a monophyletic *Dicynodon* sensu lato, and constraining *Dicynodon* to be monophyletic requires a minimum of 12.526 additional steps under the settings used in our primary phylogenetic analysis. Moreover, our unconstrained analyses show that it is not possible to redefine *Dicynodon* such that it consists of the type species *Dicynodon lacerticeps* and some or all of the remaining species in a monophylum to the exclusion of all other dicynodonts. Only *Dicynodon huenei* meets this criterion in the results of our primary phylogenetic analysis, and attempting such a redefinition with the results from the analyses in which the continuous characters were excluded or treated as discrete-state characters essentially requires synonymizing *Dicynodon* with Dicynodontoidea. Instead of a clade, available evidence suggests that *Dicynodon* sensu lato primarily consists of a paraphyletic assemblage of basal dicynodontoids as well as probable members of Cryptodontia (see above) and Lystrosauridae (see below), and at least one potential stem kannemeyeriiform (see below). When combined with the results of most other recent phylogenetic analyses (Angielczyk and Kurkin, 2003a; Surkov et al., 2005; Angielczyk, 2007; Fröbisch, 2007; Surkov and Benton, 2008; Fröbisch and Reisz, 2008, 2011; Angielczyk and Rubidge, 2010, in press; Fröbisch et al., 2010), it is clear that the null hypothesis of a monophyletic *Dicynodon* should be rejected, and below we propose a taxonomic framework that better accommodates our current understanding of dicynodont relationships.

The second important result from our phylogenetic analyses is that there does not appear to be a strong geographic signal present among the species of *Dicynodon* sensu lato (i.e., species from specific geographic areas do not consistently group together). For example, in the results of our primary analysis Laurasian and Gondwanan species cluster together (e.g., Laurasian "*Dicynodon*" *amalitzkii* forms a clade with Gondwanan *Dinanomodon gilli* and *Daptocephalus leoniceps*), and rerunning the analysis with *Dicynodon* species from southern Africa, western Laurasia (Scotland and Russia), and China constrained to form monophyletic clades results in most parsimonious trees that are 24.339 steps longer. Likewise, there is a mixture of geographically widespread and restricted subclades when *Dicynodon* is constrained to be monophyletic as opposed to only endemic clades. These data suggest that although Permian dicynodont faunas show some provinciality (Fröbisch, 2009), dispersal was possible for basal dicynodontoids.

Lystrosauridae—Traditionally, species of the morphologically distinctive genus *Lystrosaurus* have been considered to form a monophyletic group within Dicynodontoidea, but the exact placement of *Lystrosaurus* relative to *Dicynodon* sensu lato and Kannemeyeriiformes has been uncertain (e.g., compare the results of Angielczyk, 2001, 2002a, 2007; Maisch, 2002a; Surkov et al., 2005; Fröbisch, 2007; Fröbisch and Reisz, 2008; and Surkov and Benton, 2008). The number of valid *Lystrosaurus* species and their relationships to one another also have been subjects of debate (e.g., Cluver, 1971; Colbert, 1974, 1982; Cosgriff et al., 1982; Li, 1988; Lucas, 2001; Liu et al., 2002; Ray, 2005; Surkov et al., 2005; Grine et al., 2006; Botha and Smith, 2007; Camp, 2010), and Maisch (2002a) hypothesized that *Kwazulusaurus shakai* represented a basal lystrosaurid, perhaps shedding light on the evolution of the clade's unusual anatomy. We included the 'core' South African *Lystrosaurus* species (*L. curvatus*, *L. declivis*, *L. maccaigi*, *L. murrayi*) in our analysis as well as a single OTU (*Lystrosaurus hedini*) to which we assigned most known Chinese specimens (based on Camp, 2010, and our personal observations). We also included *K. shakai*, but excluded the Russian *Lystrosaurus georgi* because it can be coded for very few cranial and mandibular characters.

In the results of our primary phylogenetic analysis, the five *Lystrosaurus* species and *Kwazulusaurus* form a monophyletic group that receives relatively strong decay support and is based on 13 synapomorphies (relative length of the preorbital region, relative width of the interorbital skull roof, relative width of the intertemporal bar, relative length of the temporal fenestra, relative width of the median pterygoid plate, relative area of the internal nares, marked expansion of preorbital region present, postorbital bar with thickenings and rugosities, parietals widely exposed on skull roof, interparietal does not contribute to skull roof, sutural contact of premaxilla and palatine absent, ectopterygoid absent, nasofrontal suture with a distinct anterior process). The topology within this clade shows a mixture of similarities and differences to previous hypotheses of *Lystrosaurus* relationships. For example, *Lystrosaurus curvatus* is recovered as the most basal species, and *Lystrosaurus declivis* and *Lystrosaurus murrayi* are closely related (similar to the hypotheses of Cluver, 1971, and Liu et al., 2002; also see Camp, 2010). The grouping of *Lystrosaurus maccaigi*, *Lystrosaurus hedini*, and *Kwazulusaurus shakai* is novel to our analysis, and is surprising given that *K. shakai* has previously been thought to be a basal lystrosaurid (Maisch, 2002a) and *L. maccaigi* and *L. hedini* (as defined here) are two of the earliest-appearing *Lystrosaurus* species (e.g., Cheng and Lucas, 1993; Lucas, 1996, 2001; Botha and Smith, 2007). However, we are reluctant to assign a great deal of weight to the topology within *Lystrosaurus* because decay support is very low within the genus, and this portion of the tree is unstable in the analyses in which the continuous characters are excluded or treated as discrete-state characters, and when *Dicynodon* sensu lato is constrained to be monophyletic.

Perhaps more interesting than the topology within the genus *Lystrosaurus* is the fact that the 'core lystrosaurids' (i.e., *Lystrosaurus* and *Kwazulusaurus*) are nested within a larger clade that includes several former *Dicynodon* species in the most parsimonious cladograms from our primary analysis. This clade is supported by only two synapomorphies (ratio of length to height of the mandibular fenestra in lateral view, nasofrontal suture relatively straight, interdigitated or gently bowed), but it is noteworthy that most of the included taxa are characterized by features reminiscent of *Lystrosaurus* (e.g., a deepened snout and/or downturned snout, exposure of the parietals on the intertemporal skull roof) and that the specimen TSK 2 was previously identified as *Lystrosaurus* (King and Jenkins, 1997; see Angielczyk et al., in press, for details on why the specimen is unlikely to be *Lystrosaurus*). Decay support for this 'expanded' Lystrosauridae is relatively weak, and it is not consistently resolved when the continuous characters are excluded or run as discrete-state characters (this grouping is precluded when *Dicynodon* sensu lato is constrained to be monophyletic, although TSK 2 still groups with *Lystrosaurus* and *Kwazulusaurus* in that analysis).

Further testing of this hypothesis in future phylogenetic analyses is clearly necessary, particularly to answer the question of whether characters such as the deepened snout of "*Dicynodon*" (*Euptychognathus*) *bathyrhynchus* or the broadly exposed parietals of "*Dicynodon*" (*Basilodon*) *woodwardi* represent true synapomorphies shared with *Lystrosaurus* or if they are the result of convergent evolution. If additional support for an expanded Lystrosauridae is found, this hypothesis would have important implications for studies of the causes of the end-Permian extinction. Specifically, it would imply that evolution of many of the distinctive features found in *Lystrosaurus* began well before the end-Permian extinction, in *Cistecephalus* Assemblage Zone times (likely upper Wuchiapingian; Rubidge, 2005) and were likely independent of associated biotic and environmental changes. Functional studies of the additional lystrosaurid taxa also could be used to test the scenarios that have been proposed for the evolution of *Lystrosaurus* (e.g., Cluver, 1971), and to understand the emergence of some of the distinctive stress-relieving features of its skull (Jasinoski et al., 2009, 2010a, 2010b).

Although it has been recognized for some time that *Lystrosaurus* (and by extension Lystrosauridae) falls within Dicynodontoidea, its exact phylogenetic placement has been variable in recent phylogenetic hypotheses. Some authors have recovered it as the sister taxon of Kannemeyeriiformes (e.g., Angielczyk, 2001, 2002a; Surkov et al., 2005; Fröbisch, 2007; Fröbisch and Reisz, 2008; Fröbisch et al., 2010), whereas others have placed it outside of a clade including *Vivaxosaurus* + Kannemeyeriiformes (e.g., Angielczyk and Kurkin, 2003a; Angielczyk, 2007) or even basal to *Dicynodon* sensu lato (Maisch, 2002a). The results of our phylogenetic analysis do not provide a complete resolution to this problem. In the most parsimonious cladograms from our primary phylogenetic analysis, Lystrosauridae is reconstructed as the sister taxon of a clade including *Turfanodon* + Kannemeyeriiformes, but only two synapomorphies support this grouping to the exclusion of Lystrosauridae (raised, rugose circumorbital rim absent, ectopterygoid absent) and decay support for the branch is relatively weak. This topology also is not stable in the various permutations of the data set we investigated: Lystrosauridae is completely unresolved and its constituent species are part of a large polytomy at the base of Dicynodontoidea when the continuous characters are excluded, *Turfanodon* is reconstructed as a basal lystrosaurid and Lystrosauridae is the sister taxon of a clade containing "*Dicynodon*" (*Syops*) *vanhoepeni* + Kannemeyeriiformes when the continuous characters are run as discrete-state characters, and Lystrosauridae is the sister taxon of Kannemeyeriiformes when *Dicynodon* sensu lato is constrained to be monophyletic. We suspect that this instability may stem in part from missing data in some of the critical taxa in question. For example, *Turfanodon bogdaensis* and "*Dicynodon*" (*Syops*) *vanhoepeni* have among the highest proportions of missing data in our matrix (53.7% and 74.1%, respectively). If these taxa are excluded from the analysis, Lystrosauridae is consistently reconstructed as the sister taxon of Kannemeyeriiformes, regardless of how the continuous characters are treated, although this change also consistently moves the remaining 'non-core lystrosaurids' to a more basal position within Dicynodontoidea. Therefore, resolution of the exact position of Lystrosauridae within Dicynodontoidea (and its taxonomic composition) may not be possible until additional information is available on *T. bogdaensis* and "*D*." *vanhoepeni*.

Kannemeyeriiformes—The origin of Kannmeyeriiformes, or how kannemeyeriiforms are related to Permian dicynodonts, has long been a subject of speculation and debate. For much of the 20th century, it was recognized that kannemeyeriiforms were most likely related to the Upper Permian dicynodonts now classified within Dicynodontoidea, with *Dicynodon* or *Daptocephalus* usually being identified as the Permian ancestor of the group (e.g., Pearson, 1924; Toerien, 1953; Ewer, 1961; Keyser, 1974). However, other taxa occasionally received attention in this context, including Broom's (1932) inclusion of *Kannemeyeria* in his chapter of anomodonts sharing affinities with *Aulacephalodon*, Camp's (1956) suggestion that the ancestor of Triassic dicynodonts was a Russian Permian species similar to "*Gordonia*," Sun's (1963) conclusion that *Jimusaria sinkianensis* was a link between Permian and Triassic dicynodontoids, and Cox's (1965) speculation that kannemeyeriiforms were likely derived from *Dicynodon* or *Aulacephalodon*. Cruickshank (1964, 1967) invoked a *Daptocephalus*-like ancestor of Triassic dicynodontoids and suggested that *Lystrosaurus* and *Tetragonias* were intermediates between that Permian ancestor and taxa such as *Kannemeyeria*. Keyser (1979), Keyser and Cruickshank (1979), and Cruickshank (1986) differed from most previous authors in proposing a polyphyletic origin of Kannemeyeriiformes. They hypothesized that taxa such as *Kannemeyeria* were descended from *Dinanomodon*, whereas taxa such as *Tetragonias* and *Dinodontosaurus* were descendants of *Daptocephalus*. Moreover, given our current understanding of Permian dicynodont phylogeny, their suggestion that *Daptocephalus* itself was a descendent of *Odontocyclops* would imply that at least some Triassic dicynodonts were cryptodonts.

The application of cladistic analysis to studies of dicynodont phylogeny altered the discussion of the origin of Triassic dicynodontoids inasmuch as the search for Permian ancestors became the search for Permian sister taxa. However, because most phylogenetic analyses focused strongly on either Permian or Triassic taxa, it remained difficult to fully explore the relationships between kannemeyeriiforms and Permian dicynodontoids. Many analyses (e.g., Cluver and King, 1983; King, 1988; Angielczyk, 2001, 2002a; Surkov et al., 2005; Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Surkov and Benton, 2008; Fröbisch et al., 2010) suggested that *Dicynodon lacerticeps* was the sister taxon of a Lystrosauridae + Kannemeyeriiformes clade. However, other hypotheses have also been proposed. For example, Maisch (2002a) and Damiani et al. (2007) posited that *Dinanomodon* was the sister taxon of Kannemeyeriiformes (interestingly, the latter paper also found some support for Keyser and Cruickshank's hypothesis that *Daptocephalus* was a cryptodont). Angielczyk and Kurkin (2003a; also see Kalandadze and Kurkin, 2000; Angielczyk, 2007; Govender and Yates, 2009; Angielczyk and Rubidge, 2010, in press) reconstructed *Vivaxosaurus* as the sister group of *Kannemeyeria* (and by extension Kannemeyeriiformes), resurrecting Camp's (1956) hypothesized origin for the clade in the Permian of Russia. However, not all analyses that included *Vivaxosaurus* recovered a similar topology (Fröbisch, 2007; Fröbisch and Reisz, 2008, 2011; Fröbisch et al., 2010). No cladistic analysis has provided evidence suggesting that one or more species of *Dicynodon* sensu lato are Permian members of kannemeyeriiform subclades, although most have not had sufficiently detailed taxon sampling to fully address this issue. The closest any work has come to such a result is the placement of *Vivaxosaurus* within Kannemeyeriiformes as the sister taxon of a kannemeyeriid + sinokannemeyeriid + stahleckeriid clade in Govender and Yates' (2009) analysis when they excluded postcranial data for *Dolichuranus*.

Because our data set is the first to include a large sample of Permian and Triassic dicynodonts, it can provide new insight into historical hypotheses of kannemeyeriiform relationships, as well as the question of whether any species of *Dicynodon* sensu lato represent Permian members of kannemeyeriiform subclades. Our primary phylogenetic analysis, as well as the analyses excluding continuous characters, running the continuous characters as discrete-state characters, and constraining *Dicynodon* to be monophyletic, recovered a monophyletic Kannemeyeriiformes that is nested within Dicynodontoidea. Five synapomorphies support this clade in our primary phylogenetic analysis (nasal bosses present as paired swellings that meet in the midline to form a swollen anterodorsal surface on the snout, postfrontal absent, dorsolateral notch in squamosal below zygomatic arch absent, intertuberal ridge absent, converging ventral keels on posterior portion of anterior pterygoid rami absent), but it does not receive strong decay support. No Permian dicynodont is reconstructed as a member of a kannemeyeriiform subclade in these analyses, but *Turfanodon bogdaensis* is reconstructed as the sister taxon of Kannemeyeriiformes in our primary phylogenetic analysis and "*Dicynodon*" (*Syops*) *vanhoepeni* occupies a similar position when the continuous characters are transformed using Thiele's (1993) method. Although these results are tantalizing because they suggest that some members of *Dicynodon* sensu lato represent stem kannemeyeriiforms, we are hesitant to ascribe too much significance to them. Our codings for *Turfanodon* and "*D*." *vanhoepeni* both include a large amount of missing data, and few synapomorphies support their potential relationships with Kannemeyeriiformes (two for *Turfanodon*: raised, rugose circumorbital rim present, ectopterygoid absent; one for "*D*." *vanhoepeni* in the alternate analysis: nasal bosses present as paired swellings that meet in the midline to form a swollen anterodorsal surface on the snout). Regardless of whether "*D*." *vanhoepeni*, *Turfanodon*, Lystrosauridae, or another taxon is the sister taxon of Kannemeyeriiformes, the fact that no Permian taxa are members of kannemeyeriiform subclades and that kannemeyeriiforms do not appear in the fossil record until the Olenekian and Anisian (e.g., Lucas, 2010) implies a ghost lineage for the clade that spans at least part of the Late Permian and the lower part of the Early Triassic. Similarly, the near simultaneous appearance of several kannemeyeriiforms in the late Early Triassic and early Middle Triassic implies either a rapid radiation of the clade or a considerable amount of missing history for it in the Induan.

Relationships within Kannemeyeriiformes also have been the subject of considerable debate. Older classifications (e.g., von Huene, 1948; Camp, 1956) tended to lump the few known Triassic dicynodonts into a single group (Kannemeyeriidae), although Romer (1956) is noteworthy for placing the Triassic taxa within his Dicynodontidae and not distinguishing them as a separate subgroup. Although at first glance this would appear to to be similar to classifying the main Triassic taxa only as members of Dicynodontoidea in the framework of Kammerer and Angielczyk (2009), the diversity of taxa that Romer (1956) included within Dicynodontidae would make it equivalent to Therochelonia or Dicynodontia (depending on whether pylaecephalids are the sister taxon of emydopoids or occupy a more basal position on the phylogeny). Beginning in the 1960s, as more Triassic taxa were described, more finely subdivided classifications were proposed. For example, Lehman (1961) divided Kannemeyeriidae into Kannemeyeroinae and Stahleckeroinae, whereas Cox (1965) favored a threefold subdivision into Kannemeyeriidae, Shansiodontidae, and Stahleckeriidae. Sun (1963) and Cruickshank (1964, 1967, 1970) did not propose explicit classifications, but did discuss evolutionary scenarios that had phylogenetic implications. For example, Sun (1963) suggested that the Chinese Triassic taxa she considered (*Parakannemeyeria*, *Shansiodon*, and *Sinokannemeyeria*), *Stahleckeria*, and *Dinodontosaurus* were most closely related to *Kannemeyeria* (although she noted that *Shansiodon* retained some seemingly primitive characters), and *Placerias* represented a separate lineage. Cruickshank (1964, 1967) hypothesized that Triassic taxa such as *Kannemeyeria* were descended from an evolutionary sequence including *Lystrosaurus* and *Tetragonias*, whereas in 1970 he divided the Triassic dicynodontoids into three main groups (one including *Stahleckeria*, one including the shansiodontids and *Kannemeyeria*, and one including *Placerias*, *Ischigualastia*, and similar taxa), with *Sinokannemeyeria* as a potential ancestral stock. Keyser and Cruickshank (1979) proposed four main Triassic taxa (Kannemeyeriinae, Dinodontosaurinae, Stahleckeriinae, and Jachaleriinae), but in his comment on this paper, Cooper (1980) proposed only two taxa distinguished primarily on the presence or absence of tusks. Cox and Li (1983) also extensively discussed Keyser and Cruickshank's classification and presented new evidence in support of Cox's (1965) classification.

The application of cladistic analysis to the problem of kannemeyeriiform phylogeny has produced a range of results. Cluver and King (1983) did not consider the relationships of Triassic taxa in detail, but King (1988) divided them into five clades, Shansiodontini, Kannemeyeriini, Sinokannemeyeriini, Stahleckeriini, and Placeriini. She did not evaluate relationships within these clades in detail, but her groupings of taxa shows somewhat more similarity to Cox and Li's (1983) classification than to Keyser and Cruickshank's (1979) classification. Maisch (2001) performed the first computerized phylogenetic analysis of kannemeyeriiforms and obtained results very similar to King's (1988) non-computerized analysis. He found shansiodontids to occupy a basal position on the phylogeny, followed by kannemeyeriids and stahleckeriids, the latter of which he subdivided into four subclades. Subsequent analyses also have recovered a shansiodontid clade at the base of Kannemeyeriiformes in at least some of their results (Surkov and Benton, 2004, 2008; Vega-Dias et al., 2004; Surkov et al., 2005; Damiani et al., 2008; Govender and Yates 2009), although membership in this clade has varied, particularly in terms of whether *Angonisaurus* is a shansiodontid. Most of these studies also recovered a clade (Stahleckeriidae sensu Maisch, 2001) including *Placerias*, *Stahleckeria*, *Ischigualastia*, and *Jachaleria* (when the latter has been included); *Angonisaurus* also often occurs in this clade (Vega-Dias et al., 2004; Surkov et al., 2005; Damiani et al., 2007; Surkov and Benton, 2008; Govender and Yates, 2009). The relationships of the remaining kannemeyeriiforms have been somewhat more difficult to resolve. Some analyses recovered a clade including *Parakannemeyeria* and *Sinokannemeyeria* (Sinokannemeyeriinae sensu Maisch, 2001; *Dinodontosaurus* often is associated with this clade, but Maisch [2001] classified it in its own family, Dinodontosauridae) and *Kannemeyeria* as successive outgroups to the stahleckeriids (Maisch, 2001; Govender and Yates, 2009), although other works suggested a more pectinate arrangement of taxa (Surkov and Benton, 2008) or had difficulty resolving this portion of the cladogram (Vega-Dias et al., 2004). Surkov and Benton (2004) proposed a derived position for *Kannemeyeria* with taxa such as *Placerias* and *Stahleckeria* as outgroups.

We recovered a monophyletic 'core Shansiodontidae' consisting of *Vinceria*, *Tetragonias*, *Shansiodon*, and *Rhinodicynodon* in our primary phylogenetic analysis, as well as when we excluded the continuous characters or treated them as discrete-state characters. This clade is supported by six synapomorphies in our primary analysis (ratio of height of postdentary bones to dentary ramus, relative length of the deltopectoral crest, relative width of the distal end of the radius, nasal bosses present as paired swellings near the dorsal or posterodorsal margin of external nares, five sacral vertebrae, femoral head offset dorsally from dorsal margin of femur). Interestingly, our primary analysis reconstructs a clade including *Dinodontosaurus*, *Rechnisaurus*, and *Dolichuranus* as the sister taxon of the 'core shansiodontids' within an expanded Shansiodontidae. However, this grouping is supported by only four characters (relative width of the temporal bar, preparietal present with dorsal surface relatively flat and flush with the skull roof, fossa on ventral surface of intertemporal bar absent, insertion of M. iliofemoralis into a lateral crest that is split into a distinct first trochanter and third trochanter), receives poor decay support, and is not stable when the continuous characters are excluded or treated as discrete-state characters. Therefore, we regard it as a tentative hypothesis at best. Regardless of this detail, the shansiodontids are consistently recovered as the most basal kannemeyeriiform subclade (or a paraphyletic assemblage at the base of Kannemeyeriiformes when *Dicynodon* is constrained to be monophyletic), corroborating the basal placement of this clade in most previous cladistic analyses.

Moving up the most parsimonious cladograms from our primary analysis, we next encounter *Angonisaurus* and *Xiyukannemeyeria*, and then a clade consisting of several taxa that have been variously included in Kannemeyeriidae and Sinokannemeyeriidae in previous analyses. This 'kannemeyeriid' subclade is supported by only three synapomorphies (relative length of the preobital region, relative width of the median pterygoid plate, angle between the ascending and zygomatic process of the squamosal), and it received very low decay support. Similarly, this clade breaks down into a more pectinate topology when the continuous characters are excluded or treated as discrete-state characters, and *Dinodontosaurus*, *Dolichuranus*, and *Rechnisaurus* frequently nest among this assemblage as well (unsurprising given the very close similarity between *Rechnisaurus* and *Uralokannemeyeria*). Based on these observations and the results of previous analyses, it seems likely that these 'kannemeyeriids' and 'sinokannemeyeriids' (sensu Maisch, 2001) occupy an intermediate position on the phylogeny between the shansiodontids and stahleckeriids, but resolution of the exact membership of these groups and their relationships will require further investigation.

A consistent feature of the most parsimonious cladograms from all of our analyses (except the analysis based on only the continuous characters) is a stahleckeriid clade including *Stahleckeria*, *Sangusaurus*, *Ischigualastia*, *Jachaleria*, *Placerias*, *Moghreberia*, *Rhadiodromus*, and *Wadiasaurus*. Most of these taxa have been reconstructed in a monophyletic group in recent phylogenetic analyses (e.g., King, 1988; Maisch, 2001; Vega-Dias et al., 2004; Damiani et al., 2007; Surkov and Benton, 2008; Govender and Yates, 2009), although the composition of the group differs slightly from some traditional concepts of Stahleckeriidae (e.g., Cox, 1965; Cox and Li, 1983; although see Keyser and Cruickshank, 1979). This clade is supported by five synapomorphies (preparietal present and its dorsal surface relatively flat and flush with the skull roof, postparietal makes a large contribution to the intertemporal skull roof, anterolateral trough on the angular for the posterior process of the dentary absent, anterior edge of scapula extended laterally to form a strong crest, femoral head offset from the dorsal end of femur), but it receives poor decay support despite its stability in the analyses based on the various permutations of our data set. The inclusion of *Wadiasaurus*, *Sangusaurus*, and *Rhadiodromus* in this clade is somewhat unexpected, given that these taxa frequently have been included among the kannemeyeriids, sinokannemeyeriids, or in an uncertain position (e.g., Cox, 1969; Keyser and Cruickshank, 1979; Cox and Li, 1983; Cruickshank, 1986; Bandyopadhyay, 1988, 1989; King, 1988; Maisch, 2001; Vega-Dias et al., 2004; Surkov and Benton, 2008; Govender and Yates, 2009). However, all three are known from relatively incomplete and/or poorly preserved material and most are coded as '?' for the synapomorphies supporting Stahleckeriidae. Therefore, further investigation will be necessary to test whether these taxa are part of this clade.

Finally, within Stahleckeriidae the clade composed of *Placerias* + *Moghreberia* is noteworthy for receiving some of the highest decay and symmetric resampling support of any clade on the phylogeny. Seven synapomorphies support this grouping (posterior median palatal ridge with flattened expanded anterior area, parietal posterolateral process slender and elongate, parietals well exposed on skull roof and relatively flat, zygomatic portion of squamosal with thin dorsoventral expansion posterior to postorbital bar, contact between periotic and parietal absent, postorbitals do not extend the entire length of intertemporal bar, such that the posterior portion of the bar is formed only by the parietals, circular central depression on the occipital condyle absent). Some authors have suggested that *Placerias* and *Moghreberia* may be synonyms (Cox, 1991; Lucas and Wild, 1995; Lucas, 1998c). Although our topology is consistent with this suggestion, we recommend retaining the North American and North African taxa as separate because these taxa differ in our codings for at least four discrete-state characters in our data set, and possibly more depending on the codings for missing data. Furthermore, we recommend additional testing of this hypothesis because *Moghreberia* has been excluded from all previous computerized cladistic analyses of Triassic dicynodonts.

Taxonomic Revision of *Dicynodon* sensu lato

Although the precise topology of Dicynodontoidea is highly variable in our analyses, the non-monophyly of *Dicynodon* sensu lato relative to the predominantly Triassic clades Lystrosauridae and Kannemeyeriiformes is recovered in all unconstrained analyses. This result necessitates a higher-level taxonomic revision of "*Dicynodon*" species, with several possible approaches. The first approach would be to make *Dicynodon* monophyletic by including all lystrosaurids and kannemeyeriiforms within the genus. Such a reversion to 19th century inclusivity in *Dicynodon* would needlessly complicate and confuse the already tortuous taxonomic histories of the groups in question, and we do not advocate this approach.

Lucas (2005b) advocated a gradistic approach to *Dicynodon* taxonomy, maintaining the traditional composition of the genus by treating it as an explicitly paraphyletic, phenetically determined taxon including all non-lystrosaurid, non-kannemeyeriiform dicynodontoids. Even disregarding philosophical arguments with regards to the recognition of paraphyletic taxa, this proposal is problematic on a practical basis. Some species included within *Dicynodon* by Lucas (2001, 2005a, 2005b) (e.g., *Daqingshanodon limbus*) are, as indicated by our phylogeny, not even dicynodontoids, so retaining them within *Dicynodon* would move this taxon from paraphyly to polyphyly. Furthermore, some of these species blur the phenetic distinction between *Dicynodon* and the Triassic dicynodontoids: "*Dicynodon*" *bathyrhynchus*, which we recover as a basal lystrosaurid, has a *Dicynodon*-like, narrow intertemporal bar with extensive postorbital-parietal overlap, but a *Lystrosaurus*-like, tall, strongly deflected snout. Which of these characters should take precedence in determining generic attribution?

The third, and in our view optimal, approach to the "*Dicynodon*" genus problem is to restrict *Dicynodon* to the smallest monophyletic unit containing the type species *D. lacerticeps* and not Lystrosauridae or Kannemeyeriiformes, and separate out species not falling within that clade as distinct genera. Many of these species were either originally placed in separate genera (e.g., *Daqingshanodon*, *Gordonia*, *Turfanodon*) that were subsequently synonymized with *Dicynodon* on a phenetic basis, or had been separated from *Dicynodon* by previous workers (e.g., *Daptocephalus*, *Jimusaria*, *Sintocephalus*). Here we resurrect several of these available generic names to refer to species that do not fall within *Dicynodon* sensu stricto, but this still leaves five valid "*Dicynodon*" species without a generic name: "*D*." *amalitzkii*, "*D*." *bathyrhynchus*, "*D*." *benjamini*, "*D*." *vanhoepeni*, and "*D*." *woodwardi*. Although the precise position of some of these species ("*D*." *vanhoepeni* especially) on the tree is variable between analyses (see above), in no unconstrained analyses do these species form a clade with *D. lacerticeps* to the exclusion of Triassic dicynodontoids. Indeed, "*D*." *benjamini* is recovered as a cryptodont, and "*D*." *bathyrhynchus* and "*D*." *vanhoepeni* are recovered as basal lystrosaurids ("*D*." *vanhoepeni* is alternatively recovered as a basal kannemeyeriiform in some analyses). Because retaining any of these species in the genus *Dicynodon* would make that taxon an unnatural unit, here we establish new genera for these species.

Lucas (2005b:194) decried such "cladotaxonomic" practice, arguing that "the amount of and significance of variation in the genus has never been fully documented and analyzed," rendering breakup of the genus as proposed by Angielczyk and Kurkin (2003a) untenable. In the present work, we have documented and analyzed inter- and intraspecific variation in "*Dicynodon*" using descriptive, phylogenetic, and morphometric approaches, and although there are many characters that are indeed subject to possible population-level variation (e.g., size of the preparietal, degree of facial rugosity), the general conclusion of Angielczyk and Kurkin (2003a) stands: much of "*Dicynodon*" is only distantly related to the type species, and should not be treated as if it were a coherent unit.

SYSTEMATIC PALEONTOLOGY

SYNAPSIDA Osborn, 1903
THERAPSIDA Broom, 1905a
ANOMODONTIA Owen, 1860a
DICYNODONTIA Owen, 1860a
BIDENTALIA Bain vide Owen, 1876
CRYPTODONTIA Owen, 1860a
DAQINGSHANODON Zhu, 1989

Type Species—*Daqingshanodon limbus* Zhu, 1989.
Diagnosis—As for the type species.

DAQINGSHANODON LIMBUS Zhu, 1989
(Fig. 75)

Daqingshanodon limbus Zhu, 1989:12.
Dicynodon limbus Lucas, 1998b:85.

Holotype—IVPP V7940.
Referred Material—None.
Diagnosis—A small dicynodont characterized by the following autapomorphies: posterolateral edge of quadrate ramus of squamosal curls over itself at midheight, sharp ridge extending from base of zygomatic arch to anterolateral edge of caniniform process. Distinguished from *Keyseria benjamini* by the relatively shorter postorbital bar, narrowing posteriorly (the transverse width of the intertemporal bar expands posteriorly in *Keyseria*), more horizontal orientation of the postorbitals in the intertemporal bar, relatively shorter palatal exposure of the premaxilla, absence of a ridge on the lateral surface of the premaxillary-maxillary suture, well-developed lacrimal process around the lacrimal foramen, and median pterygoid plate located in a more posterior position of the skull.

KEYSERIA, gen. nov.

Types Species—*Dicynodon benjamini* Broom, 1948.
Diagnosis—As for the type species.
Etymology—Named in honor of André W. Keyser for his contributions to dicynodont systematics. In particular, Dr. Keyser undertook the first major revisions of *Dicynodon* sensu Broom, removing many species from the genus and synonymizing them with *Tropidostoma microtrema* and *Oudenodon bainii* (Keyser, 1973, 1975). Feminine.

KEYSERIA BENJAMINI (Broom, 1948), comb. nov.
(Fig. 16)

Dicynodon benjamini Broom, 1948:606.

Holotype—RC 63.
Referred Material—CGP S125b.
Diagnosis—A small- to medium-sized dicynodont characterized by the following unique combination of characters: broad intertemporal bar with wide exposure of parietals, expanding in width posteriorly, large pineal foramen, vertical orientation of the postorbitals in the intertemporal bar, temporal arch with concave lateral edge anteriorly and strongly convex lateral edge posteriorly in dorsal view, with squamosal flaring laterally near the tip, well-developed ridge on lateral premaxillary-maxillary suture, ovoid, paired nasal bosses overhanging the external nares, postcaniniform crest present, elongate premaxillary portion of palate terminating in a triangular tip, and a well-developed embayment anterior to caniniform process.

DICYNODONTOIDEA (Owen, 1860a)

BASILODON, gen. nov.

Type Species—*Dicynodon woodwardi* Broom, 1921.
Diagnosis—As for the type species.
Etymology—'King tooth,' from the ancient Greek *βασιλεύς* (king) and *ὀδούς* (tooth), named in honor of Gillian M. King for her many contributions to dicynodont research, including the first book devoted specifically to this group (The Dicynodonts: A Study in Palaeobiology). Masculine.

BASILODON WOODWARDI (Broom, 1921), comb. nov.
(Figs. 151, 161E, F)

Dicynodon woodwardi Broom, 1921:655.
Dicynodon microdon Broom, 1936:376.
Dicynodon calverleyi Broom, 1940b:179.
Dicynodon weatherbyi Broom, 1941:200.

Holotype—MMK 4166.
Referred Material—BSP 1934 VIII 516, MMK 5264, RC 39, RC 117, SAM-PK-K7841, TM 267, and USNM 24646.
Diagnosis—A medium-sized dicynodontoid characterized by the following autapomorphy: well-developed triangular depressions on the dorsal surface of the postorbital contribution to the postorbital bar. Distinguished from all dicynodontoids other than *Syops vanhoepeni* by a distinctly biplanar snout profile in which the break in slope is between the premaxilla and nasal. Further diagnosed by the following unique combination of characters: short intertemporal bar with parietal exposed throughout but narrowing in exposure posteriorly, horizontal orientation of the postorbitals in the intertemporal bar, anterior rami of pterygoids bowed outwards, palatal rim without distinct embayment anterior to caniniform process, and elongate premaxillary portion of palate terminating in distinctly squared-off tip.

DAPTOCEPHALUS van Hoepen, 1934

Type Species—*Dicynodon leoniceps* Owen, 1876.
Diagnosis—As for the type species.

DAPTOCEPHALUS LEONICEPS (Owen, 1876)
(Figs. 70, 161C, D)

Dicynodon leoniceps Owen, 1876:32.
Dicynodon leontops Broom, 1913c:451.
Dicynodon lissops Broom, 1913c:450.
Dicynodon osborni Broom, 1921:651.
Dicynodon watsoni Broom, 1921:653.
Daptocephalus leoniceps van Hoepen, 1934:88.
Dicynodon leontocephalus Broom, 150:246.
Dicynodon daptocephaloides Toerien, 1955:70.

Holotype—NHMUK 47047.
Referred Material—AMG 4945, AMNH FARB 5508, AMNH FARB 5582, AMNH FARB 5598, BP/1/555, BP/1/769, BP/1/832, BP/1/2188, BP/1/2784, BP/1/3427, BP/1/4233, BSP 1934 VIII 49, CAMZM T773, CGP GHG140, GPIT/RE/7176, NHMUK R3600, NMQR 26, NMQR 75, NMQR 960, NMQR 1400, NMQR 1544, SAM-PK-6044, SAM-PK-K10022, SAM-PK-K10570, TM 1496, UCMP 33431, UMCP 42692, USNM 23337, and USNM 23353.
Diagnosis—A very large Permian dicynodontoid characterized by the following unique combination of characters: a steeply angled, sloping snout, anteroposteriorly short premaxilla with weakly 'hooked' tip, ventrally directed caniniform process, rugose orbital rim, squamosal with broadly rounded dorsal margin in lateral view, postfrontals exposed as thin, strap-like bones at the anteromedian edges of the postorbitals, extremely long, narrow intertemporal bar with extremely narrow or no median exposure of parietals, and vertical orientation of the postorbitals in the intertemporal bar.

DELECTOSAURUS Kurkin, 2001

Type Species—*Delectosaurus arefjevi* Kurkin, 2001.

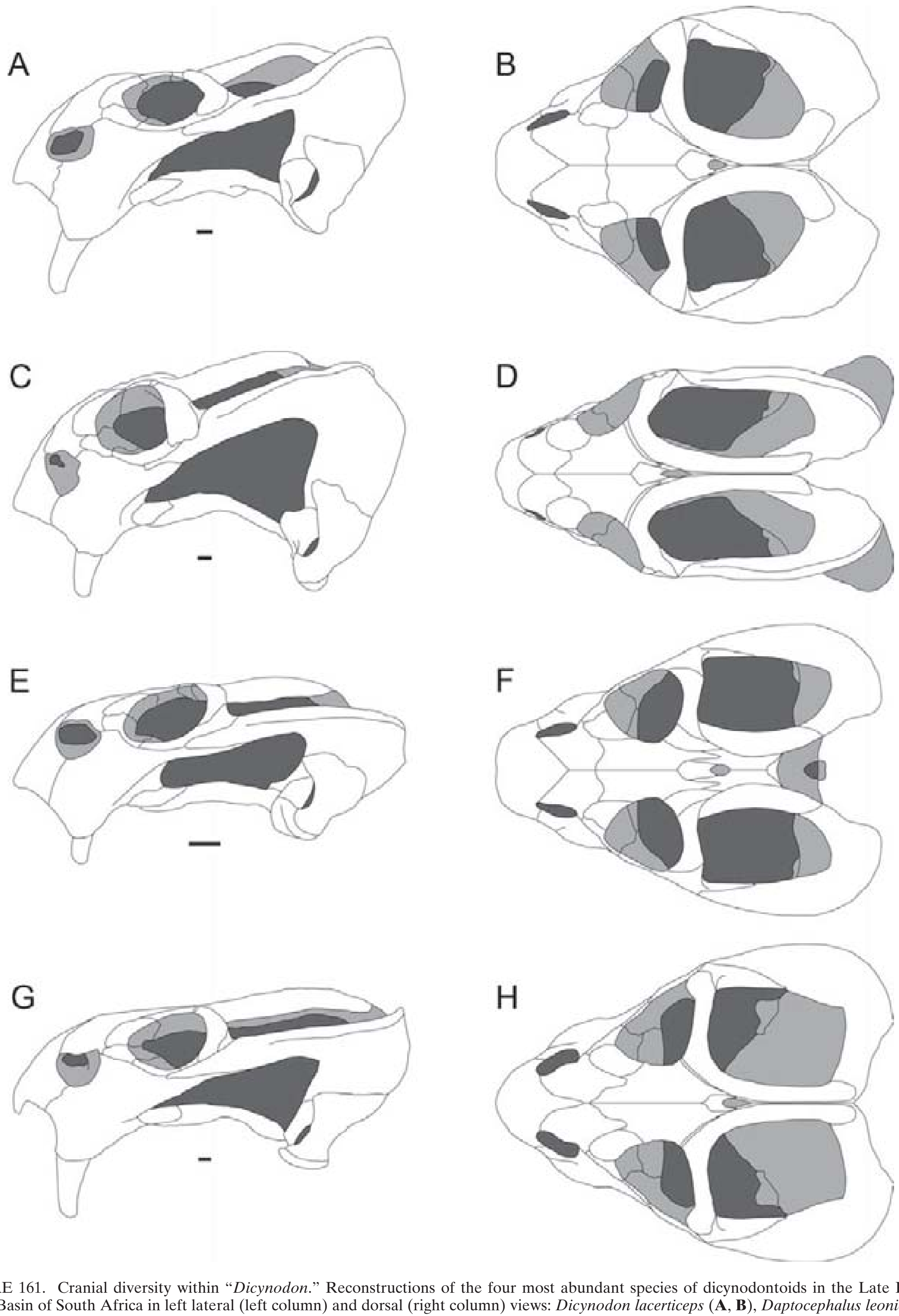

FIGURE 161. Cranial diversity within "*Dicynodon*." Reconstructions of the four most abundant species of dicynodontoids in the Late Permian Karoo Basin of South Africa in left lateral (left column) and dorsal (right column) views: *Dicynodon lacerticeps* (**A**, **B**), *Daptocephalus leoniceps* (**C**, **D**), *Basilodon woodwardi* (**E**, **F**), and *Dinanomodon gilli* (**G**, **H**). Scale bars equal 2 cm.

Diagnosis—As for the type species. A second nominal species, *D. berezhanensis*, is very similar, although Kurkin (2001) considered the shape of the frontals to distinguish them.

DELECTOSAURUS AREFJEVI Kurkin, 2001

Delectosaurus arefjevi Kurkin, 2001:56.

Holotype—PIN 4644/1.

Referred Material—None.

Diagnosis—A small dicynodontoid distinguished from *Dicynodon lacerticeps* by the presence of a floccular fossa and the relatively short interpterygoid vacuity. Further diagnosed by the following unique combination of characters: narrow intertemporal bar with extensive postorbital-parietal overlap but with narrow parietal exposure for length of the bar, anteroposteriorly short premaxilla with weakly 'hooked' tip, distinctly triangular in ventral view, and palatal margin with weakly developed embayments anterior to the caniniform process.

DICYNODON Owen, 1845

Type Species—*Dicynodon lacerticeps* Owen, 1845.

Referred Species—*Dicynodon huenei* Haughton, 1932.

Diagnosis—Medium to large Permian dicynodontoid characterized by the following unique combination of characters: anteriorly directed caniniform process, premaxillae squared-off in palatal view, squamosals narrow in lateral view, with the zygomatic and quadrate rami forming an acute angle, interorbital width greater than intertemporal, and relatively short intertemporal bar with narrow or no exposure of the parietals.

DICYNODON LACERTICEPS Owen, 1845
(Figs. 65, 161A, B)

Dicynodon lacerticeps Owen, 1845:62.
Dicynodon pardiceps Owen, 1876:42.
Dicynodon taylori Broom, 1932:181.
Dicynodon kitchingi Broom, 1937a:143.
Dicynodon dutoiti Broom and Schepers, 1937:729.
Dicynodon cadlei Broom, 1940:82.
Dicynodon trigonocephalus Broom, 1940:182.
Dicynodon aetorhamphus Broom, 1948:605.

Holotype—NHMUK 36233.

Referred Material—BP/1/156, BP/1/780, BP/1/889, BP/1/2880, BP/1/3170, BP/1/4026, BSP 1934 VIII 515, CAMZM T770, CAMZM T774, CGP GHG8, CGP K31, CGP R42, NHMUK 47045, NMQR 199, RC 23, RC 38, RC 85, SAM-PK-4008, SAM-PK-8784, SAM-PK-K1191, SAM-PK-K7011, SAM-PK-K7591, SAM-PK-K7806, SAM-PK-K9949, SMFNS 51922, TM 345, TM 1495, TM 1502, USNM 25183, and USNM 25211.

Diagnosis—Medium to large Permian dicynodontoid distinguished from *Dicynodon huenei* by the relatively narrower zygomatic arch and postorbital bar.

DICYNODON HUENEI Haughton, 1932
(Fig. 56)

Dicynodon huenei Haughton, 1932:639.

Holotype—SAM-PK-10630.

Referred Material—CAMZM T799, CAMZM T979, CAMZM T982, CAMZM T983, CAMZM T1089, CAMZM T1122, CAMZM T1126, CAMZM T1280, and CAMZM T1292, SAM-PK-10634, TSK 14, TSK 27, TSK 37, TSK 83.

Diagnosis—Medium to large dicynodontoid distinguished from *Dicynodon lacerticeps* by the transversely and dorsoventrally thickened zygomatic arch, an expanded ventral portion of the postorbital bar, forming a flat plate on its anterior edge, and rugosity on the posterior surface of the caniniform process.

DINANOMODON Broom, 1938

Type Species—*Dinanomodon rubidgei* Broom, 1938.

Diagnosis—As for *Dinanomodon gilli* (senior synonym of the type species *Dinanomodon rubidgei*).

DINANOMODON GILLI (Broom, 1932)
(Figs. 43, 161G, H)

Dicynodon gilli Broom, 1940:176.
Dinanomodon rubidgei Broom, 1938:247.
Dicynodon macrodon Broom, 1940a:81.
Dicynodon anneae Broom, 1940b:181.
Dinanomodon gigas Broom, 1940b:176.
Dicynodon galecephalus Broom and Robinson, 1948:404.

Holotype—SAM-PK-4008.

Referred Material—BP/1/112, BP/1/4029, BP/1/5287, NHMUK R3598, NMQR 68, NMQR 1449, RC 9, RC 22, RC 36, RC 42, RC 77, SAM-PK-7839, SAM-PK-K10220, SAM-PK-K10618, and TM 4506.

Diagnosis—Very large Permian dicynodontoid characterized by the following autapomorphies: extremely anteroposteriorly elongate premaxilla with strongly 'hooked' tip and nasal bosses above external nares give nares a 'saddle-shaped' appearance in lateral view. Distinguished from all dicynodontoids other than *Peramodon amalitzkii* and *Vivaxosaurus trautscholdi* by an elongate anterior process of the frontals, and from all dicynodontoids other than *Turfanodon bogdaensis* and *Vivaxosaurus trautscholdi* by an elongate ascending process of premaxilla extending posteriorly to near or contact the frontals. Further diagnosed by the following unique combination of characters: extremely long, narrow intertemporal bar (decreasing in width posteriorly) with narrow or no median exposure of parietals, vertical orientation of postorbitals on the intertemporal bar, median ridge on on the midfrontal suture, and premaxillary portion of palate with triangular tip.

GORDONIA Newton, 1893

Type Species—*Gordonia traquairi* Newton, 1893.

Diagnosis—As for the type species.

GORDONIA TRAQUAIRI Newton, 1893
(Fig. 134)

Gordonia traquairi Newton, 1893:436.
Gordonia huxleyana Newton, 1893:445.
Gordonia duffiana Newton, 1893:450.
Gordonia juddiana Newton, 1893:462.
Dicynodon traquairi von Huene, 1940:280.
Dicynodon duffianus von Huene, 1940:280.
Dicynodon huxleyanus von Huene, 1940:280.
Dicynodon juddianus von Huene, 1940:280.

Holotype—BGS GSE11703.

Referred Material—BGS GSE11704, ELGNM 1890.3, ELGNM 1978.549, ELGNM 1978.559, ELGNM 1995.5.1, ELGNM 1995.5.2, and ELGNM 1999.22.

Diagnosis—A small dicynodontoid characterized by the following autapomorphy: lateral dentary shelf rod-like, angled anterodorsally. Further diagnosed by the following unique combination of characters: long, narrow intertemporal bar with narrow exposure of parietals, vertical orientation of the postorbitals in the intertemporal bar forming sagittal crest, short snout, and short, steep mandibular symphysis.

JIMUSARIA Sun, 1963

Type Species—*Dicynodon sinkianensis* Yuan and Young, 1934.

Diagnosis—As for the type species.

JIMUSARIA SINKIANENSIS (Yuan and Young, 1934)
(Fig. 124)

Dicynodon sinkianensis Yuan and Young, 1934:563.
Jimusaria sinkianensis Sun, 1963:107.
Jimusaria taoshuyuanensis Sun, 1973:53.

Holotype—IVPP 341407.

Referred Material—IVPP V3420.1, IVPP V3420.2, and IVPP V3420.3.

Diagnosis—A medium-sized dicynodontoid characterized by the following autapomorphies: a sharp, blade-like lateral dentary shelf expanding anteriorly into a thick swelling, a short, rounded caniniform process with equivalent curvature anteriorly and posteriorly. Further diagnosed by the following unique combination of characters: narrow intertemporal bar with no dorsal exposure of parietals, squamosals narrow in lateral view, with the zygomatic and quadrate rami forming an acute angle, and prominent grooves arcing between the postfrontals and postorbitals.

PERAMODON, gen. nov.

Type Species—*Dicynodon amalitzkii* Sushkin, 1926.

Diagnosis—As for the type species.

Etymology—'Distant land tooth,' from the Vepsian word perama (far-away land) and the ancient Greek ὀδούς (tooth). The name of the Russian city of Perm (after which the Permian Period is named) may be derived from perama; this taxon is named *Peramodon* in reference to its status as a Russian Permian dicynodont and its geographic disjunction from true *Dicynodon* (*D. lacerticeps*). Masculine.

PERAMODON AMALITZKII (Sushkin, 1926), comb. nov.

(Fig. 9)

Dicynodon amalitzkii Sushkin, 1926:323.

Holotype—PIN 2005/38.

Referred Material—None.

Diagnosis—A medium-sized dicynodont that can be distinguished from all dicynodontoids other than *Syops vanhoepeni*, *Turfanodon bogdaensis*, and *Vivaxosaurus trautscholdi* by the presence of a preparietal depression immediately anterior to the pineal foramen. Distinguished from all dicynodontoids other than *Dinanomodon rubidgei* and *Vivaxosaurus trautscholdi* by the anterior process of the frontals. Further diagnosed by the following unique combination of characters: relatively short, very narrow intertemporal bar with steeply sloping snout profile, broadly rounded dorsal margin of squamosal in lateral view, anteriorly directed canine, and broad, round caniniform process, more curved anteriorly than posteriorly.

SINTOCEPHALUS van Hoepen, 1934

Type Species—*Dicynodon alticeps* Broom and Haughton, 1913.

Diagnosis—As for the type species.

SINTOCEPHALUS ALTICEPS (Broom and Haughton, 1913)

(Fig. 8)

Dicynodon alticeps Broom and Haughton, 1913:37.
Sintocephalus alticeps van Hoepen, 1934:87.

Holotype—SAM-PK-2347.

Referred Material—None.

Diagnosis—Medium-sized Permian dicynodontoid characterized by the following autapomorphy: thickened region of temporal arch immediately after postorbital bar with convex ventral margin in lateral view. Further diagnosed by the following unique combination of characters: large orbits (relative to dicynodontoids of equal size), steeply angled, sloping snout, broad intertemporal region (equal in width to interobital region anteriorly, but constricting posteriorly), broad exposure of parietals, and lateral margins of adductor musculature attachment sites do not overlap on intertemporal midline.

SYOPS, gen. nov.

Type Species—*Dicynodon vanhoepeni* Boonstra, 1938.

Diagnosis—As for the type species.

Etymology—'Hog face,' from the ancient Greek συς (hog) and ωψ (face), referring to the piglike appearance of the skull (relatively long and low-snouted for a dicynodont, with stout, recurved tusks). Also an allusion to the numerous warthogs at the type locality in the Luangwa Valley. Masculine.

SYOPS VANHOEPENI (Boonstra, 1938), comb. nov.

(Fig. 142)

Dicynodon vanhoepeni Boonstra, 1938:373.
Dicynodon roberti Boonstra, 1938:383.

Holotype—SAM-PK-11311.

Referred Material—SAM-PK-11325A and SAM-PK-11325B.

Diagnosis—A medium-sized dicynodontoid distinguished from all dicynodontoids other than *Basilodon woodwardi* by the sharp break in snout slope between the nasal and premaxilla, and from all dicynodontoids other than *Peramodon amalitzkii*, *Turfanodon bogdaensis*, and *Vivaxosaurus trautscholdi* by a depressed preparietal immediately anterior to the pineal foramen. Further diagnosed by the following unique combination of characters: narrow intertemporal bar with narrow exposure of the parietals, prominent ridge on lateral premaxillary-maxillary suture, relatively long, low snout, and anteriorly directed canines.

TURFANODON Sun, 1973

Type Species—*Turfanodon bogdaensis* Sun, 1973.

Diagnosis—As for the type species.

TURFANODON BOGDAENSIS Sun, 1973

(Fig. 17)

Turfanodon bogdaensis Sun, 1973:56.
Striodon magnus Sun, 1978:19.
Dicynodon bogdaensis King, 1988:90.
Dicynodon sunanensis Li, Cheng, and Li, 2000:150.

Holotype—IVPP V3241.

Referred Material—IGCAGS V296 and IVPP V4694.

Diagnosis—A large Permian dicynodontoid distinguished from all dicynodontoids other than *Syops vanhoepeni*, *Peramodon amalitzkii*, and *Vivaxosaurus trautscholdi* by the depressed preparietal anterior to the pineal foramen, and distinguished from all dicynodontoids other than *Dinanomodon gilli* and *Vivaxosaurus trautscholdi* by the elongate ascending process of the premaxilla. Further diagnosed by the following unique combination of characters: facial region heavily pitted, intertemporal bar long and narrow, with narrow exposure of the parietals, vertical orientation of the postorbitals in the intertemporal bar, snout tall with steeply sloping profile, broadly rounded dorsal margin of the squamosal in lateral view, and relatively broad interorbital region.

VIVAXOSAURUS Kalandadze and Kurkin, 2000

Type Species—*Vivaxosaurus permirus* Kalandadze and Kurkin, 2000.

Diagnosis—As for *Vivaxosaurus trautscholdi* (senior synonym of the type species *Vivaxosaurus permirus*).

VIVAXOSAURUS TRAUTSCHOLDI (Amalitzky, 1922), comb. nov.

(Fig. 135)

Dicynodon trautscholdi Amalitzky, 1922:332.
Gordonia annae Amalitzky, 1922:333.
Gordonia rossica Amalitzky, 1922:333.
Oudenodon venyukovi Amalitzky, 1922:334.

Dicynodon annae Sushkin, 1926:326.
Dicynodon rossicus von Huene, 1940:278.
Dicynodon venyukovi von Huene, 1940:278.
Vivaxosaurus permirus Kalandadze and Kurkin, 2000:643.

Holotype—PIN 2005/1.

Referred Material—PIN 1536/1, PIN 2005/3, PIN 2005/5, and PIN 2005/6.

Diagnosis—A medium-sized dicynodontoid characterized by an autapomorphic morphology of the caniniform process: narrow and anteroventrally directed with a rounded lobe anterior to the tusk. Distinguished from all dicynodontoids other than *Peramodon amalitzkii*, *Syops vanhoepeni*, and *Turfanodon bogdaensis* by a depression on the preparietal immediately anterior to the pineal foramen. Distinguished from all dicynodontoids other than *Dinanomodon gilli* and *Peramodon amalitzkii* by the elongate anterior processes of the frontals, and and from all dicynodontoids other than *Dinanomodon gilli* and *Turfanodon bogdaensis* by the elongate ascending process of the premaxilla.

LYSTROSAURIDAE Broom, 1903
EUPTYCHOGNATHUS, gen. nov.

Type Species—*Dicynodon bathyrhynchus* von Huene, 1942.

Diagnosis—As for the type species.

Etymology—'Well-folded jaw,' from the ancient Greek *ευ* (good, well), *πτυχος* (folded), and *γνάθος* (jaw), referring to the distinct biplanarity of the snout profile and to *Ptychognathus*, Owen's original (but preoccupied) name for *Lystrosaurus*. Masculine.

EUPTYCHOGNATHUS BATHYRHYNCHUS (von Huene, 1942), comb. nov.

Dicynodon bathyrhynchus von Huene, 1942:160.

Holotype—GPIT/RE/7104.

Referred Material—CGP/1/310, CGP AF107-83, and UCMP 42714.

Diagnosis—A medium-sized dicynodontoid characterized by the following autapomorphies: arcuate ridge curving across snout between prefrontal bosses, very short premaxillary portion of palate with blunt, rounded tip and separated from rest of palate by distinct embayment in the palatal rim anterior to the caniniform processes. Further diagnosed by the following unique combination of characters: snout very tall, ventrally deflected, snout distinctly biplanar in profile, with the break in slope between the nasals and frontals, intertemporal bar very short and narrrow, with intertemporal width less than interorbital width, extensive but incomplete postorbital-parietal overlap, vertical orientation of the postorbitals in the intertemporal bar, well-developed prefrontal bosses, and a swelling at the base of the postorbital bar.

BIOSTRATIGRAPHY AND BIOGEOGRAPHY OF *DICYNODON*

Biostratigraphy of "*Dicynodon*" Species and Their Utility as Index Fossils

Because they are the most common terrestrial vertebrate fossils in middle-Upper Permian and Early Triassic deposits, dicynodonts have been extensively utilized in vertebrate biostratigraphy (e.g., Broom, 1906; Watson, 1914b; Drysdall and Kitching, 1963; Kitching, 1977; Sun, 1980; Cox, 1991; Lucas, 1993, 1998a, 1998b, 1999, 2006, 2010; Rubidge, 1995, 2005; Gay and Cruickshank, 1999; Golubev, 2000). Of particular importance is the fact that since the late 1970s, *Dicynodon* (or *Daptocephalus*) has served as an index fossil for the uppermost Permian biostratigraphic assemblage in the Karoo Basin (e.g., Keyser and Smith, 1977–1978; Kitching, 1977; SACS, 1980; Rubidge, 1995, 2005), and the last appearance of *Dicynodon* has been used as a biostratigraphic marker for the end-Permian extinction in recent studies of this event in the Karoo (Smith, 1995; MacLeod et al., 2000; Ward et al., 2000, 2005; Smith and Ward, 2001; Retallack et al., 2003; although see Gastaldo et al., 2009).

Lucas (1998a, 2001, 2002, 2005a, 2005b, 2005c, 2006, 2009) has been the strongest recent proponent of the biostratigraphic utility of *Dicynodon* sensu lato, arguing that it characterizes and permits global correlation of the 'Platbergian land vertebrate faunachron' (LVF) (defined as the span from the first to last appearance of *Dicynodon*). Under this scheme, the Platbergian LVF would be equivalent to the uppermost *Cistecephalus* Assemblage Zone and all of the *Dicynodon* Assemblage Zone of Rubidge (1995). This is the youngest of the three Late Permian LVFs, the others being the Hoedemakeran (defined by the first appearance of *Tropidostoma*) and the Steilkransian (defined by the first appearance of *Cistecephalus*). The separation between these LVFs is problematic even within the Karoo basin, because the first appearance of *Dicynodon* sensu lato is concurrent with that of *Cistecephalus*, and the definition of the LVFs lacks the multitaxic and lithologic context of the defined assemblage zones of the Beaufort Group (Rubidge, 1995). Far more problematic, however, is the use of *Dicynodon* sensu lato to correlate various basins with the Platbergian LVF. Our phylogenetic analyses corroborate Angielczyk and Kurkin's (2003a, 2003b) hypothesis that *Dicynodon* sensu lato is not monophyletic. Therefore, "*Dicynodon*" specimens in various basins do not represent the same taxon, and there is no guarantee that they had similar temporal ranges. Lucas (2005b) acknowledges the likely paraphyly of "*Dicynodon*," but argues that the gradistic "*Dicynodon*" (all non-lystrosaurid, non-kannemeyeriiform dicynodontoids) still represents a phenetically discrete unit with global biostratigraphic utility. We disagree that the various "*Dicynodon*" species form a phenetically discrete grade (see above), but of greater importance is the fact that Lucas' definition of *Dicynodon* necessarily excludes its ability to separate the Platbergian LVF from the other Late Permian LVFs and thus be of any correlative value. If *Dicynodon* is defined as all non-Triassic dicynodontoids (and Lucas' [2005b] inclusion of even *Elph borealis* in *Dicynodon* indicates that this is his preferred definition), then this gradistic 'genus' must have originated no later than *Tropidostoma* AZ times (given that Dicynodontoidea and Cryptodontia, including *Tropidostoma*, are sister taxa). This results in a catch-22: in order to correlate the Platbergian LVF globally one must include all basal dicynodontoids (e.g., *Gordonia* in Scotland, *Vivaxosaurus* in Russia, *Turfanodon* in China, etc.) within *Dicynodon*, but in doing so one creates a range for *Dicynodon* that logically must completely overlap with the other Late Permian LVFs, rendering it useless for all but the broadest correlations.

We are of the opinion that there is no benefit in continuing to use an inaccurate and outdated gradistic concept of *Dicynodon* for biostratigraphic purposes when it is unable to resolve a time unit finer than the Lopingian. Instead, attention should now turn to better documenting the stratigraphic ranges of the valid species of "*Dicynodon*" (Fig. 162) and collecting additional data that will allow a more strongly supported resolution of basal dicynodontoid linages. Pending additional study of the biostratigraphy of South African dicynodontoids, we recommend the use of *Daptocephalus leoniceps* as an index taxon for the *Dicynodon* AZ within the Karoo Basin, but limit its utility to within that basin. Although it seems clear that *Daptocephalus leoniceps* is one of the last Permian dicynodonts to become extinct in South Africa, it is not clear how precisely this last occurrence correlates with the marine end-Permian extinction or the geochronologically defined Permo-Triassic boundary (e.g., De Kock and Kirschvink, 2004; Ward et al., 2005; Steiner, 2006; Coney et al., 2007; Gastaldo et al., 2009). With the exception of *Euptychognathus bathyrhynchus* and *Dicynodon huenei* (found in South Africa/Tanzania and Tanzania/Zambia, respectively; note that we consider the specimen

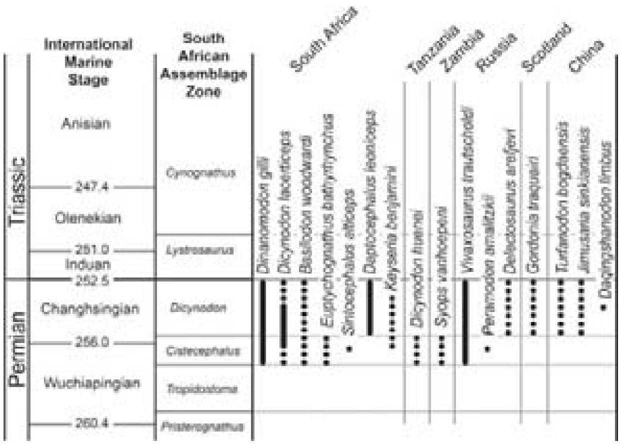

FIGURE 162. Stratigraphic ranges of Permian "*Dicynodon*" species recognized as valid herein. Solid lines indicate that the taxon is known from multiple specimens of well-resolved stratigraphic position within a South African Assemblage Zone or extrabasinal equivalent. Dotted lines indicate that the taxon is known from few specimens of unknown or poorly resolved stratigraphic position within an Assemblage Zone or equivalent. Single dots indicate that the taxon is known only from the holotype. All taxa are basin endemics except for *Euptychognathus bathyrhynchus* (known from South Africa and Tanzania) and *Dicynodon huenei* (known from Tanzania and Zambia). Equivalence of the Scottish and Chinese records with the *Dicynodon* AZ should be considered very tentative. Although part of the "*Dicynodon*"-bearing Cangfanggou Group (Xinjiang, China) is clearly latest Permian, the fossiliferous section is over 600 m thick (Lucas, 1998a) and may also include *Cistecephalus* AZ equivalents lower in section.

described by Wild et al. [1993] to be *D. huenei*, not *D. lacerticeps*), no basal dicynodontoid species are present in basins in different countries, and as such cannot be used to correlate these basins. Battail (2009) recently published a photograph of a Laotian specimen that shows some similarities to *Daptocephalus leoniceps*, raising the possibility that this species has the potential to be used for limited correlations beyond the Karoo Basin. However, we have not examined this specimen personally, and cannot confirm or deny its identity as *D. leoniceps* at this time.

Dicynodont Turnover at the Permo-Triassic Boundary

Our revised taxonomy of *Dicynodon* sensu lato has important implications for measures of tetrapod extinction severity at the Permo-Triassic boundary (PTB). As the most abundant, species-rich tetrapod group in the Late Permian, dicynodonts have played a central role in studies of vertebrate turnover during this mass extinction. Although at least four distinct dicynodont lineages survived the greatest mass extinction of all time, the clade suffered a severe decrease in overall numbers of genera and species (Fröbisch 2007, 2008). Recent alpha taxonomic revisions of many anomodonts have enabled major advances in diversity estimates within the clade (see Fröbisch, 2008, 2009). However, previous estimates of dicynodont species turnover both within the Karoo Basin and globally have been hampered by the taxonomic confusion surrounding *Dicynodon*. Our revised list of 15 valid "*Dicynodon*" species (including seven in the Karoo Basin) permits a more accurate tabulation of dicynodont turnover at the PTB than has been possible in previous analyses. Depending on whether species or genera were utilized as OTUs, previous analyses of turnover at the PTB have either overestimated or underestimated the severity of this extinction in dicynodonts. The loss of *Dicynodon* did not involve the extinction of 30 species in the Karoo at the end of the Permian, as species counts in the most recent reviews of the genus (Cluver and Hotton, 1981; King, 1988) would indicate. Recognizing the problematic nature of *Dicynodon* alpha taxonomy, most recent studies of vertebrate turnover at the PTB have treated *Dicynodon* as a single genus-level taxon (e.g., Angielczyk et al., 2005b; Smith and Botha, 2005; Ward et al., 2005; Botha and Smith 2006; Roopnarine et al., 2007), although Fröbisch (2008) considered richness at both the genus and species levels (including 13 of the 15 valid "*Dicynodon*" species). However, this approach masks the extinction of a number of distinct lineages of Permian dicynodontoids. In the Karoo Basin, *Dicynodon lacerticeps*, *Daptocephalus leoniceps*, *Dinanomodon gilli*, and *Basilodon woodwardi* are all present in the latest Permian *Dicynodon* Assemblage Zone, and at least *Daptocephalus* and *Dinanomodon* are among the last Permian taxa to become extinct. The holotype of *Keyseria benjamini* is also from the *Dicynodon* Assemblage Zone, but based on this single specimen the survival of this species until the PTB is uncertain (the referred specimen CGP S125b is from the *Cistecephalus* Assemblage Zone). Similarly, the rarity of *Sintocephalus alticeps* and *Euptychognathus bathyrhynchus* (the former known only from a *Cistecephalus* AZ skull, the latter known from three *Cistecephalus* AZ specimens) precludes robust conclusions as to their stratigraphic ranges. Thus, between the *Dicynodon* and *Lystrosaurus* assemblage zones there is the loss of at least six distinct dicynodontoid taxa in the Karoo, although at present we are certain of only two of those taxa (*Daptocephalus* and *Dinanomodon*) surviving until the PTB proper. Extrabasinal analyses using "*Dicynodon*" at the genus level also underestimate the severity of the extinction for dicynodontoids (e.g., Benton et al., 2004; Lucas, 2009): Russian and Chinese "*Dicynodon*" each consist of at least three distinct lineages in the terminal Permian (*Delectosaurus arefjevi*, *Peramodon amalitzkii*, and *Vivaxosaurus trautscholdi* in Russia and *Daqingshanodon limbus*, *Jimusaria sinkianensis*, and *Turfanodon bogdaensis* in China).

Finally, our results have implications for the recovery following the mass extinction event. The fact that some species of "*Dicynodon*" may fall within Lystrosauridae does not strongly alter our picture of this clade's diversity dynamics across the boundary. The presence of *Lystrosaurus maccaigi* and *Lystrosaurus curvatus* in the Late Permian demonstrate that *Lystrosaurus* is a survivor of the extinction, and the appearance of *Lystrosaurus declivis*, *Lystrosaurus hedini*, and *Lystrosaurus murrayi* in the Early Triassic shows that it participated in the burst of tetrapod diversification that appears to have followed the event (Smith and Botha, 2005; Botha and Smith; 2006, 2007). Our results do suggest that at least some aspects of the cranial morphology of *Lystrosaurus* began to evolve as early in the Permian as the *Cistecephalus* AZ, implying that they were not adaptations to specific ecological or environmental conditions at the boundary even if they proved advantagous at that time. Depending on the exact identity of its sister taxon (see above), our cladograms imply a ghost lineage for Kannemeyeriiformes extending at least to *Dicynodon* AZ times, and possibly back to the *Cistecephalus* AZ. However, because no Late Permian or earliest Triassic taxa can be identified as members of any kannemeyeriiform subclade, it is difficult to assess how strongly this clade was affected by the end-Permian extinction and the pace of their diversification. If shansiodontids are the most basal kannemeyeriiforms, and the biostratigraphic framework that places the global first appearance of shansiodontids after the first appearance of *Kannemeyeria simocephala* in the Karoo Basin (e.g., Lucas, 2010) is correct, this would imply that kannemeyeriiform diversification was well underway by the Induan but that most of this history is missing from the known fossil record. When combined with the fact that our phylogeny implies that all major lineages of kannemeyeriiforms are represented in the fossil record by the Anisian, the picture that emerges is one of rapid dicynodont diversification following the end-Permian extinction. This echoes discoveries that push back the origins of other Triassic clades (e.g., Nesbitt et al., 2010), suggesting that although the end-Permian extinction had profound effects on terrestrial communities, recovery proceeded relatively quickly.

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APPENDIX 1. Specimens used in the morphometric analysis. All specimens listed below were digitized for the analysis of snout profile. Specimens marked with an asterisk were also digitized for the analysis of squamosal shape.

Dicynodon lacerticeps

BP/1/156
BP/1/780
BP/1/889
BP/1/2880*
BP/1/3170
BP/1/4026*
CAMZM T770*
CGP K31*
CGP S52*
NHMUK 36233
NMQR 199
RC 23*
RC 38*
RC 85*
SAM-PK-8784
SAM-PK-K1191
SAM-PK-K7591
SAM-PK-K7806
SAM-PK-K10514*
TM 1495
TM 1502*
USNM 25183*
USNM 25211

Daptocephalus leoniceps

BP/1/832
BP/1/2188*
BP/1/2784
BP/1/3427*
BP/1/3744
CGP AF156–83*
CGP GHG36a*
CGP GHG140*
CGP JW83–65*
CGP K93*
NHMUK 47045
NHMUK 47047*
NMQR unnumbered
NMQR 26*
NMQR 75
NMQR 960*
NMQR 1400
NMQR 1544
RC 96
SAM-PK B88*
SAM-PK-4026
SAM-PK-6044
SAM-PK-K10570*
SAM-PK-K10695
UCMP 33431*
USNM 23337*
USNM 25214

APPENDIX 2. Characters and codings used in phylogenetic analysis.

CHARACTERS USED IN PHYLOGENETIC ANALYSIS

Character list for the phylogenetic analysis performed in this study. The primary source of each character is listed behind the character definition.

Morphometric Characters

(1) Length of preorbital region of skull relative to basal length of skull. (Modified from Modesto et al., 1999: char. 6)
(2) Relative length of premaxillary secondary palate (From Angielczyk 2007: char. 63)
(3) Minimum width of interorbital skull roof relative to basal length of skull. (New)
(4) Relative width of temporal bar at level of postorbital bar versus the relative width at the junction of the intertemporal bar with the occipital plate. (New)
(5) Length of temporal fenestra relative to basal length of skull. (New)
(6) Width of median pterygoid plate relative to basal skull length. (New)
(7) Angle formed by the posterior pterygoid rami. (New)
(8) Length of interpterygoid vacuity relative to basal length of skull. (Modified from Angielczyk and Kurkin, 2003a: char. 33)
(9) Relative area of the internal nares. (From Angielczyk, 2007: char. 64)
(10) Angle between ascending and zygomatic processes of the squamosal. (Modified from Fröbisch and Reisz 2008: char. 75)
(11) Angulation of the occiput relative to the palate, expressed as the ratio of dorsal and basal lengths of the skull. (Modified from Cox and Li, 1983)
(12) Ratio of length to height of mandibular fenestra in lateral view. (Modified from Rubidge and Hopson, 1996: char. 5; and Modesto et al., 1999: char. 36)
(13) Ratio of height of dentary ramus to height of dentary symphysis. (New)
(14) Ratio of maximum height of postdentary bones (excluding reflected lamina of angular) to the height of the dentary ramus. (New)
(15) Ratio of minimum width of the scapula to maximum width of dorsal end of scapula. (From Angielczyk, 2007: char. 72)
(16) Length of the deltopectoral crest relative to total length of the humerus. (From Angielczyk, 2007: char. 68)
(17) Maximum width of the distal end of the radius relative to the maximum length of the radius. (From Angielczyk, 2007: char. 69)
(18) Ratio of posterior iliac process length to acetabulum diameter. (From Sidor and Hopson, 1998: char. 157)
(19) Ratio of anterior iliac process Length to acetabulum diameter. (From Sidor and Hopson, 1998: char. 158)
(20) Length of trochanteric crest on femur relative to length of femur. (New)

Discrete-State Characters

(21) Premaxillae unfused (0) or fused (1). (From Angielczyk and Kurkin, 2003a: char. 3)
(22) Paired anterior ridges on palatal surface of premaxilla absent (0), present and converge posteriorly (1), or present and do not converge (2). (From Angielczyk and Kurkin, 2003a: char. 7)
(23) Lateral anterior palatal ridges absent (0) or present (1). (From Angielczyk, 2007: char. 60)
(24) Posterior median ridge on palatal surface of premaxilla absent (0), present with a flattened, expanded anterior area

(1), or present without a flattened, expanded anterior area (2). (From Angielczyk and Kurkin, 2003a: char. 8)

(25) Palatal surface of premaxilla with well-defined depressions with curved sides lateral to median ridge (if present) (0), with groove-like depressions that have straight sides and a rounded anterior end (1), or relatively flat with poorly defined or no depressions present (2). (From Angielczyk and Kurkin, 2003a: char. 9)

(26) Location of premaxillary teeth lateral (0), medial (1), or absent (2). (From Angielczyk and Kurkin, 2003a: char. 2)

(27) Posterior exposure of the premaxilla on the palate: absent (0), present (1). (From Hopson and Barghusen, 1986: char. 6.8)

(28) Palatine shelf ventral to internal naris: absent (0), present (1). (From Hopson and Barghusen, 1986: chars. 20.3 and 21.4)

(29) Anterior tip of snout rounded (0) or squared off (1). (From Maisch and Gebauer, 2005: char. 11)

(30) Marked anterior expansion of preorbital region absent (0) or present (1). (Modified from Maisch and Gebauer, 2005: char. 2)

(31) Snout roughly parallel to long axis of skull (0) or strongly angled ventrally (1). (New)

(32) Snout open to back of the skull (0) or anterior margin of orbit extended posteromedially to partly close off the snout from the rest of the skull (1). (From Angielczyk and Kurkin, 2003a: char. 25)

(33) Septomaxilla posterodorsal spur present and widely separates nasal and maxilla (0), spur present but does not separate maxilla and nasal (i.e., nasal-maxilla suture present and well defined in this region) (1), septomaxilla spur absent (2). (Modified from Modesto et al., 1999: char. 8)

(34) Notch on dorsal edge of narial opening absent (0) or present (1). (New)

(35) Postnarial excavation absent (0), present, relatively small, and rounded posteriorly (1), or present, very large, and elongate (2). (Vega-Dias et al., 2004: char. 8)

(36) Maxillary alveolar region short, occupying less than 53% of the ventral length of the bone (0) or tooth bearing region long, occupying 72% or more of the ventral length of the bone (1). (From Modesto et al., 1999: char. 9)

(37) Palatal surface of premaxilla exposed in lateral view (1) or not exposed in lateral view (0). (New)

(38) Maxillary canine present as large member of tooth series (0), absent (1), or present as tusk (2). (From Modesto et al., 2003: char. 6)

(39) Maxillary non-caniniform teeth located near lateral margin of maxilla (0), located more medially (1), or absent (2). (From Angielczyk and Kurkin, 2003a: char. 4)

(40) Shelf-like area lateral to the maxillary non-caniniform teeth absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 5)

(41) Fine serrations on maxillary teeth present (0), serrations absent (1), or coarse serrations present (2). (From Modesto et al., 1999: char. 3)

(42) Sutural contact of maxilla and prefrontal present (0) or absent (1). (From Modesto et al., 2003: char. 10)

(43) Caniniform process absent (0) or present (1). (Modified from Angielczyk and Kurkin, 2003a: char. 6)

(44) Caniniform depression: has the form of an embayment of palatal rim anterior to caniniform process or tusk (1), has the form of a notch in palatal rim anterior to caninfiorm process (2), or absent (0). (Modified from Angielczyk and Kurkin, 2003a: chars. 6 and 14)

(45) Keel-like extension of the palatal rim posterior to the caniniform process absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 1)

(46) Postcaniniform crest absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 28)

(47) Ventral edge of the caniniform process or dorsal edge of the erupted portion of the canine tusk anterior (0) to, or at the same level to slightly posterior to (1) the anterior orbital margin. (From Angielczyk and Kurkin, 2003a: char. 44)

(48) Nasal bosses absent (0), present as a median swelling with a continuous posterior margin (1), present as paired swellings near the dorsal or posterodorsal margin of external nares (2), present as paired swellings that meet in the midline to form a swollen anterodorsal surface on the snout (3). (Modified from Angielczyk and Kurkin, 2003a: char. 23)

(49) Transverse crest approximately at level of naso-frontal suture absent (0) or present (1). (From Maisch, 2002a: char. 18)

(50) Prefrontal bosses absent (0), present but separate from nasals (1), or present and confluent with nasal bosses (2). (New)

(51) Raised, sometimes rugose, circumorbital rim absent (0) or present (1). (New)

(52) Postfrontal bone present on dorsal surface of skull (0) or absent (1). (From Maisch, 2002a: char. 8)

(53) Postorbital bar without (0) or with thickenings and rugosities (1). (From Maisch and Gebauer, 2005: char. 5)

(54) Temporal portion of skull roof relatively straight, without a strong break in slope (0), or temporal portion of skull roof angled dorsally with a strong break in slope near its anterior end (1). (Modified from Vega-Dias et al., 2004: char. 16)

(55) Preparietal bone absent (0), present and its dorsal surface relatively flat and flush with the skull roof (1), present and with a depressed dorsal surface relative to the surrounding skull roof (2), present with ridges running along it which may surround the pineal foramen (3). (From Angielczyk and Kurkin, 2003a: char. 45)

(56) Parietals' contribution to skull table transversely as broad as long (0), longer anteroposteriorly than broad (1), or shorter anteroposteriorly than broad (2). (From Modesto and Rybczynski, 2000: char. 16)

(57) Parietal posterolateral process slender and elongate (0), or short (1). (From Modesto and Rybczynski, 2000: char. 17)

(58) Parietals well exposed on the skull roof and relatively flat (0), parietals exposed in midline groove or channel (1), or narrow and crest-like, with postorbitals overlapping parietals extensively (2). (New)

(59) Orientation of the temporal portion of the postorbital: relatively flat, so that most of the exterior surface of the bone faces dorsally (0), close to vertical, so that most of the exterior surface of the bone faces laterally (1), or bi-planar, with approximately equally sized dorsal and lateral surfaces that are close to perpendicular (2). (New)

(60) Fossa on the ventral surface of the intertemporal bar formed by the postorbital and parietal large (0), reduced (1), or absent (2). (From Angielczyk and Kurkin, 2003a: char. 53)

(61) Pineal foramen surrounded by a thin, smooth, chimney-like boss (0), flush or nearly flush with dorsal surface of skull (1), surrounded by a strong, often rugose boss (2), surrounded by a boss but with pineal canal angled anteriorly (3), or absent (4). (Modified from Angielczyk and Kurkin, 2003a: char. 26)

(62) Interparietal does not contribute to intertemporal skull roof (0), makes a small contribution to intertemporal skull roof (1), or makes a large contribution to intertemporal

skull roof (2). (Modified from Angielczyk and Kurkin, 2003a: char. 48; Maisch 2001: char. 2; Vega-Dias et al., 2004: char. 15)

(63) Squamosal without (0) or with (1) lateral fossa for the origin of the lateral branch of the M. adductor mandibulae externus. (From Angielczyk and Kurkin, 2003a: char. 21)

(64) Distinct dorsolateral notch in squamosal below zygomatic arch in posterior view absent (0) or present (1). (Modified from Angielczyk and Kurkin, 2003a: char. 32)

(65) Squamosal posteroventral process short such that there is relatively extensive exposure of quadrate and quadratojugal in posterior view and the quadrate foramen (if present) is visible in posterior view) (0) or long such that nearly all of the quadrate and quadratojugal are covered by the squamosal in posterior view and the quadrate foramen (if present) is not visible in posterior view (1). (Modified from Modesto et al., 1999: char. 15)

(66) Zygomatic portion of the squamosal of nearly constant thickness (0), with posterior portion thickened and/or downturned (1), or with thin dorsoventral expansion posterior to postorbital bar (2). (Modified from Angielczyk and Kurkin, 2003a: char. 51)

(67) Zygomatic process of squamosal parasagittally deep (0), narrow and rod-like (1), or transversely expanded (2). (From Modesto et al., 1999: char. 12)

(68) Squamosal zygomatic process narrowly based and in line with occipital condyle (0) or widely based and flares posteriorly beyond occipital condyle (1). (From Modesto et al., 2003: char. 15)

(69) Sutural contact of squamosal and maxilla absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 34)

(70) Squamosal separated by tabular bone from supraoccipital (0) or contacts supraoccipital (1). (From Modesto et al., 1999: char. 20)

(71) Quadratojugal narrow and rod-like (0) or plate-like distally (1). (From Modesto et al., 1999: char. 17)

(72) Quadrate with a dorsal lobe that has a convex, rounded anterior edge that rests against quadrate ramus of pterygoid (0) or with a dorsal lobe that is developed into a distinct process that extends anteriorly along the quadrate ramus of the pterygoid and is triangular to sub-triangular in shape (1). (New)

(73) Vomers unfused (0) or fused (1). (From Angielczyk and Kurkin, 2003a: char. 11)

(74) Mid-ventral plate of vomers with an expanded, oval-shaped area posterior to junction with premaxilla (0) or without a notable expanded area posterior to junction with premaxilla (1). (From Angielczyk and Kurkin, 2003a: char. 12)

(75) Mid-ventral plate of vomers relatively wide in ventral view (0), more narrow and blade-like in ventral view (1). (Modified from Angielczyk and Kurkin, 2003a: char. 13)

(76) Trough on mid-ventral plate of vomers (i.e., ventral surface concave ventrally with raised edges): present (0) or absent (1). (New)

(77) Palatine dentition present (0) or absent (1). (From Modesto et al., 1999: char. 25)

(78) Palatal surface of the palatine without evidence of a keratinized covering (0), relatively smooth but with fine pitting and texturing suggestive of a keratinized covering (1), highly rugose and textured, suggesting a keratinized covering, with a raised posterior section and an anterior section that is smoother and flush with the secondary palate (2), or moderately rugose with pitting suggesting a keratinized covering for all of surface and flush with the secondary palate (3). (Modified from Angielczyk and Kurkin, 2003a: char. 22)

(79) Palatine widest at its approximate midpoint of length (0), widens posteriorly (1), widens anteriorly forming a palatine pad (2), or width relatively constant for entire length (3). (Modified from Rybczynski, 2000: char. 23; and Angielczyk, 2004: char. 30)

(80) Foramen on the palatal surface of the palatine absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 24)

(81) Lateral palatal foramen absent (0), present at level of the anterior, expanded palatal exposure of the palatines (1), present posterior and dorsal to the level of the anterior, expanded palatal exposure of the palatines (2). (From Angielczyk and Kurkin, 2003a: char. 35)

(82) Sutural contact of palatine and premaxilla absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 27)

(83) Ectopterygoid extends further posteriorly than palatine in palatal aspect (0), or does not extend further posteriorly than palatine in palatal aspect (1), or absent (2). (Modified from Modesto et al., 1999: char. 24)

(84) Pterygoids contact anteriorly (0) or separated by vomers (1). (Modified from Modesto et al., 1999: char. 29)

(85) Transverse flange of pterygoid projects laterally, free of posterior ramus (0), projects laterally, bound by posterior ramus (1), ventrally directed and relatively large, wing-like (2), or ventrally directed and low, keel-like (3). (Modified from Modesto et al., 2003: char. 31; and Rybczynski, 2000: char. 27)

(86) Contact of pterygoid and maxilla absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 46)

(87) Ventral surface of the median pterygoid plate depressed (0), smooth and flat (1), with a thin median ridge (2), with a wide, boss-like median ridge (3), or with a low rugose median swelling (4), or with a conical ventral projection (5). (Modified from Angielczyk and Kurkin, 2003a: char. 43)

(88) Pterygoid dentition present (0) or absent (1). (From Modesto et al., 1999: char. 26)

(89) Posterior edges of the interpterygoid vacuity located dorsal to the median pterygoid plate (0) or extended ventrally such that they are flush with the median pterygoid plate (1). (New)

(90) Development of the pila antotica as a rod-like process on the anterior edge of the periotic with a corresponding notch for the trigeminal never posterior to it (0), or pronounced pila antotica absent and trigeminal notch is a horizontal hollow in the anterior edge of the periotic (1). (From Surkov and Benton, 2004: char. 12)

(91) Contact between periotic and parietal absent (0) or present (1). (From Surkov and Benton, 2004: char. 15)

(92) Parasphenoid excluded from (0) or reaches (1) interpterygoid vacuity. (From Modesto et al., 1999: char. 32)

(93) Basisphenoid contribution to the basisphenoid-basioccipital tubera slopes anterodorsally at a shallow angle, forming elongate ridges on the basicranium that are close to the same height as the tubera for most of their length (0), slopes anterodorsally at a steeper angle such that the parabasisphenoid conribution is still somewhat ridge-like but the portion of the ridge on the anterior surface of the tuber is more vertically oriented (1), or is nearly vertical, forming very weak ridges if any (2). (From Angielczyk and Rubidge in press: char. 77)

(94) Stapedial facet of basisphenoid-basioccipital tuber exposed laterally (0), exposed ventrolaterally (1), or exposed ventrolaterally and open distally (2). (Modified from Angielczyk and Kurkin, 2003a: char. 42)

(95) Margin of fenestra ovalis formed predominantly by parabasisphenoid, with little or no contribution from

basioccipital (0), formed by approximately equal portions of parabasisphenoid and basioccipital (1), or formed predominantly by basioccipital, with little or no contribution by parabasisphenoid (2). (From Angielczyk, 2007: char. 54)

(96) Intertuberal ridge absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 49)

(97) Dorsal process on anterior end of epipterygoid footplate absent (0) or present (1). (From Angielczyk and Rubidge 2010: char. 73)

(98) Stapedial foramen present (0) or absent (1). (From Angielczyk and Kurkin, 2003a: char. 29)

(99) Dorsal process of the stapes present (0) or absent (1). (From Fröbisch, 2007: char. 72)

(100) Tabular contacts opisthotic (0) or separated from opisthotic by squamosal (1). (From Modesto et al., 1999: char. 21)

(101) Exoccipital and basioccipital contributions to the occipital condyle distinct (0) or co-ossified into a single unit (1). (New)

(102) Floccular fossa present (0) or absent (1). (From Angielczyk and Kurkin, 2003a: char. 41)

(103) Mandibular fenestra absent (0), present (1), or present but occluded by a thin sheet of the dentary (2). (Modified from Rubidge and Hopson, 1996: char. 5; and Modesto et al., 1999: char. 36)

(104) Jaw ramus straight in dorsal view, without strong lateral bends (0), or bends strongly laterally (1) posterior to symphysis. (New)

(105) Dentaries sutured (0) or fused (1) at symphysis. (From Modesto et al., 1999: char. 33)

(106) Teeth present on dorsal surface of dentaries (0), medially displaced, sometimes on a swelling or shelf (1), or absent (2). (From Angielczyk and Kurkin, 2003a: char. 10)

(107) Fine serrations on dentary teeth present (0), serrations absent (1), or coarse serrations present (2). (Modified from Modesto et al., 1999: char. 3)

(108) Denticulated cingulum on dentary teeth absent (0) or present (1). (Modified from Modesto et al., 1999: char. 4)

(109) Symphyseal region of lower jaw smoothly rounded and at same level as rest of dentary ramus in lateral view (0), with an upturned margin that is raised above the level of the dorsal surface of the jaw rami and has a scooped-out depression on its posterior surface (1), drawn into a sharp, spiky beak (2), or shovel-shaped with a rounded or squared-off edge and a weak depression on its posterior surface (3). (From Angielczyk and Kurkin, 2003a: char. 18)

(110) Dentary table absent (0) or present (1). (From Angielczyk and Rubidge, in press: char. 15)

(111) Posterior dentary sulcus absent (0), present but does not extend past dentary teeth (if present) (1), present and extends past dentary teeth (if present), but is relatively wide and shallow (2), or present, extends past dentary teeth (if present) and is narrower and deeper (3). (From Angielczyk and Rubidge, in press: char. 16)

(112) Tall, dorsally convex cutting blade on medial edge of dorsal surface of dentary absent (0) or present (1). (From Angielczyk and Rubidge, in press: char. 78).

(113) Lateral dentary shelf absent (0), present but relatively small (1), present and well developed (2). (Modified from Fröbisch and Reisz, 2008: char. 82)

(114) Anterodorsal edge of lateral dentary shelf relatively flat (0), with a groove (1), or developed into a rounded swelling (2). (New)

(115) Splenial symphysis unfused (0) or fused (1). (From Sidor, 2001: char. 26)

(116) Spenial contribution to dentary symphysis: anterior process on splenial present in ventral view (0) or absent (1). (New)

(117) Coronoid bone present (0), or absent (1). (From Modesto et al., 1999: char. 38)

(118) Angular with anterolateral trough for the posterior process of the dentary absent (0) or present (1) (New)

(119) Prearticular with (0) or without (1) lateral exposure posteriorly. (From Modesto et al., 1999: char. 39)

(120) Articular distinct (0) or at least partially fused to prearticular (1). (From Sidor, 2003: char. 48)

(121) Surangular vertical lamina present and lateral to articular (0) or absent (1). (From Modesto et al., 1999: char. 37)

(122) Jaw articulation permits strictly orthal closure (0) or permits parasagittal movement (1). (From Rybczynski, 2000: char. 37; and Angielczyk, 2004: char. 41)

(123) Enlarged dentary caniniform present (0) or absent (1). (New)

(124) Number of sacral vertebrae three (0), four (1), five (2), or six (3). (From Angielczyk and Kurkin, 2003a: char. 36)

(125) Cleithrum absent (0) or present (1). (From Angielczyk and Kurkin, 2003a: char. 39)

(126) Acromion process: absent or very small (0) or present and well defined (1). (Modified from Sidor and Hopson, 1998: char. 134; and Vega-Dias et al., 2004: char. 27)

(127) Procoracoid foramen or notch entirely contained within the procoracoid (0) or formed by contributions of the procoracoid and scapula in lateral view (1). (From Angielczyk, 2007: char. 66)

(128) Procoracoid does not participate in formation of glenoid (0) or participates in formation of glenoid (1). (From Angielczyk, 2007: char. 67)

(129) Proximal articular surface of humerus formed by a slightly convex area on proximal surface of the bone without much expansion onto the dorsal surface (0), somewhat expanded with some encroachment onto the dorsal surface (1), or strongly developed and set off from rest of humerus by a weak neck (2). (From Angielczyk and Kurkin, 2003a: char. 30)

(130) Insertion of M. subcoracoscapularis on humerus a rounded, rugose area on proximal end of humerus (0), large elongate process (1), or short, pinna-like process (2). (Modified from Angielczyk, 2007: char. 58)

(131) Insertion of M. latissimus dorsi at rugose tuberosity on the posteroventral surface of humerus (0) or extended into a dorsoventrally flattened pinna-like process (1). (From Angielczyk and Kurkin, 2003a: char. 50)

(132) Ectepicondylar foramen on humerus present (0) or absent (1). (From Angielczyk and Kurkin, 2003a: char. 38)

(133) Radial and ulnar condyle continuous (0) or well ossified and separate (1) on ventral surface of humerus. (From Surkov et al., 2005: char. 12)

(134) Dorsal edge of ilium: unnotched (0) or notched (1). (New)

(135) Ulna with small olecranon process that does not extend far past the articular surface for the humerus (0), or with a large olecranon process that extends well past the articular surface for the humerus (1). (Angielczyk, 2007: char. 61)

(136) Pubic plate is significantly expanded anteroposteriorly, such that its length is comparable to that of ischium (0) or anteroposteriorly short, so that it is much shorter than ischium (1). (New)

(137) Distinct cranial process on anterior end of pubis absent (0) or present (1). (New)

(138) Proximal articular surface of the femur present as a weak swelling that is mostly limited to the proximal surface of the bone (0) or present as a more rounded, hemispherical swelling that has some encroachment on the anterior

surface of the femur (1). (Modified from Angielczyk and Kurkin, 2003a: char. 31)

(139) Insertion of M. iliofemoralis present as a low rugosity on the dorsolateral portion of the femur (0), developed into a distinct crest that extends down part of the lateral surface of the femur (1) or a lateral crest that is split into a distinct first trochanter and third trochanter (2). (Modified from Angielczyk and Kurkin, 2003a: char. 52; and Govender and Yates, 2009: char. 85)

(140) Distal carpal 5: present as a distinct element (0), not present as a distinct element (1). (Modified from Sidor and Hopson, 1998: char. 151)

(141) Greatly enlarged vascular channels present (1) or absent (0). (From Angielczyk, 2007: char. 74)

(142) Curved ridge that follows the profile of the symphysis present on the edge between the anterior and lateral surfaces of the dentary absent (0) or present (1). (New)

(143) Mediolateral flattening and anteroposterior expansion of postorbital bar for most or all of its length absent (0) or present (1). (New)

(144) Occipital condyle round to subspherical in posterior view (0) or distinctly tri-radiate (1) in posterior view. (New)

(145) Pubic plate is significantly expanded ventrally such that it is nearly the same height as ischium (0) or reduced ventrally such that it is shorter than ischium (1). (Modified from Surkov et al., 2005: char. 14)

(146) Postorbitals extend the entire length of intertemporal bar (0) or do not extend the entire length of intertemporal bar, such that the posterior portion of the bar is formed only by the parietals (1). (Modified from Maisch, 2001: char. 1; and Vega-Dias et al., 2004: char. 13)

(147) Circular central depression or fossa on the occipital condyle between the exoccipitals and basioccipital present (0) or absent (1). (New)

(148) Lateral dentary shelf relatively thick, with distinct dorsal and ventral surfaces above the mandibular fenestra (0) or a thin ventrolaterally directed sheet that forms the dorsal margin of the mandibular fenestra (1). (New)

(149) Anterior and distal edges of deltopectoral crest close to perpendicular (0) or very obtuse (1) (Modified from Govender and Yates, 2009: char. 78).

(150) Converging ventral keels on posterior portion of anterior pterygoid rami absent (0) or present (1). (New)

(151) Lacrimal does not contact septomaxilla (0) or does contact septomaxilla (1). (From Vega-Dias et al., 2004: char. 9).

(152) Distinct lateral caniniform buttress absent (0), present (1), or present with posteroventral furrow (2). (From Damiani et al., 2007: char. 25)

(153) Posterior process of the premaxilla with a non-bifurcated posterior tip (0) or with a bifurcated posterior tip (1). (New)

(154) Naso-frontal suture relatively straight, interdigitated, or gently bowed (0), with a distinct anterior process (1), or with a distinct posterior process (2). (Modified from Vega-Dias et al., 2004: char. 7)

(155) Nasals with a long median suture that separates the premaxilla from the frontals (0) or with a short median suture and frontals and premaxilla in close proximity (1) (Modified from Vega-Dias et al., 2004: char. 4)

(156) Snout dorsoventrally shallow (0) or dorsoventrally deepened (1). (New)

(157) Oblique ridge on lateral side of zygomatic arch giving triangular cross-section and overhanging a weak groove present (1) or absent (0). (New)

(158) Reflected lamina of angular closely approaches or touches articular (0) or widely separated from articular (1). (From Maisch, 2001: char. 28)

(159) Anterior edge of scapula extended laterally to form a strong crest (1) or not (0). (Modified from Vega-Dias et al., 2004: char. 28)

(160) Origin of triceps on posterior surface of scapula relatively low (0) or developed into a prominent posterior projection (1). (Modified from Vega-Dias et al., 2004: char. 26)

(161) Number of sternal bosses: 2 (0), 4(1). (From Vega-Dias et al., 2004: char. 32)

(162) Femoral head continuous with the dorsal margin of femur (0) or offset dorsally from dorsal margin (1). (Modified from Govender and Yates, 2009: char. 84)

(163) Labial fossa surrounded by maxilla, jugal, and palatine absent (0) or present (1). (From Angielczyk, 2001: char. 19; Angielczyk and Kurkin 2003a: char. 19)

CODINGS USED IN PHYLOGENETIC ANALYSIS

Continuous Codings

Biseridens
? ? ? 1.032 ? ? ? ? ? 11.0 ? ? 0.956 ? ? ? ? ? ? ?

Anomocephalus
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Otsheria
0.381 10.95 0.231 ? 0.512 0.181 5.3 0.108 5.893 15.5 0.86 ? ? ? ? ? ? ? ? ?

Ulemica
0.47 10.903 0.125 1.06 0.407 0.216 4.9 ? 5.922 15.4 1.098 0.294 0.939 1.135 ? ? ? ? ? ?

Suminia
0.352 10.455 0.205 ? 0.225 0.198 5.0 0.09 5.802 11.6 0.902 0.395 0.842 1.094 0.558 0.296 0.13 0.557 0.758 0.0

Patranomodon
0.29 11.029 0.228 0.914 0.272 0.202 6.0 0.043 ? 13.7 0.744 0.476 1.25 1.059 ? ? ? ? ? 0.0

Galeops
0.339 10.384 0.18 ? 0.327 0.136 4.1 ? 5.832 ? ? 0.489 0.831 0.968 0.646 0.351 0.181 ? ? ?

Galepus
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0.149 ? ? 0.0

Galechrius
? ? ? ? ? ? ? ? ? ? ? 0.355 0.865 0.7 ? 0.401 0.206 ? ? 0.0

''*Eodicynodon*'' *oelofseni*
0.351 ? ? 0.968 0.435 ? ? ? ? 12.0 ? 0.259 0.708 ? ? ? ? ? ? ?

Eodicynodon oosthuizeni
0.321 10.521 0.24 0.909 0.525 0.143 9.1 0.168 5.876 9.0 0.839 0.242 0.686 1.026 0.454 0.473 0.242 0.686 1.143 0.0

Colobodectes
0.203 10.177 0.195 ? 0.52 0.149 6.6 0.206 5.852 ? 0.948 ? ? ? ? ? ? ? ? ?

Lanthanostegus
? ? ? 0.661 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Chelydontops
0.25 9.373 0.152 ? 0.546 0.108 6.4 ? 5.945 11.3 ? 0.155 0.758 0.736 ? ? ? ? ? ?

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Eosimops
0.19 9.311 0.238 0.746 0.519 0.123 8.7 0.175
5.913 11.4 0.83 0.402 0.803 0.904 0.633 0.466
0.26 ? ? 0.0

Prosictodon
0.198 9.78 0.156 ? 0.548 0.09 7.3 0.131 5.876
7.6 0.821 ? 0.834 0.637 ? ? ? ? ? 0.0

Diictodon
0.239 9.375 0.189 0.611 0.545 0.134 7.7 0.212
5.881 10.4 0.89 0.23 0.754 0.883 0.424 0.49
0.273 0.748 1.525 0.0

Robertia
0.238 9.508 0.202 0.717 0.56 0.105 8.3 0.198
5.895 9.8 0.852 0.14 0.647 0.848 0.487 0.504
0.228 ? ? 0.0

Pristerodon
0.222 9.481 0.172 1.009 0.586 0.116 9.9 0.207
5.85 10.7 0.815 0.184 0.714 0.917 0.561 0.447
? 0.348 0.727 0.0

Endothiodon
0.314 9.687 0.384 0.275 0.588 0.11 8.9 0.147
6.051 7.3 0.96 0.405 0.816 0.745 0.536 0.509
0.431 0.296 0.818 0.0

Emydops
0.23 9.554 0.202 0.893 0.543 0.116 9.8 0.179
5.802 9.0 0.843 0.348 0.706 0.933 0.626 0.42
0.23 0.946 1.752 0.0

Dicynodontoides
0.266 9.726 0.227 0.759 0.555 0.083 8.4 0.175
5.969 11.55 0.882 ? 0.725 0.917 0.304 0.529 ?
0.143 0.81 0.403

Kombuisia
0.193 9.645 0.202 0.4 0.555 0.195 ? ? 5.866 ?
0.746 ? 0.684 ? ? ? ? ? ? ?

Myosaurus
0.251 9.725 0.259 0.955 0.474 0.085 9.15 0.208
5.771 9.05 0.858 0.348 0.958 0.942 0.586 ? ? ?
? ?

Cistecephalus
0.265 9.99 0.278 1.143 0.528 0.118 9.7 0.0
5.861 9.2 0.873 0.4 0.687 0.784 0.46 0.412
0.317 0.618 1.629 0.0

Cistecephaloides
0.311 10.305 0.425 1.319 0.372 0.194 ? ? 5.835
12.5 0.632 0.346 0.796 0.914 ? ? ? ? ? ?

Kawingasaurus
0.306 9.933 0.329 1.429 0.399 0.135 10.55 ?
5.77 10.0 0.844 0.286 ? 0.964 0.298 0.419 ? ?
? ?

Rhachiocephalus
0.318 9.114 0.264 0.704 0.592 0.091 8.65 0.14
6.097 12.6 0.975 0.145 0.742 0.778 0.501 0.506
? ? ? ?

Kitchinganomodon
0.323 9.708 0.322 0.743 0.567 0.114 7.7 0.074
6.112 11.7 0.919 0.156 0.818 0.736 ? 0.466 ? ?
? ?

Oudenodon bainii
0.282 9.221 0.171 0.853 0.604 0.09 8.3 0.137
5.995 11.3 0.863 0.274 0.799 0.743 0.61 0.495
0.365 0.636 0.938 0.376

Tropidostoma
0.291 8.945 0.198 0.878 0.579 0.095 8.35 0.131
5.977 12.4 0.853 0.217 0.743 0.735 0.552 0.499
? 0.45 1.3 0.293

Australobarbarus
0.338 9.822 0.184 0.68 0.536 0.11 6.1 0.16
5.974 13.35 0.895 0.256 0.745 0.75 ? ? ? ? ? ?

Odontocyclops
0.37 9.807 0.234 0.964 0.594 0.097 10.3 0.116
6.09 12.55 0.933 0.221 0.778 0.784 0.609 0.524
0.386 0.385 1.0 0.469

Idelesaurus
0.367 10.118 0.175 1.022 0.5 0.107 8.25 0.173
6.006 13.45 0.969 0.193 0.693 0.762 ? ? ? ? ?
?

Aulacephalodon
0.3 9.274 0.326 0.852 0.586 0.118 6.6 0.124
6.069 13.65 0.82 0.194 0.755 0.781 0.55 0.526
0.345 1.024 1.195 0.395

Pelanomodon
0.293 9.386 0.301 0.885 0.574 0.105 9.6 0.153
6.0 12.0 0.81 ? 1.038 0.879 ? ? ? ? ? ?

Geikia locusticeps
0.263 9.374 0.281 0.88 0.545 0.098 9.4 0.141
5.96 13.9 0.761 0.205 0.818 0.848 ? ? ? ? ? ?

Geikia elginensis
0.366 ? 0.521 0.846 0.529 ? ? ? ? 13.1 0.829
0.212 0.9 0.987 ? ? ? ? ? ?

Elph
0.279 ? 0.186 0.64 0.544 0.157 8.9 ? 5.879
12.95 0.914 ? 0.781 ? ? ? ? ? ? ?

Interpresosaurus
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Katumbia
0.18 9.927 0.22 0.527 0.541 0.11 9.4 0.132
5.942 14.4 ? ? 0.833 0.822 ? ? ? ? ? ?

Delectosaurus
0.369 9.798 0.258 0.702 0.546 0.119 7.8 0.13
5.952 14.7 0.985 ? ? ? ? ? ? ? ? ?

Dicynodon lacerticeps
0.316 9.864 0.236 0.621 0.529 0.115 7.5 0.117
5.974 12.0 0.916 0.178 0.771 0.752 ? ? ? ? ? ?

Dicynodon huenei
0.304 9.79 0.248 0.567 0.56 0.108 8.3 0.111
6.047 11.55 0.976 0.206 0.756 0.818 0.538
0.573 0.317 0.667 1.4 0.374

Daptocephalus leoniceps
0.269 9.235 0.231 0.564 0.56 0.118 6.5 0.107
6.071 ? 0.858 0.23 0.764 0.751 ? 0.545 ? ?
2.143 ?

Daqingshanodon limbus
0.282 9.34 0.26 0.619 0.442 0.08 ? 0.189 5.863
10.3 0.808 0.212 0.677 0.819 ? ? ? ? ? ?
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Dinanomodon gilli
0.344 9.781 0.21 0.407 0.608 0.119 7.1 0.11
6.084 9.9 1.046 0.186 ? 0.724 ? ? ? ? ? ?

Peramodon amalitzkii
0.272 ? 0.224 0.563 0.553 ? ? ? ? 9.5 0.839
0.167 0.676 0.68 0.463 ? ? ? ? ?

Vivaxosaurus trautscholdi
0.361 10.247 0.226 0.667 0.478 0.118 7.9 0.111
6.002 13.9 1.023 0.203 0.702 0.731 0.317 0.544
? ? ? ?

Jimusaria sinkiangensis
0.307 ? 0.278 0.672 0.767 0.089 7.2 0.098 ?
8.9 0.992 0.251 ? 0.699 ? ? ? ? ? ?

Sintocephalus alticeps
0.354 9.399 0.244 0.516 0.522 0.124 6.5 0.132
5.979 ? 1.022 ? ? ? ? ? ? ? ? ?

Turfanodon bogdaensis
? ? ? 0.588 ? ? ? ? ? 10.3 0.895 ? ? ? ? ? ? ?
? ?

Keyseria benjamini
0.244 ? 0.159 1.034 0.605 0.083 6.3 ? 5.961
9.0 0.831 ? ? ? ? ? ? ? ? ?

Gordonia traquairi
0.239 ? 0.139 0.65 0.585 ? ? ? ? ? 0.924 0.188
? 0.773 0.543 0.49 0.144 ? ? ?

Euptychognathus bathyrhynchus
0.327 9.663 0.13 0.562 0.56 0.091 6.5 0.084
6.015 10.25 0.792 ? 0.79 0.815 ? ? ? ? ? ?

Syops vanhoepeni
? ? ? 0.484 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Kwazulusaurus
0.287 10.349 0.243 0.806 0.342 0.168 9.2 0.078
5.929 10.7 0.888 ? ? ? ? ? ? ? ? ?

TSK 2
0.385 9.866 0.24 0.321 ? 0.135 ? 0.124 5.947 ?
0.997 ? ? ? ? ? ? ? ? ?

Lystrosaurus hedini
0.336 10.203 0.433 0.687 0.398 0.167 9.2 0.08
5.927 11.2 0.693 0.28 0.651 0.792 ? ? ? ? ? ?

Lystrosaurus maccaigi
0.263 9.931 0.341 0.656 0.325 0.159 9.0 0.087
6.027 10.9 0.805 0.354 0.711 0.706 ? 0.526
0.54 ? ? 0.389

Lystrosaurus curvatus
0.292 10.088 0.382 0.613 0.431 0.159 7.05
0.084 5.939 8.8 0.871 ? 0.767 0.643 0.466
0.479 0.516 0.943 1.577 0.322

Lystrosaurus declivis
0.327 10.285 0.408 0.708 0.414 0.155 8.85
0.105 5.947 9.95 0.838 0.348 0.756 0.719 0.418
0.459 0.466 1.0 1.733 0.341

Lystrosaurus murrayi
0.292 10.297 0.432 0.672 0.463 0.176 8.35
0.104 5.916 12.55 0.804 0.296 0.802 0.751
0.475 0.459 0.447 1.06 1.845 0.392

Kannemeyeria simocephala
0.425 10.584 0.402 0.272 0.527 0.149 9.85
0.071 6.072 13.6 1.151 0.179 0.826 0.671 0.63
0.557 0.34 ? 1.261 0.359

Sinokannemeyeria
0.439 10.469 0.488 0.57 0.393 0.161 5.9 0.109
6.106 ? 0.918 0.243 0.549 0.385 0.494 0.489
0.556 0.523 1.365 0.408

Dolichuranus
0.412 10.467 0.347 0.28 0.485 0.133 7.45 0.091
6.079 10.7 0.959 0.192 0.756 0.542 ? 0.536 ? ?
? 0.425

Parakannemeyeria
0.442 9.649 0.362 0.367 0.357 0.122 7.5 0.104
6.106 12.4 0.923 0.166 0.79 0.515 0.467 0.52
0.48 0.6 2.105 0.4

Xiyukannemeyeria 0.286 10.027 0.413 0.46 0.433
0.168 8.45 0.086 6.042 8.9 0.795 0.32 ? 0.667
? ? ? ? ? ?

Tetragonias
0.35 9.992 0.354 0.233 0.574 0.125 6.8 0.088
6.005 10.4 1.004 0.205 0.858 0.796 0.447 0.481
0.3 0.674 1.825 0.286

Shansiodon
0.315 9.78 0.338 0.164 0.52 0.12 7.2 0.1 5.968
9.8 1.116 0.286 0.821 0.84 0.575 0.479 ? 0.784
1.409 0.363

Vinceria
0.267 10.552 0.352 0.201 0.49 0.137 7.0 0.153
5.993 11.25 0.983 ? ? ? ? ? ? ? ? ?

Rhinodicynodon
0.304 9.174 0.253 0.5 0.523 0.1 ? ? 5.982 10.1
0.879 0.24 0.875 0.734 ? ? ? ? ? ?

Angonisaurus
0.339 10.206 0.514 0.667 0.572 0.19 6.6 0.06
6.037 10.0 1.012 0.143 0.785 0.722 ? 0.524 ?
0.579 2.274 ?

Dinodontosaurus
0.4 10.154 0.347 0.231 0.465 0.137 7.4 0.074
6.046 10.4 0.937 0.191 0.85 0.587 0.398 0.51
0.423 0.667 1.739 0.305

Stahleckeria
0.489 10.284 0.489 0.726 0.49 ? ? ? 6.109 8.65
0.953 0.238 0.857 0.897 0.442 0.53 ? 0.346
1.962 0.447

Jachaleria
0.392 10.269 0.393 0.199 0.379 0.161 4.0 0.084
6.103 ? 0.766 ? 0.822 0.766 0.427 ? 0.529 ?
0.791 0.434

Ischigualastia
0.499 10.023 0.403 0.291 0.468 0.141 5.65
0.064 6.133 ? 1.03 ? 0.9 0.841 0.41 0.577
0.561 ? 0.96 0.412

Rabidosaurus
0.464 ? ? 0.268 0.607 ? ? ? ? ? ? ? ? ? ? ? ?
? ? ?

Rhadiodromus
0.509 10.023 0.403 0.285 0.574 0.122 6.9 0.088
6.076 10.8 1.085 ? ? ? ? ? 0.604 ? ? ?

Wadiasaurus
0.423 ? 0.337 0.539 0.506 0.218 ? ? 6.065 10.6
1.052 0.344 0.9 0.81 0.607 0.563 0.45 0.471
1.039 0.417

Rechnisaurus
? 0.436 0.154 ? 0.14 9.9 ? 6.066 ? ? ? ? ? ? ?
? ? ? ?

Kannemeyeria lophorhina
0.361 10.401 ? ? ? 0.149 ? 0.063 6.078 ? ?
0.077 0.786 0.542 ? ? ? ? ? ?

Sangusaurus
0.339 ? 0.447 0.618 ? ? ? ? 6.064 ? ? ? ? ? ?
? ? 0.676 2.22 0.311

Uralokannemeyeria
0.49 ? 0.407 0.526 0.454 0.147 ? 0.091 ? 11.9
1.154 ? ? ? ? ? ? 0.819 1.193 ?

Placerias
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0.49 0.499 ? ? ?

Moghreberia
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?

Basilodon woodwardi
0.304 9.393 0.207 0.7 0.492 0.129 6.1 0.133
5.971 11.1 0.802 ? ? ? ? ? ? ? ? ?

Discrete-State Codings

Biseridens
0000200000001001?000100???00001000020010200000
0100??00000010000000?01??????0???00?0010100000
0?00001???0??????????????????010?00??00?00000?
?????0

Anomocephalus
?????0????0??0?1??001?0????0?0??0?????????0??0
0?0?1???????????????????????????????1??0100???
0?????????????????????????????0????????????00?
?????

Otsheria
00002010000?1001?100?00????000000002?01?000000
1101??11??1000011000011???0000???11???????????
??????????????????????????????0??0???00?00000?
????0

Ulemica
00002011000?1001?000100???0000100002001?001000
110?0011001130011010011??10010?10?101010110000
10(0 1)00010011??????????????????00??000?00?00
0000????0

Suminia
0000201100001001?100200????000000002101?001000
1?01001100?1302110100110?1000001010?1000210000
1000000001100000000000000001?00100?0010?010000
00?00

Patranomodon
0000?011?0002000?100100????0000000101000100000
10000000001010?01000011??00000?1010?10?0100000
0???00000010?????????0???000?001?00??10?000001
???01

Galeops
0000201100002000?100100????1000000??1000??1000
110?0100001?10?01000110?1?1?????????1000??0000
10?11100011?000000010?0?????000????00?0?0??001
01???

Galepus
?0002?1???0??0????????0?????????0?????????????
?????????????????????????????????????0?0100000
??????????1???1?0000??00?00???0?0???1??????0??
???0?

Galechrius
00?0?01?0?0??000?1001?0????1?0????????????????
??0?????????????????????????????????10?0100??0
?????0????1??00??0?00?00?000?0??0???1?0?0??0?1
00?0?

``*Eodicynodon*'' *oelofseni*
?????0110000200001001?0?????0000001??010001010
20????00001120???12?310??000?0?????01011101000
101?1???111??????????????????001?000?1?????001
?????

Eodicynodon oosthuizeni
0001021100002000020010100001000000101010101110
2101100000112010112031001000000111101010101100
201011111110010000011001000?100100000100010000
00?00

Colobodectes
01010211000020000200101000010001001110001?1110
2101??0001112010112031001000100??1????????????
??????????????????????????????0??0???10001000?
????0

Lanthanostegus
???????1???0?????200?1????0?00100011?01020???0
0?0???0???11201?1120310?100?10????????????????
??????????????????????????????1??0??????????0?
????0

Chelydontops
10012211000020000211?11000010010?011101020111?
?1?11?11001120101130310010002001?11?1011201120
10??111?111??????????????????0?0?000?1000?00?1
????0

Eosimops
1111021100002000021011120011001000111010201110
211110101111201011203100?0001001?11?1011??3011
100011?11110111?00001001000??01100000100100001
00?00

Prosictodon
1111021100002000011011?20011?0100011120???1110
21111010001120101120210??0001001111?1011??1111
10?01???111??????????????????001?000?10????001
????0

Diictodon
1111021100002000022??1120011001000111200(1 2)0
11102111101111112010113021000000200111101012??
1111101011111111111100000001000?0000000001001(
0 1)(0 1)00100?00

Robertia
1111021100002000021011120011001000111010201110
211110100011201011302100?0001001?1101011101111
10?01111111011?000000?0?000??001?0000100100001
00?00

Pristerodon

```
1101221100002000021011100001001000111010111110
2111101000112021112021001000200111101011201120
201011111112110000010001000????1?0000100000001
10?00
```

Endothiodon

```
10002111000020100111200????20100111111112?1110
2101101000112021113031000000200 1?1101011202120
101011111111010?0001000??00?0001?000010?0??001
00?00
```

Emydops

```
1011121100002000020011111011000000111010101010
21111011111201111(2 3)021000001200101101011(1
2)030202110111111?11??00000?0??00??001?00000
00000001?0?00
```

Dicynodontoides

```
1012021100012000022??1111001000100411200101110
2101101000112011113021000001200101102012??3000
2110111111110110120010?1011101011000000000001
10000
```

Kombuisia

```
1012121100012?00012??011101100010011021?(1 4)0
1?102?011?1???1120111?30?1??1001200101 0?2012??
3100201?1110111??????????????????101?100?00000
0001????0
```

Myosaurus

```
1002121100012000012??1111011000100120020101010
2101101111102111112021001001200111101012??3000
21??11??111011101010?0???????101?0001100020001
10??0
```

Cistecephalus

```
1012121100012010012??11110110(0 1)11(0 1)00210
2011101020111011011121111112021?00?0120001?1?11
12??302021101111111010012110101101010001000000
0000000110?10
```

Cistecephaloides

```
1002121100012010012??0111001000100021020111010
20011011011?2?11113??1????0110?1??1?1112??3020
211?1111111??????????????????001?000?000000001
????0
```

Kawingasaurus

```
1002121100012010012??01110000001000210204?1010
201?101101112111113011????0110?0??101012???000
10111?11111?100?21001?1???????01?000000002000?
10??0
```

Rhachiocephalus

```
1202221110002000012??1100102010010111200301110
2111101111122011113021000012200111101112??1130
1010111111?01(0 1)110110?0??11?1001?000011000
000101?00
```

Kitchinganomodon

```
1202221110002000012??1100102010010111200311111
2111111101122011112031?0?0122011?11?1112??11?0
12???11?111?????10?10????????001?0010110000001
00??0
```

Oudenodon bainii

```
1202221110002000012??1100102001000111100111111
2111101111122011113021000012200111101112??1130
121011111112010010110001111?0001100101(0 1)101
000100000
```

Tropidostoma

```
1202221110002000021011100102001000111100111111
211110110012201111302100?012200111101111??1130
121?111111120100101100 0??11?0001?0010111010001
00?00
```

Australobarbarus

```
12022211100020000210?1100102001000111100111111
2111101111122010113121 0??0122011111?1111201130
121?11??111??????????????????001?001?1?10?0001
????0
```

Odontocyclops

```
1202221110002000022??1100102020000311100011111
211110111112201111302100?0122011?11?1112??1130
12??111?111201??10110001111??00110010111000001
00000
```

Idelesaurus

```
1202221110002000022??1100102010000112100101111
2111101100122011112021000002201??10?1112??1130
121?1111111??????????????????101?001?111010001
????1
```

Aulacephalodon

```
1202221111002000022??1100002120(0 1)1030101020
111121111011011220111130210000122(0 1)01111011
12??1130121111111112010010110001111?1001000101
1100000100101
```

Pelanomodon

```
1202221111002000012??1100102120110301010201111
211110111112201111312100?0122101111???????????
?????????1????????????????????01?00??11100000?
????1
```

Geikia locusticeps

```
1202221111002000012??1100102121110311100201011
2111101111122011113121000022210 1111?1112??1130
1010111111?010???????????????101?001?111000001
0???1
```

Geikia elginensis

```
1202221111002000012??1100112?21?10???100?01111
21??1?11111220?1?13?210?10??????????1012??1130
12??????111??????011?????????10??0?10??1001001
?????
```

Elph

```
1??2021100002010022??1100010001000111200101110
211110????1220111?3011?0001220???11?1112??1130
1211????11???????????????????001?001??0100000?
????0
```

Interpresosaurus

```
120??2110000201 0022??11000100010??1??21???????
??????1???1?20????????????????????????????????
??????????????????????????????????????010??0??
????0
```

Katumbia

```
12022211?000??10022??110001100100031120010111?
211?10111112201111312 10??01221111?0?1112??1130
1211????11???????????????????101?001?00000000?
????0
```

Delectosaurus

```
1202221100002100022??1100001001000211211101110
2111101111132011(1 2)1312110?01221???100??????
??????????????????????????????????01?00??10101
000?????1
```

Dicynodon lacerticeps
1202221100002000022??1100001011000211211101110
2111101111132011113021000022211111111112??1130
2211111111?????????????????101?001?1010(0 1)
0001????1

Dicynodon huenei
1202221100002000022??1100001011(0 1)0021121110
1111211110111113201111312100002221111111112??
11302211111111120101101100011111???011001010100
000100?01

Daptocephalus leoniceps
1202221100002000022??1100011011000211211101110
21111011111320111131111010122111111111112??1130
2211111111?????101100?11????10110111001010001
????1

Daqingshanodon limbus
1202221100002000022??110010200010031110010111?
2111101 1??1220111130210?00????????11?1112??1130
121?1111111?????????????????101?0?1?1?1000001
?????0

Dinanomodon gilli
1202221100002110122??1100001011000211211101110
2111101111132011113121 1??01221111111?1??????3?
12???11?11????????????????????101?0?1?00101(0 1
)002????0

Peramodon amalitzkii
1???????0000201002???11?00110010002112 1?101110
211?10??????????????13?21?0?0?221?11???111???1???
2211?11?11?31101?????????????????101?0?1??01010001
00???

Vivaxosaurus trautscholdi
1202221100002010022??1100001000000211111110110
211110110013 2011(1 2)1312110?0222(0 1)?1?11111
12??113022??1110111?0??110110?????????101?00111
010110010 0??1

Jimusaria sinkiangensis
120??2111000200002???1100001001000211211111110
211110????1?201?1130211010222111?1??1112??1130
221001 1?111?????????????????????10??0?1??02000001
????1

Sintocephalus alticeps
1202221100 0?2000022??1100000010000111111?1111?0
2?1????????13201111312 10??0?????????????????????
??????????1??????????????????????0??0????1001000?
?????

Turfanodon bogdaensis
12???211?000???0?22??1100011010 0?02112111111110
21?1???????13201?2131211??01221???111???????????
???????????????????????????????1?00??10101100?
?????

Keyseria benjamini
1202221100 0?2000022??110011200000011100?101110
211110 11??1220?11130210??01?210111 1???????????
??????????1??????????????????????01?00??00100000?
?????

Gordonia traquairi
1202?211000??000022??1100012001?0011121?1?1111
211?10?1??1?2????131?1???0??2??11???1112??1?30
22???1??111??1??10?1000????????01?0?10??1???001
00???

Euptychognathus bathyrhynchus
1202221110102000022??110001011 0000?112111?1110
21111011111320?1?13?210??022?11??11?1112??1130
221??????11??????????????????????101?001?1?10??101
?????

Syops vanhoepeni
1?????1?100?2000022??11001120 1?0?021?2111?????
????????????????????13?????????????????????1???1???
????????????????????????????????0???0?????10000??
?????

Kwazulusaurus
1202221110102000022??11000000 00?0001?101?101110
2111??11111?20?1213141 1??0222 1???11????????????
??????????????????????????????????01?0???00?01110?
?????

TSK 2
1202221110102000022??1100000011 0?011111?1???1?
?1?1??111113201111312100002221???11????????????
???????????????????????????????????1?00???11001??
?????

Lystrosaurus hedini
1202221111102000022??1100002010010211011101110
21111011111320112131411??022210??1111112??1130
22101101 11??1?????????????????101?001?011000101
????1

Lystrosaurus maccaigi
1202221111?2000022??11000100 11?102?101?101110
21111?11111320102131411??022210??11?1112??1130
22??11??1113?????0110?01?01?110110010011011101
???01

Lystrosaurus curvatus
1202221111102000022??1100012011010211011101110
21111011111320102131211000222 1???101111???????
2210?11?11??01??1011?10??01??101?0010111010101
00?01

Lystrosaurus declivis
1202221111102000022??1100012111010211011101110
21111011111320102131211000222101110111 12??1130
221011101111301??1011010 1111?1101100111101010 1
???01

Lystrosaurus murrayi
1202221111102000022??11000121100101110111011 10
21111011111320102131211?0022211111101112??1130
2210111011 1?0111101101 0?111?1101?001111100010 1
00?01

Kannemeyeria simocephala
1202221100002110022??0100003000111111212111110
21111011111320112131111110222 01??1111112??1130
22101111111301001011000111 1?110010010002020001
01001

Sinokannemeyeria
1202221100002120022??110000301011121121111101 0
21111111111?201?2131211??02220?111111112??1130
121??01?1112010?1211001??11??100?0010??1010001
0000?

Dolichuranus
1202221110002110022??110000301011011121211101 0
21111011111320101131211 0?02220???11?1112??1130
121?101?111?00??12010?1??12??100?001010200000 1
00?01

Parakannemeyeria
1202221110002020122??1100003010111211211111010
211110111113201?21311110?022201111111112??11?0
12??1?1?1113010010110001111??100100100120?0011
00?(0 1)1

Xiyukannemeyeria
120??211100?2020022??11000130101112112111?1010
211110111113201?2131211??02220?1110?1112??1???
121?1?1?111??1??121?000??11??100?00100120?0011
0??01

Tetragonias
1202221110002000022??1100012010100111212111010
21111011111320102131211010?2211111111112??1130
121010111112010012110001112??1011101000(1 2)00
001100011

Shansiodon
1202221110002000022??1100012011100111212111010
21111?????13201?2131?1?0?02220?111111112??1130
2210?0??111201??1211101??11??001?1010?010??011
00?11

Vinceria
12022211100?2000022??1100012010100111212111010
2111??11111?20??2131211??022?0?1111?1??2??????
????????111???????????????????01?1???0?200000?
????1

Rhinodicynodon
1202221110002000022??1100012011100111212101010
211110????1320?12131?1?0?022?????10?1112??1130
22??1???111?010010110001112??1011101??01010011
00?11

Angonisaurus
1202221110002?00112??110001?010110211011111010
2111??11111?20?1?131?110?02220???1111112??1130
1210101?1113?100?20100?11????1011101??01???001
00???

Dinodontosaurus
1202221110002010022??1100013010100111212111010
2111101111?200011311111?1022211???1111112??1130
1210101?1113010012010011112??10011010001010010
00001

Stahleckeria
1202021110002020112??1100003010111011011121010
21111011111320111131111110222111?1111112??1130
121011111113010012110011111??10010010001010000
10111

Jachaleria
1202221110002010112??1100013010110111212121010
21111111111320102131111?1022200??11??112??11?0
????????111200???????011111???00110??01101000?
0111?

Ischigualastia
1202221110002120112??1100003010111?11212121010
20111111111320??2131511?102220?1111?1112??1130
1?????1?1112001012010011111??100110?0001010000
10111

Rabidosaurus
1202221100002110022??110000301011121?01?1?111?
2111??????122010?13111???0?2??1??1?1??????????
???????????????????????????????0??0???0?0??0??
????1

Rhadiodromus
1202221110002010012??11000030101113112121?1010
2111??11111320?11131?1?1102220???11???????????
??????????????????????????????01?00???(0 1)201
000??????

Wadiasaurus
12022211000?2010012??110000?010?01?1101?101010
21?110????1?20??2131?1???02220???11?1112??1130
??????1?111201?012110011111???011???1?0?0??001
10011

Rechnisaurus
12022211100?2010022??110000301010111?2121?1??0
2?????????1?20?01131?1???02220????????????????
??????????????????????????????0??00???0?0000??
????1

Kannemeyeria lophorhina
1202221100002110122??0100003020101111212111110
21111?111113201?213111101022201??10?1112??1130
12??1010111?????12?100???????100?0011101020000
00??1

Sangusaurus
12022211100??010112??1100003010?0??1121211101?
?11??0????13201??13111???02221????111112???130
12????1?1112?????????0?1111??1001001???10??0?0
???1?

Uralokannemeyeria
12022211100?2??0122???10000??1?11121101?1?101?
21111011111?20???13?211??02220???11???????????
?????????1?2?????????0????????00?00??10????00?
?????

Placerias
1200221?0000?000022??1110003010111110011121012
211110???????????1??5111002220?111111112??1130
??10?1??111?01001?0101?1111?1000111?00?0?10001
1101?

Moghreberia
1?002211000??020022???1000030?01111100111210?2
21???01111132011??3??1??0?2220????1?1112??1130
1210???111?????????????????????0?111???20??000
?????

Basilodon woodwardi
1202221110002000022??1100002011000111110111110
21111011111320111131210??01221?1?11?1?1???????
22???????1???????????????????101?001??10000001
????1