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Chapter 7

Permian and Triassic Dicynodont (Therapsida: Anomodontia) Faunas of the Luangwa Basin, Zambia: Taxonomic Update and Implications for Dicynodont Biogeography and Biostratigraphy

Kenneth D. Angielczyk, Jean-Sébastien Steyer, Christian A. Sidor, Roger M. H. Smith, Robin L. Whatley, and Stephen Tolan

Abstract Dicynodont fossils were first collected in the Luangwa Basin, Zambia, in the 1920s, but limited detailed study and taxonomic uncertainty have obscured their biostratigraphic utility and their implications for topics such as dicynodont biogeography and the effects of the end-Permian extinction. Here we present a comprehensive taxonomic revision of the dicynodonts of the Luangwa Basin, taking into account specimens in all major museum collections and new material collected by our team in 2009. We recognize 14 dicynodont species from the Upper Permian Upper Madumabisa Mudstone: *Pristerodon mac-kayi*, *Endothiodon* sp., *Diictodon feliceps*, *Compsodon helmoedi*, *Emydops* sp., *Dicynodontoides* cf. *D. nowacki*, a new tusked cistecephalid, cf. *Katumbia parringtoni*,

Kitchinganomodon crassus, *Oudenodon bainii*, *Odontocyclops whaitsi*, *Dicynodon huenei*, *Syops vanhoepeni*, and a new lystrosaurid. Previous reports of *Lystrosaurus* in the basin appear to be in error. In addition, we found no significant partitioning of dicynodont taxa in the northern and southern parts of the basin, despite substantial differences in preservation, indicating the presence of a single faunal assemblage in the Upper Permian. The Madumabisa dicynodont assemblage is best correlated with the *Cistecephalus* Assemblage Zone of South Africa. The shared presence of *Dicynodon huenei* and possibly *Katumbia* in the Luangwa Basin and the Ruhuhu Basin of Tanzania suggests that the Tanzanian Usili Formation also can be correlated with the *Cistecephalus* zone. Interestingly, the Madumabisa assemblage from Zambia is more similar to the coeval assemblage from South Africa, despite its closer geographic proximity to Tanzania. The Karoo and Ruhuhu basins also include more endemic species in the Permian than the Luangwa Basin. The Middle Triassic Ntawere Formation preserves four dicynodont species (*Kannemeyeria lophorhinus*, “*Kannemeyeria*” *latirostris*, *Zambiasaurus submersus*, *Sangusaurus edentatus*), which occur at two stratigraphic levels. The lower Ntawere assemblage resembles that of the Omingonde Formation of Namibia in the presence of *Kannemeyeria lophorhinus* and potentially *Dolichuranus* (if “*K.*” *latirostris* represents this taxon). The upper Ntawere assemblage shares the genus *Sangusaurus* with that of the Manda beds of Tanzania and includes the endemic *Zambiasaurus*. Comparisons of these assemblages to the Omingonde and Manda suggest that both are best correlated with the *Cynognathus* C subzone. When combined with data on other tetrapod taxa, our revised dicynodont assemblages contribute to an emerging picture of broad faunal similarity in southern and eastern Africa during the Late Permian, and increasing differentiation between the South African and other Karoo basins following the end-Permian extinction.

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Keywords *Cistecephalus* Assemblage Zone • East Africa • Karoo Basins • Ntawere Formation • Upper Madumabisa Mudstone

Introduction

Dicynodonts number among the most successful Permian and Triassic nonmammalian synapsids in terms of their species richness, abundance, and stratigraphic distribution. The clade was also cosmopolitan, with dicynodont fossils having been discovered on every continent (King 1992; Rubidge 2005; Fröbisch 2009). However, the detail with which the dicynodont faunas from particular areas are known varies greatly depending on factors such as available outcrop area and the cumulative collecting effort expended by paleontologists. Thus, the Karoo Basin of South Africa, which has extensive fossiliferous exposures and a history of continuous paleontological research spanning over 150 years, has produced more than 15,000 cataloged dicynodont specimens (Nicolas and Rubidge 2009, 2010), making it by far the best window into the evolutionary history of the clade. However, even other well-studied areas, such as the fore-Ural region of Russia, have produced far fewer specimens (e.g., Ivakhnenko et al. 1997), and some geographically significant dicynodont records consist of very small samples (e.g., 10 specimens from Scotland: Cruickshank et al. 2005; five published specimens from Laos, one of which is lost: Battail 2009a, b; Steyer 2009). This unevenness in sampling obscures biogeographic and biostratigraphic patterns, and it makes it difficult to determine whether apparent absences of particular dicynodont taxa in a given area are real or artifactual. An extreme example can be found in the geographic distribution of *Diictodon feliceps*, which is known from South Africa, Zambia, and China, but not fossiliferous basins in between (Angielczyk and Sullivan 2008). Obviously there was a route that *D. feliceps* used to disperse between these widely separated areas, but was that route outside of areas where Permian tetrapod fossils were preserved, or would more intensive collecting in intermediate areas reveal novel geographic occurrences?

A related issue is the complex taxonomic history of dicynodonts. Over the course of the past four decades, much of dicynodont taxonomy, particularly for Permian taxa, has been extensively revised (e.g., Cox 1964; Keyser 1973a, b, 1975, 1993; Tollman et al. 1980; Cluver and Hotton 1981; King 1988; King and Rubidge 1993; Sullivan and Reisz 2005; Grine et al. 2006; Botha and Angielczyk 2007; Fröbisch and Reisz 2008; Angielczyk et al. 2009; Kammerer et al. 2011), greatly improving our knowledge of the clade's diversity. However, because the majority of

named dicynodont species are based on material from the Karoo Basin, most revisions have focused on South African taxa. Even when non-South African taxa have been included, it is often difficult to trace a particular valid name or synonym through the literature. If a particular name or reported occurrence has not been dealt with explicitly in a revision, it can be a daunting task to attempt to identify a specimen short of personally examining it. Many of the original reports of material from outside of South Africa consist of very brief descriptions of fragmentary specimens accompanied by figures that are little more than sketches (e.g., Haughton 1926, 1932; Boonstra 1938). The dicynodont faunas of the Luangwa Basin of Zambia exemplify many of these issues.

The first tetrapod fossils discovered in the Luangwa Basin were two fragmentary pieces of dicynodont postcrania (SAM-PK-7424, SAM-PK-7425) collected in 1925 by G. Prentice (Dixey 1937). The geologist F. Dixey made the first significant collections of fossils, mostly from the northern part of the basin, in 1928 and 1935 (Dixey 1937; Boonstra 1938) (Fig. 7.1a). Additional collecting in the northern part of the basin was carried out in 1960 and 1961 by the Geological Survey of Northern Rhodesia and the Bernard Price Institute for Palaeontological Research (Brink 1963; Drysdall and Kitching 1963; Kitching 1963), and by the British Museum (Natural History)—University of London Joint Palaeontological Expedition in 1963 (Attridge et al. 1964). A decade later, in 1972, members of the Geological Survey of Northern Rhodesia discovered additional localities in the central Luangwa Basin. As a direct result, fossil collections were made in 1974 in collaboration with the Oxford University Museum of Natural History (Kerr 1974; Kemp 1975). A short subsequent reconnaissance to the same area was made in 2000 by T. S. Kemp (Oxford University Museum of Natural History), J. G. Theime (former director of the Geological Survey of Zambia), and associates (T. S. Kemp, personal communication, 2009). Most recently, our team spent three weeks in July, 2009 working in both the northern and central parts of the basin.

To date, collecting efforts have resulted in several hundred specimens that are distributed among the Iziko: South African Museum (Prentice's and Dixey's collections), the Bernard Price Institute for Palaeontological Research (specimens from the 1960 and 1961 expeditions), The Livingstone Museum (a small number of specimens from the 1963 expedition), and The Natural History Museum (most specimens from the 1963 expedition); material from the 1974 expedition is currently housed at Oxford University but it and specimens from the 2009 expedition will be returned to the National Heritage Conservation Commission of Zambia. Much of this material is all but unstudied, and only a handful of papers focusing on dicynodonts from the

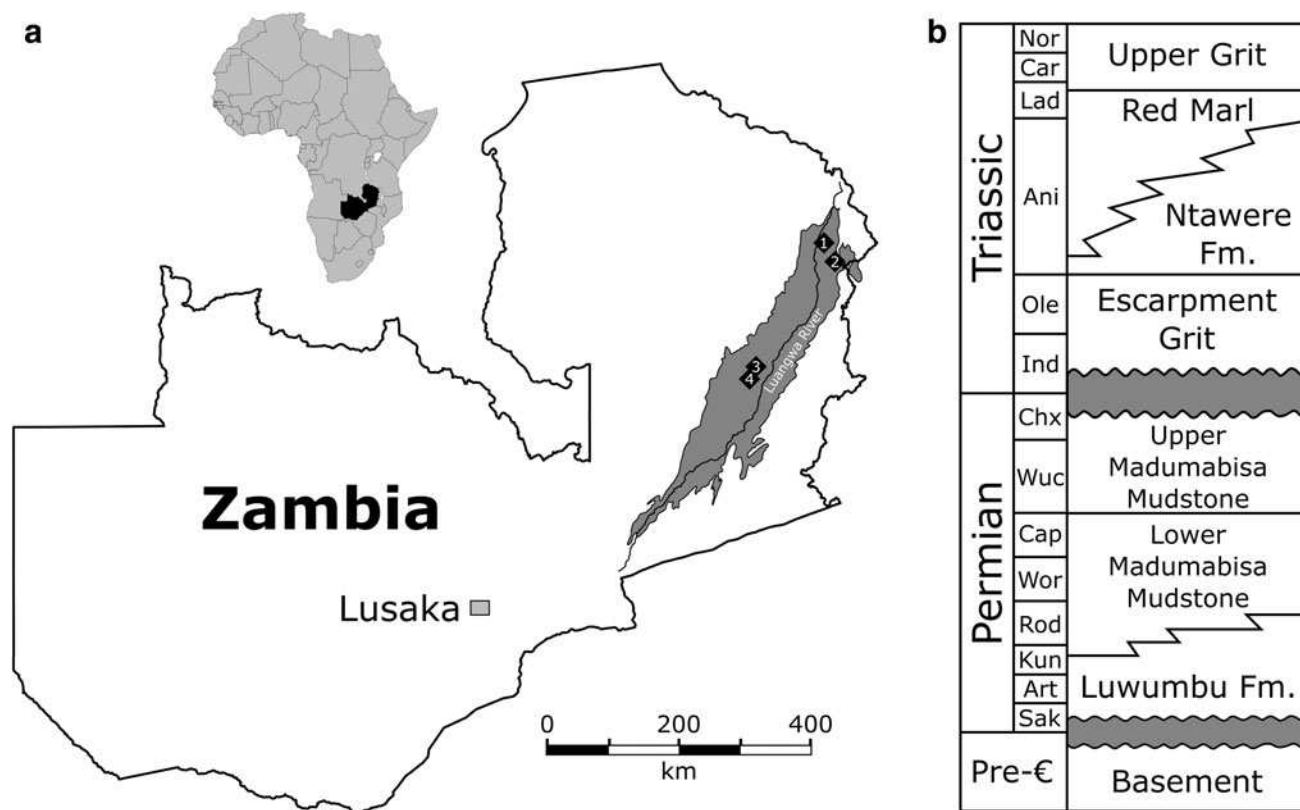


Fig. 7.1 **a** Map showing location of the Luangwa Basin and the approximate locations of the main areas in which vertebrate fossils have been collected; *inset* map shows the location of Zambia in Africa. *Area 1* corresponds to the northern Permian localities of Dixey (1937; Boonstra 1938), Drysdall and Kitching (1962, 1963), Kitching (1963), and Attridge et al. (1964). *Area 2* corresponds to the Triassic localities of Drysdall and Kitching (1962, 1963), Kitching (1963), and Attridge et al. (1964). *Area 3* corresponds to the localities of Kerr (1974) and Kemp (1975) in North Luangwa National Park. *Area 4* corresponds to

the localities of Kerr (1974) and Kemp (1975) in the Munyamadzi Game Management Area. Specimens were collected in all four of these areas by the 2009 expedition. **b** Generalized stratigraphy of the Luangwa Basin. Lithostratigraphy based on Banks et al. (1995). Correlations between lithostratigraphy and marine stages approximate and based on Nyambe and Utting (1997), Nyambe (1999), Cairncross (2001), and Catuneanu et al. (2005). Note that relative thicknesses of the marine stages are not scaled to their relative temporal durations

Luangwa Basin have been published (Boonstra 1938; Cox 1969; Crozier 1970; Keyser 1979; Keyser and Cruickshank 1979; King 1981; Gale 1988; King and Jenkins 1997; Angielczyk 2002), although some described particular specimens in great detail. Of the material that has been published, a considerable proportion has been included in taxonomic revisions, and in some cases multiple revisions (Keyser 1973c, 1975; Keyser and Cruickshank 1979; Angielczyk 2002; Renaut et al. 2003; Botha and Angielczyk 2007; Kammerer et al. 2011). There is also an unpublished report of at least one additional new taxon that has never been formally described (Freeman 1993). These facts make it difficult to compile accurate faunal lists for the Luangwa Basin, but such data are necessary if broader studies of dicynodont biogeography and biostratigraphy, and the end-Permian mass extinction, are to produce meaningful results.

Here we review the Permian and Triassic dicynodont faunas of the Luangwa Basin, based on our personal observations of most of the Zambian dicynodont specimens

in museum collections and supplemented with observations of dicynodont fossils in the field. Although the review uses up-to-date dicynodont taxonomy, we provide links between modern and older names, and provide justifications for our identifications and images of voucher specimens for each taxon. Finally, we discuss the biogeographic and biostratigraphic implications of the revised faunal lists.

Anatomical Abbreviations: Al, alveolus; Ect, ectepic-ondylar foramen; Dpc, deltopectoral crest; Nb, nasal boss; Pct, “postcanine” tooth; Pds, posterior dentary sulcus; Sq, squamosal.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York City, NY, USA; BP, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; CAMZM, University Museum of Zoology, Cambridge, UK; CGP, Council for Geosciences, Pretoria, South Africa; GPIT, Institut für Geowissenschaften, Tübingen, Germany; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; LM, Livingstone

Museum, Livingstone, Zambia; NHCC, National Heritage Conservation Commission, Lusaka, Zambia; NHMUK, Natural History Museum, London, UK; NMQR, National Museum, Bloemfontein, South Africa; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; RC, Rubidge Collection, Graaff-Reinet, South Africa; TSK, T. S. Kemp Collection, Oxford University, Oxford, UK.

Geological Context

Stratigraphy and Sedimentology

The Karoo basins of south-central Africa formed during the assembly and breakup of Pangaea under two distinct tectonic regimes sourced from the southern and northern margins of Gondwana. The southern tectonic regime, generated by subduction and orogenesis along the Panthalassan (paleo-Pacific) margin of Gondwana resulted in the formation of the Gondwanide mountain belt with a series of retroarc foreland basins. Subsidence and sedimentation in these basins was primarily controlled by flexural and dynamic loading of the crust (Catuneanu et al. 2005). The main Karoo Basin in South Africa is the best exposed of these foreland basins and contains the litho- and biostratigraphic reference sections for the Upper Carboniferous–Middle Jurassic Karoo Supergroup.

North of the main Karoo Basin, tectonic regimes were dominated by extensional or transtensional stresses that propagated southwards into the supercontinent from the Tethyan margin of Gondwana. The sedimentary fills of these rift basins show a pronounced similarity due to their similar structural history; the older Karoo deposits were laid down and preserved within the oldest graben structures, most of which occupy the deepest parts of the basins today. As the rifts expanded, younger sedimentary sequences progressively overstepped onto domino-style tilted horsts and younger grabens. Thus, almost continuous sedimentation took place within the deep parts of the rifts whereas the successions on the rift shoulders were interrupted by hiatuses and erosion, evidenced by unconformities and reduced sections (Tankard et al. 2009).

Climatic fluctuations also left a mark on the stratigraphic record, providing a common trend that can be identified in the sedimentary fill of most of the Karoo-aged basins formed under different tectonic regimes. The climate changed from cold to humid temperate and semi-arid during the Late Carboniferous–earliest Permian interval, to warmer and eventually hot with fluctuating precipitation from the Early Triassic through to Early Jurassic (Smith et al. 1993).

In Zambia, Karoo-aged sequences occur in the Luangwa, Luano and Zambezi rift basins. To date, tetrapod fossils

have been collected in large numbers only from the Luangwa Basin (Fig. 7.1a), although there is a report of fragmentary dinocephalian material from the Zambezi Basin (Gair 1959). The Luangwa Basin itself comprises two non-overlapping opposing half-graben separated by a transfer zone or accommodation zone that forms a structural high (Banks et al. 1995). The sub-basins are structurally and depositionally similar, and preserve essentially the same stratigraphic sequence (Fig. 7.1b). Tetrapod fossils occur in the Upper Permian Madumabisa Mudstone Formation and the Middle Triassic Ntawere Formation in the Luangwa Basin. Numerous Permian and Triassic fossils have been collected in the northern sub-basin, but nearly all of the material from the transfer zone is of Permian age. The specimen of *Luangwa drysdalli* described by Kemp (1980a; also see Kerr 1974; Kemp 1975) is the only Triassic tetrapod collected in the transfer zone to date. The vertebrate paleontology of the southern sub-basin remains almost entirely unexplored.

The Madumabisa Mudstone sediments accumulated on the floor of a wide flat-bottomed rift valley with a gentle regional slope towards the south-southwest. The sequence is interpreted as having initially been an alluvial plain dominated by low sinuosity river channels (Lower Member of Drysdall and Kitching 1963). As the graben widened and the rates of sedimentation increased, the rivers became progressively higher in sinuosity with more and more ponds and lakes until eventually the valley floor became predominantly sub-aqueous as evidenced by the extensive, thick beds of massive grey and green mudstones in the Upper Member of the Madumabisa Mudstone Formation (Yemane and Kelts 1990; Banks et al. 1995). Most of the Late Permian vertebrate fossils are found in greenish grey and pale brown massive siltstone beds, associated with and often partly enclosed within smooth surfaced calcareous nodules. The fossil rich beds are interpreted as having accumulated by episodic, possibly catastrophic, flooding of a vegetated floodplain.

The contact with the overlying pebbly sandstone of the Escarpment Grit Formation is regarded as erosional throughout the Luangwa Basin. However, the same contact in the nearby Zambezi basin is an abrupt change of depositional style, disconformable rather than unconformable (Bond 1967). In the main Karoo Basin, time-equivalent strata show a transition through the argillaceous Palingkloof member of the Balfour Formation into the arenaceous Katberg Formation, with no disconformity, and vertebrate fossils that record the End-Permian mass extinction event (Smith 1995). The synchronicity of this relatively rapid switch from cool-wet lacustrine to warm-dry fluvial depositional environments across all the Karoo basins in southern Gondwana has been attributed to CO₂ degassing from basaltic floods in northern Pangaea causing rapid global

warming, a shift in precipitation belts, and aridification of inland regions (Ward et al. 2005).

In the Luangwa sequence the Lower Triassic Escarpment Grit grades upwards into semi-arid fluvio-lacustrine redbed strata of the Middle Triassic Ntawere Formation, where the mudrocks are predominantly dark reddish brown with horizons of calcareous rhizocretions and nodules. Trough cross bedded coarse-grained gritstones with intraformational conglomerates interbedded with structureless light-red siltstone beds are interpreted as ephemeral stream channel fills incised into wind deposited loess. Stromatolitic limestone drapes over lenses of reworked brecciated mudstone with bone clasts are part of the playa lake shoreline facies in which many of the vertebrate fossils are found.

Vertebrate Taphonomy

The preservation style of dicynodonts in the fossil rich localities within the Upper Madumabisa Mudstone is most commonly isolated skulls, mostly without articulated lower jaws, and isolated limb and girdle elements, although a few complete articulated skeletons (some curled-up) and semi-associated skeletons also can be found. Most of the fully articulated specimens are of *Diictodon* and *Pristerodon* and most of the disarticulated, semi-associated skeletons are of the medium and large dicynodonts *Oudenodon* and *Odontocyclus*. The close association of the articulated skeletons with micritic nodules suggests these bones were buried while skin and connective tissue were still present. The organic matter subsequently decomposed to release hydrogen sulphide into the surrounding silt, creating reduction halos that later induced calcium carbonate to precipitate from the groundwater. Preservation of specimens in hematite-rich nodules is more common in the northern sub-basin than in the transfer zone, although a thin hematite rind sometimes is present on the bone surface of specimens from the latter area.

The dicynodonts of the Ntawere Formation have a similar taphonomic range to those of the Upper Madumabisa Formation, but with far fewer complete articulated specimens and none found in curled-up pose. This may be due to the disappearance of small-bodied dicynodonts such as *Diictodon*, *Pristerodon*, and *Emydops*, which may have inhabited underground burrows (Smith 1987). The larger kannemeyeriiforms are commonly found as patches of scattered (i.e., disarticulated but still associated) postcrania within an area of three to five square meters, suggesting that scavenging was more prevalent in the mid-Triassic. This interpretation is reinforced by the occurrence of bone bearing coprolites in and around the bone scatters (this study and Drysdall and Kitching 1963).

Note on Treatment of Fossil Localities

The various individuals and groups who collected fossils in the Luangwa Basin used different systems for identifying localities. We use three sets of locality numbers in the Systematic Paleontology section. For specimens collected in the northern part of the basin by Dixey and the 1960, 1961, and 1963 expeditions, we use the Drysdall and Kitching (1963; also see Kitching 1963) locality numbering system, which incorporates and standardizes all localities up to that time. For specimens collected by the 1974 expedition, we use the numbering system of Kerr (1974), which was used in most of the papers describing material from this collection (Kemp 1979, 1980b; Davies 1981; King 1981) and can be directly related to information provided in other publications that do not refer to localities by number (Kemp 1975; King and Jenkins 1997). Finally, we use our locality numbers for specimens collected during the 2009 expedition (i.e., NHCC specimens with locality numbers starting with “L”). Detailed locality information is available to qualified researchers from the respective museums or from KDA in the case of specimens collected by our team.

Permian Dicynodont Fauna

We use the higher-level taxonomy of Kammerer and Angielczyk (2009) for Permian dicynodonts, with minor changes reflecting the results of Kammerer et al. (2011). Our taxonomic results for Permian dicynodonts are summarized in Table 7.1.

Systematic Paleontology

Therapsida Broom, 1905

Anomodontia Owen, 1860a

Chainosauria Nopcsa, 1923

Dicynodontia Owen, 1860a

Endothiodontia Owen, 1876

Endothiodon sp.

Figure 7.2a, c

Material: BP/1/3574, NHCC LB11, NHCC LB12.

Localities: Locality 3 of Drysdall and Kitching (1963) (BP/1/3574), locality L32 (NHCC LB12), locality L49 (NHCC LB11).

Identifying Characteristics: Cox (1964), Cluver and King (1983), King (1988), and Ray (2000) provided diagnoses for *Endothiodon*, and Cox’s paper is noteworthy for its consideration of intra- and interspecific variation in the genus. The available Zambian *Endothiodon* specimens are

Table 7.1 Dicynodont taxa present in the Upper Permian Upper Madumabisa Mudstone, Luangwa Basin, Zambia, and synonyms used in the literature on the Luangwa Basin

Taxon	Synonyms in Luangwa Basin literature
<i>Endothiodon</i> sp.	<i>Endothiodon uniseries</i>
<i>Pristerodon mackayi</i>	<i>Parringtoniella</i> , <i>Emydops</i> , <i>Emydopsis</i>
<i>Diictodon feliceps</i>	<i>Dicynodon grimbeeki</i> , <i>Dicynodon sollasi</i> , <i>Dicynodon clarencei</i>
<i>Compsodon helmoedi</i>	None
<i>Emydops</i> sp.	<i>Emydops</i> sp. indet.
<i>Dicynodontoides</i> cf. <i>D. nowacki</i>	None
Cistecephalidae n. g. & sp.	<i>Cistecephalus</i> , <i>Cistecephalus microrhinus</i> , <i>Cistecephalus planiceps</i>
cf. <i>Katumbia parringtoni</i>	None
<i>Odontocyclops whaitsi</i>	<i>Rhachiocephalus dubius</i> , <i>Odontocyclops dubius</i> , <i>Dicynodon</i> cf. <i>breviceps</i> , <i>Dicynodon</i> , <i>Rhachiocephalus magnus</i>
<i>Oudenodon bainii</i>	<i>Dicynodon lutriceps</i> , <i>Dicynodon</i> cf. <i>breviceps</i> , <i>Dicynodon corstorphineii</i> , <i>Dicynodon</i> cf. <i>corstorphineii</i> , <i>Dicynodon</i> cf. <i>milletti</i> , <i>Dicynodon latirostris</i> , <i>Dicynodon luangwanensis</i> , <i>Dicynodon helenae</i> , <i>Dicynodon euryceps</i> , <i>Dicynodon parabreviceps</i> , <i>Oudenodon luangwanensis</i> , <i>Oudenodon luangwaensis</i> , <i>Oudenodon luangwensis</i>
<i>Kitchinganomodon crassus</i>	None
<i>Dicynodon hueni</i>	<i>Dicynodon lacerticeps</i> , <i>Dicynodon trigonocephalus</i> , “ <i>Dicynodon</i> ” <i>trigonocephalus</i>
<i>Syops vanhoepeni</i>	<i>Dicynodon vanhoepeni</i> , <i>Dicynodon roberti</i> , “ <i>Dicynodon</i> ” <i>vanhoepeni</i> , “ <i>Dicynodon</i> ” <i>roberti</i>
Lystrosauridae n. g. & sp.	<i>Lystrosaurus</i> cf. <i>curvatus</i>

See text for details

all very fragmentary, and appear to represent parts of the palate and/or jaws. The most diagnostic features of these fragments are their relatively large sizes and the presence of long, medially-placed tooth rows, both of which give them a close resemblance to *Endothiodon* specimens from areas such as South Africa and Mozambique (Fig. 7.2a–d). For example, comparison to more complete specimens suggests that NHCC LB12 was part of a skull with a basal length of approximately 380 mm and NHCC LB11 originated in a mandible with a length of approximately 300 mm, values that are comparable to large *Endothiodon* specimens such as AMNH 5565 (basal length of skull 430 mm; length of jaw ramus 400 mm) or BP/1/1659 (basal length of skull 345 mm). However, the specimens are too fragmentary to allow a species-level identification.

Synonyms in Luangwa Basin Literature: Fröbisch (2009) stated that Drysdall and Kitching (1963) and Kitching (1963) recorded *Endothiodon uniseries* from the Luangwa Basin. However, we can find no mention of that species in those publications. Cox (1964) reported a specimen of *E. uniseries* collected by John Attridge from the “Madumabisa shales,” but of Zimbabwe, not Zambia.

Previous Reports: Kitching (1963) and Drysdall and Kitching (1963) reported collecting two fragmentary specimens of *Endothiodon* at their Locality 3, which they included in their lower fossiliferous horizon. We relocated one of those specimens (BP/1/3574) and confirm its identification. Anderson and Cruickshank (1978), King (1988, 1992), Rubidge (2005), and Fröbisch (2009) all included

Endothiodon in the faunal lists they compiled. Cooper (1982) and Angielczyk (2002) both mentioned *Endothiodon* in their discussion of the biostratigraphic correlation of the Madumabisa Mudstone.

Eumantelliidae Broom, 1935

Pristerodon mackayi Huxley, 1868

Figure 7.2e–g

Material: BP/1/3386, BP/1/3399, BP/1/3410, BP/1/3601, NHCC LB4, NHCC LB5, NHCC LB8, NHCC LB9, NHCC LB10, SAM-PK-K7933.

Localities: Locality 4 of Drysdall and Kitching (1963) (BP/1/3386, BP/1/3399, BP/1/3410, BP/1/3601, SAM-PK-K7933), locality L6 (NHCC LB4), locality L7 (NHCC LB5), locality L50 (NHCC LB8), locality L52 (NHCC LB9, NHCC LB10).

Identifying Characteristics: Keyser (1993) and King and Rubidge (1993) provided recent diagnoses of *Pristerodon*. The Zambian *Pristerodon* specimens we identified vary greatly in quality of completeness and the degree to which they have been prepared. The most informative specimens (e.g., BP/1/3410; Fig. 7.2e, f), show numerous characters diagnostic of *Pristerodon*, including a broad temporal region in which the parietals are exposed between the postorbitals, leaf-shaped palatine pads, and the presence of maxillary “postcanine” teeth arranged in a row that is oblique to the sagittal plane of the skull. Identifications for more fragmentary and/or unprepared specimens are based on a combination of size and the presence of one or more

diagnostic characters. For example, the material from locality L52 (NHCC LB9 and NHCC LB10) consists of the remains of at least three individuals, and diagnostic material includes a palate with an exposed tusk and an oblique row of “postcanine” teeth, and two toothed dentaries, one of which also possesses the remains of a relatively large, rounded lateral dentary shelf.

Synonyms in Luangwa Basin Literature: *Parringtoniella* (Drysall and Kitching 1963; King 1988, 1992). Keyser (1993) and King and Rubidge (1993) discussed the synonymy of *Pristerodon* and *Parringtoniella*. Boonstra (1938) referred one specimen (SAM-PK-K7933) to *Emydops* or *Emydopsis*. Although the former taxon is valid, and the latter appears to be a junior synonym of it (King 1988), SAM-PK-K7933 most plausibly represents a poorly preserved specimen of *Pristerodon*.

Previous Reports: If our identification of SAM-PK-K7933 is correct, then Boonstra’s (1938) report of this specimen is the first time a Zambian specimen of *Pristerodon* was mentioned in the literature, although it was not identified as such at the time. Drysdall and Kitching (1963) noted the occurrence of “*Parringtoniella*” at their Locality 3, but it is unclear whether they collected any of these specimens because all of the *Pristerodon* material we identified at the BP originated at their Locality 4. Anderson and Cruickshank (1978), Rubidge (2005), and Fröbisch (2009) all included *Pristerodon* in their compilations. King (1988) included “*Parringtoniella*” in the faunal list for Zambia, but later King (1992) suggested that this most likely was a synonym of *Pristerodon*.

Therochelonina Seeley, 1894

Pylaecephalidae (van Hoepen, 1934)

Diictodon feliceps (Owen, 1876)

Figure 7.2h–m

Material: BP/1/3598, NHCC LB1, NHCC LB2, NHCC LB3, NHCC LB6, NHCC LB7, NHCC LB27, TSK 77, TSK 98.

Localities: Locality 4 of Drysdall and Kitching (1963) (BP/1/3598). Locality L31 (NHCC LB1), locality L38 (NHCC LB2, NHCC LB6, NHCC LB7, NHCC LB27), locality L48 (NHCC LB3). Kerr’s (1974) Locality 11 (TSK 98), Kerr’s (1974) Locality 13 (TSK 77).

Identifying Characteristics: Sullivan and Reisz (2005) and Angielczyk and Sullivan (2008) recently discussed diagnostic characters and ranges of discrete and morphometric variability for *Diictodon feliceps*. The specimens we refer to *D. feliceps* all are relatively small with square-cut caniniform processes set off from the palatal rim by a notch (Fig. 7.2i, j). In the specimens where the intertemporal region is preserved and exposed, it is relatively narrow and the postorbitals extensively overlap the parietals. A

mandible from locality L38, NHCC LB6 (Fig. 7.2h), lacks postcanine teeth, has a dentary table that grades into a short broad posterior dentary sulcus (see Angielczyk and Rubidge 2013 for information on the interpretation of the homologies of these characters), and the remains of a tall, convex cutting blade on the medial side of the dorsal surface of the dentary. The shape of the well-preserved deltopectoral crest of NHCC LB7 (Fig. 7.2k) closely resembles those of South African *D. feliceps* specimens, and other humeral fragments from locality L38 (e.g. NHCC LB27; Fig. 7.2l) also show the presence of an ectepicondylar foramen.

Synonyms in Luangwa Basin Literature: *Dicynodon grimbeeki*, *Dicynodon sollasi*, *Dicynodon clarencei* (Drysdall and Kitching 1963; Gale 1989). See King (1993) and Sullivan and Reisz (2005) for discussion of the synonymies of the first two species with *D. feliceps*. *Dicynodon clarencei* was recognized as a synonym of *Dicynodontoides recurvidens* by Angielczyk et al. (2009).

Previous Reports: Based on the species identifications given in their subsequent publications, at least some of the specimens identified as *Dicynodon* by Drysdall and Kitching (1962) likely represent *Diictodon*. Drysdall and Kitching (1962, 1963) reported specimens in what they considered the lower (Locality 3) and upper (Locality 4) fossiliferous beds of the Madumabisa Mudstone. However, they did not state whether these occurrences were based on collected specimens or field reports, making confirmation of the identifications difficult. Gale (1988) referred an assemblage of juvenile dicynodont specimens from Zambia to *Diictodon*, and King (1993) followed this identification in her discussion of *Diictodon* taxonomy. However, this identification is questionable because their sizes are larger than would be expected for *Diictodon* given their presumed early ontogenetic stage, and they lack the distinctive notched caniniform process that is typical of *Diictodon*. Gale (1989) referred the same specimens to *Dicynodon clarencei* (a synonym of *Dicynodontoides recurvidens*; see Angielczyk et al. 2009), but they also lack diagnostic characters for that species. Anderson and Cruickshank (1978), King (1988, 1992), King and Jenkins (1997), Rubidge (2005), and Fröbisch (2009) included *Diictodon* in the faunal lists they compiled for Zambia. Angielczyk and Sullivan (2008) figured a largely unprepared but diagnostic Zambian *Diictodon* specimen (BP/1/3598).

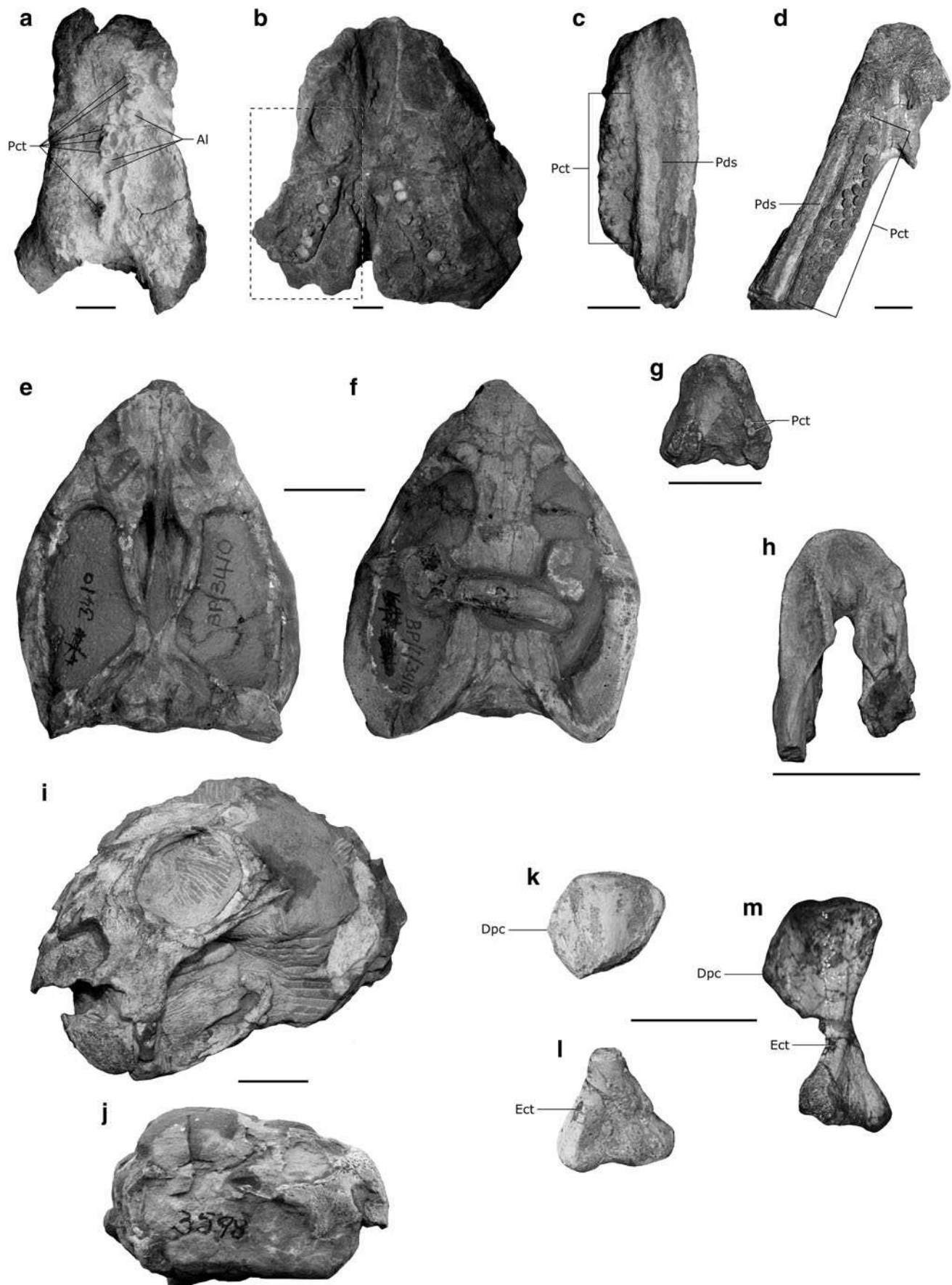
Emydopoidea (van Hoepen, 1934)

Compsodon helmoedi van Hoepen, 1934

Figure 7.3a–h

Material: NHCC LB13, NHCC LB14.

Localities: Locality L26 (NHCC LB13), locality L45 (NHCC LB14).



◀ **Fig. 7.2** Zambian specimens of *Endothiodon*, *Pristerodon*, and *Diictodon*, and comparative material. **a** Palate fragment of *Endothiodon* sp. from Zambia (NHCC LB12) in ventral view. The fragment includes a partial premaxilla, partial palatine, and several “postcanine” teeth and alveoli. **b** Comparative snout of *Endothiodon uniseries* (NHMUK R4042) from South Africa in ventral view. The dashed box shows the section of the palate preserved in NHCC LB12. **c** Partial right dentary of *Endothiodon* sp. from Zambia in dorsal view. **d** Partial mandible of *Endothiodon* sp. from Mozambique (BP/1/5489) in dorsal view. Note the similarity of the location and morphology of the “postcanine” teeth and posterior dentary sulcus to those of NHCC LB12. **e** Skull of *Pristerodon mackayi* from Zambia (BP/1/3410) in ventral view. **f** Skull of *Pristerodon mackayi* from Zambia (BP/1/

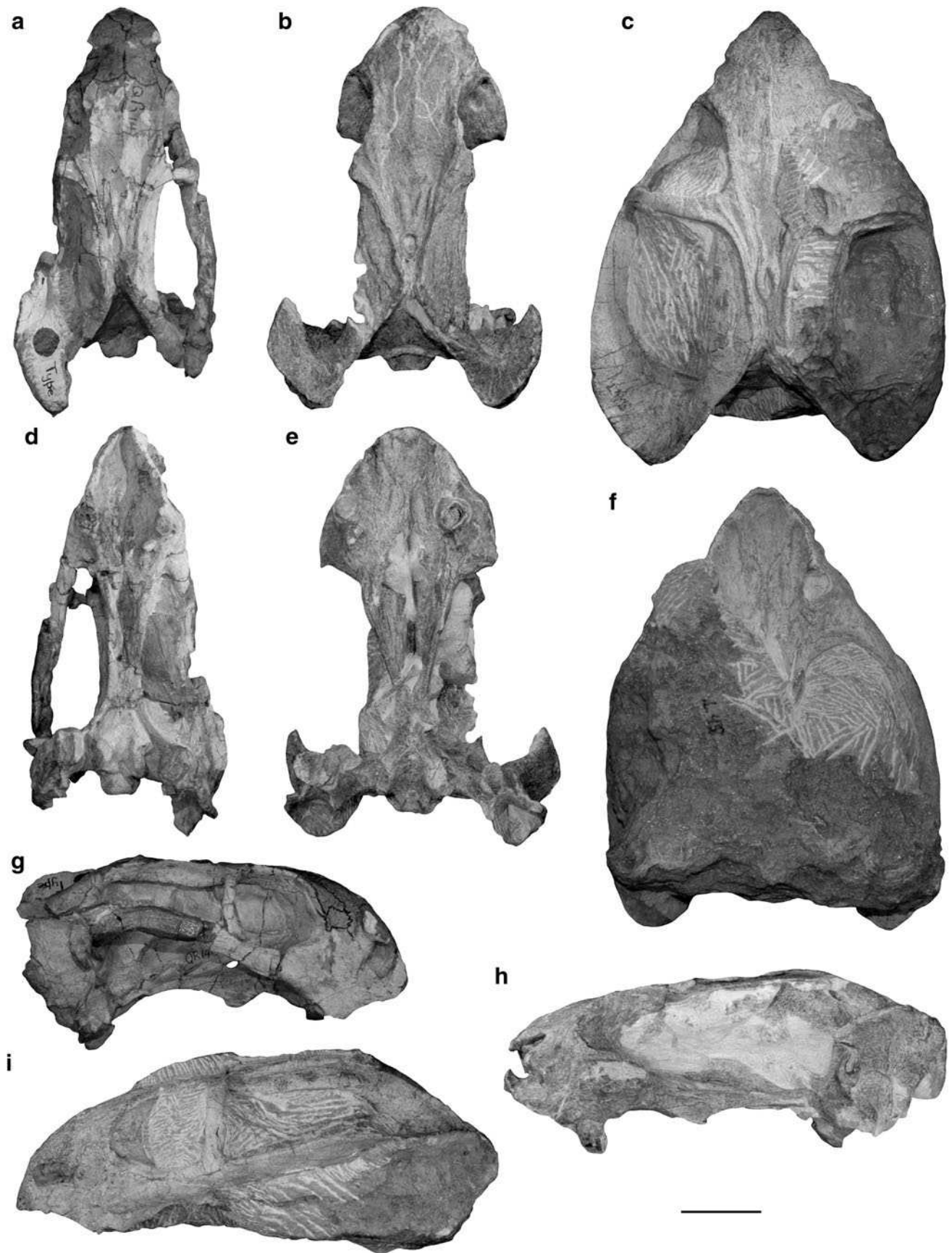
3410) in dorsal view. **g** Partial mandible of *Pristerodon mackayi* from Zambia (NHCC LB9) in dorsal view. **h** Partial mandible of *Diictodon feliceps* from Zambia (NHCC LB6) in dorsal view. **i** Partially-prepared skull and mandible of *Diictodon feliceps* from Zambia (NHCC LB3) in anterolateral view. **j** Partially-prepared skull and mandible of *Diictodon feliceps* from Zambia (BP/1/3598) in right lateral view. **k** Proximal end of a left humerus of *Diictodon feliceps* from Zambia (NHCC LB7) in dorsal view. **l** Distal end of a right humerus of *Diictodon feliceps* from Zambia (NHCC LB27) in ventral view. **m** Left humerus of *Diictodon feliceps* from South Africa (CGP STH 36). Note the similarity in shape of the deltopectoral crest to that of NHCC LB7 and the presence of an ectepicondylar foramen. Scale bars are 20 mm

Identifying Characteristics: *Compsodon helmoedi* was described by van Hoepen (1934) based on a small skull (basal length approximately 100 mm) collected in the Karoo Basin of South Africa. Toerien (1954) provided additional information on the holotype and suggested that *C. helmoedi* may be related to *Emydops*, but Cluver and King (1983) and King (1988) treated it as a valid species of uncertain affinities. Brink and Keyser (1983) considered *C. helmoedi* to be a synonym of *Tropidostoma microtrema*, but did not provide justification for this synonymy.

The holotype of *C. helmoedi* (NMQR 1460) (Fig. 7.3a, d, g) is a small, laterally compressed skull with tusks and “postcanine” teeth, relatively large but smooth palatine pads that are pierced by a palatine foramen, and long, straight anterior pterygoid rami that bear prominent, triangular ventral keels. Van Hoepen (1934) stated that a fragment of tooth associated with the specimen was serrated, and speculated that *C. helmoedi* may have had serrated tusks. However, this would be unprecedented among dicynodonts, particularly because serrations are structures associated with enamel whereas dicynodont tusks are composed only of dentine (Camp and Welles 1956; Poole 1956), and the portions of the tusks preserved in situ in NMQR 1460 show no evidence of serrations. The “postcanine” preserved on the left side of the specimen also shows no sign of serrations. An embayment of the palatal rim is present anterior to the caniniform process, and a postcaniniform keel is present. Anterior palatal ridges are absent, but a posterior median ridge is present that is flanked laterally by longitudinal depressions (although the depressions are poorly preserved due to lateral compression). A nasal boss with a continuous posterior border is present on the snout, and the lateral surface of the maxilla bears a distinctive, pocket-like depression posterior to the external naris between the anterior orbital margin and the caniniform process. On the skull roof, the midfrontal suture is slightly raised, and the edges of the orbit are slightly raised above the surface of the frontals. Posterior to the orbital rim, the postfrontals and postorbitals are raised above the posterior portion of the frontals and the preparietals, giving the skull roof in this area a slightly depressed

appearance. The preparietal itself is elongate, and roughly triangular in shape, with its apex reaching the parietal foramen. The edges of the preparietal are slightly raised, forming weak ridges that extend to the parietal foramen, which itself is surrounded by a slightly raised lip. The parietals are exposed between the postorbitals on the skull roof, although this exposure appears to be narrower than is the case in *Emydops* or *Pristerodon*. Based on this combination of character states, including the distinctive depression on the lateral surface of the premaxilla and the raised postfrontals and postorbitals, we consider *C. helmoedi* a valid taxon that is likely part of Emydopoidea. A full redescription and investigation of its phylogenetic relationships will be the subject of a subsequent publication.

NHCC LB13 (Fig. 7.3b, e, h) and NHCC LB14 (Fig. 7.3c, f, i) bear a striking resemblance to the type of *C. helmoedi*. NHCC LB13 is almost exactly the same size as NMQR 1460 (basal length approximately 103 mm) and is tusked. “Postcanines” are not preserved, but two empty alveoli are present posterior to the tusk on each side of the skull. Median anterior ridges are absent on the secondary palate, although lateral ridges similar to those found in *Diictodon* or *Emydops* are present. A posterior median ridge is also present, and is flanked by rounded grooves. Interestingly, the anterior portion of the median ridge forms a flattened, Y-shaped expanded area that is reminiscent of that seen in *Eosimops newtoni* (Angielczyk and Rubidge 2013). An embayment on the palatal rim anterior to the caniniform process is present, as is a postcaniniform keel. The palatine pads are relatively large, smooth, and pierced by a palatal foramen, and the left anterior pterygoid ramus preserves a ventral keel nearly identical to that of NMQR 1460 (the right side is damaged). The snout of NHCC LB13 is damaged, but the remains of a median nasal boss appear to be present, and a pocket-like depression is present on the lateral surface of the maxilla. The midfrontal suture is slightly raised, as are the orbital margins, and the postorbitals and postfrontals are raised above the level of the posterior portion of the frontals and the preparietal. The preparietal is of similar shape as that of NMQR 1460, and its edges form distinct ridges that extend to the parietal foramen. The



◀ **Fig. 7.3** Zambian specimens of *Compsodon helmoedi* and comparative material. **a** Holotype skull of *Compsodon helmoedi* from South Africa (NMQR 1460) in dorsal view. Note that the specimen has been laterally compressed. **b** Skull of *Compsodon hemoedi* from Zambia (NHCC LB13) in dorsal view. **c** Partially prepared skull of *Compsodon hemoedi* from Zambia (NHCC LB14) in dorsal view. **d** Holotype skull of *Compsodon helmoedi* from South Africa (NMQR 1460) in ventral view. **e** Skull of *Compsodon hemoedi* from Zambia (NHCC

LB13) in ventral view. **f** Partially prepared skull of *Compsodon hemoedi* from Zambia (NHCC LB14) in ventral view. **g** Holotype skull of *Compsodon helmoedi* from South Africa (NMQR 1460) in right lateral view. **h** Skull of *Compsodon hemoedi* from Zambia (NHCC LB13) in left lateral view. **i** Partially prepared skull of *Compsodon hemoedi* from Zambia (NHCC LB14) in left lateral view. Scale bar is 20 mm

parietal foramen is surrounded by a slightly raised lip. The postorbitals of NHCC LB13 have a larger exposure on the skull roof than those of NMQR 1460 and overlap the parietals more extensively, but given the otherwise great degree of similarity between the specimens, we interpret this as likely individual variation or preservation differences.

NHCC LB14 is larger than NMQR 1460 (basal length approximately 113 mm), and at the time of writing has only been partially prepared. Part of a tusk is exposed on the right side of the specimen, and empty alveoli for a tusk and at least one “postcanine” are present on the left side. Median anterior palatal ridges are absent, but the lateral anterior ridges are well developed. The posterior median palatal ridge also is present and bears a flattened expanded anterior section similar to NHCC LB13. The posterior median ridge is also flanked by rounded depressions. An embayment of the palatal rim anterior to the caniniform process is present, as is a postcaniniform keel. Only the left palatine pad is exposed, but it has the same shape as that of NHCC LB13 and is pierced by a palatal foramen. A median nasal boss with a continuous posterior border is present on the snout, and the pocket-like depression is well developed on the lateral surface of the maxilla. The midfrontal suture and the orbital margins are raised, and the postfrontals and postorbitals are raised above the level of the frontals and preparietal. The preparietal is triangular with raised edges that continue posteriorly to meet with the raised lip that surrounds the parietal foramen. The parietals are slightly more exposed on the skull roof than in NHCC LB13, giving this region an appearance more similar to that of NMQR 1460.

Synonyms in Luangwa Basin Literature: None.

Previous Reports: *Compsodon* has not been reported previously from the Luangwa Basin.

Emydopidae (van Hoepen, 1934)

Emydops sp.

Figure 7.4a, b, d, f

Material: BP/1/3347, NHCC LB15.

Localities: Locality 4 of Drysdall and Kitching (1963) (BP/1/3347), locality L52 (NHCC LB15).

Identifying Characteristics: Angielczyk et al. (2005) and Fröbisch and Reisz (2008) provided recent reviews of diagnostic characters of *Emydops*. Both specimens are small, possess an intertemporal region in which the parietals are broadly exposed between the postorbitals, and display a squared-off profile of the occiput in posterior view (better exposed in BP/1/3347). The mandible is preserved in NHCC LB15, and although unprepared, it is suggestive of the presence of a prominent lateral dentary shelf and shovel-like symphyseal region. Unfortunately, neither BP/1/3347 or NHCC LB15 is prepared enough at this time to determine whether it represents *Emydops arctatus*, *E. oweni*, or a new species.

Synonyms in Luangwa Basin Literature: *Emydops* sp. indet. (Fröbisch, 2009).

Previous Reports: Boonstra (1938) reported a fragmentary specimen with tusks and “postcanines” that he tentatively identified as *Emydops* or *Emydopsis*. However, as noted above, this specimen (SAM-PK-K7933) is most likely *Pristerodon*. Drysdall and Kitching (1962, 1963) and Kitching (1963) noted field observations of *Emydops* from their Localities 3 and 17, which they considered part of the lower and middle fossiliferous beds of the Madumabisa Mudstone, respectively. Strangely, they did not mention *Emydops* at Locality 4, despite the fact that the only identifiable *Emydops* specimen collected during that fieldwork of which we are aware (BP/1/3347) is from Locality 4. Anderson and Cruickshank (1978), King (1988, 1992), Rubidge (2005), and Fröbisch (2009) included *Emydops* in the faunal lists they presented, undoubtedly based on previous reports.

Kistecephalia Seeley, 1894

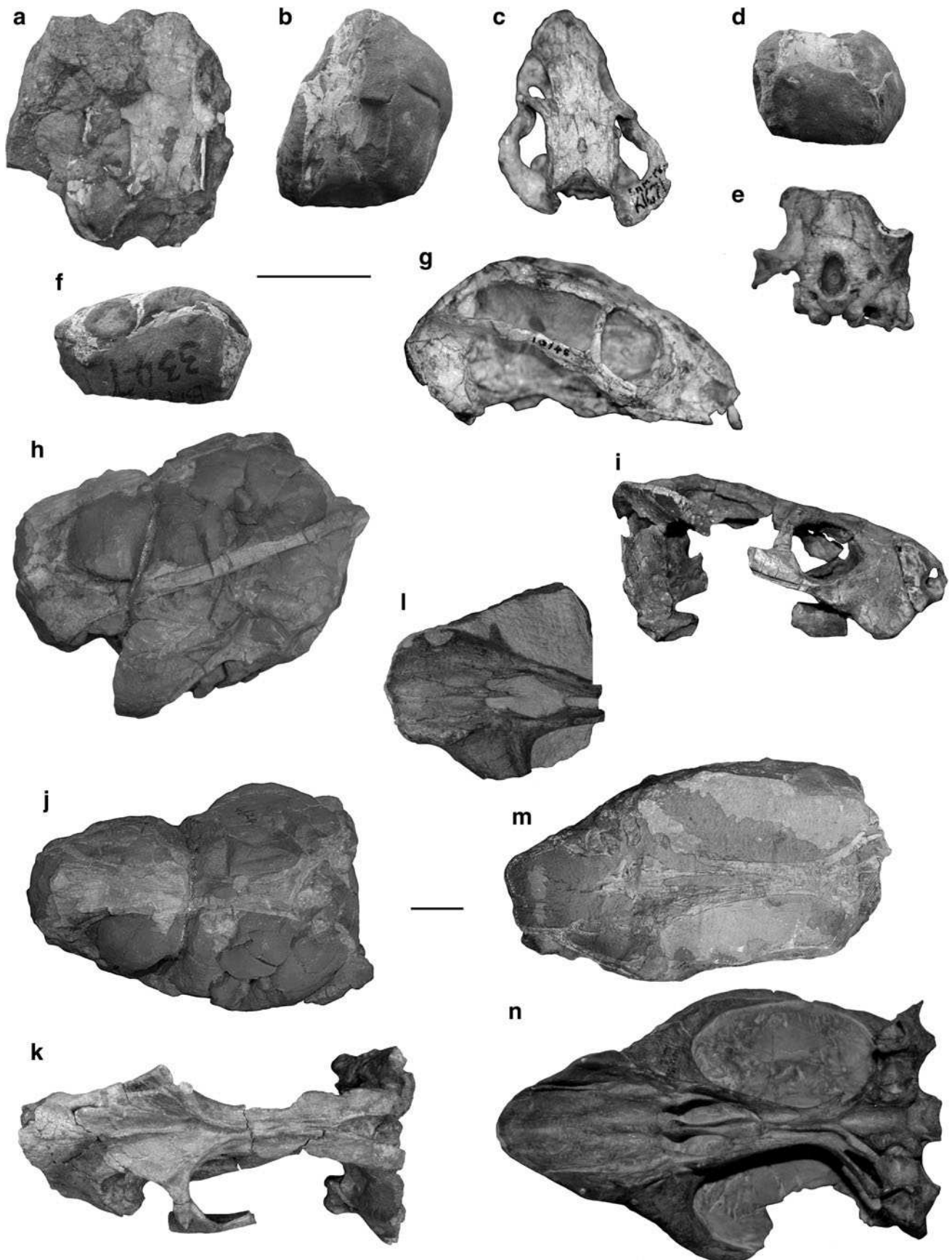
Kingoriidae King, 1988

Dicynodontoides cf. *D. nowacki* (von Huene, 1942)

Figure 7.4h, j, l, m

Material: NHMUK R15944, NHCC LB16. NHCC LB17 also may be *Dicynodontoides*, but the specimen is unprepared.

Localities: Locality 4 of Drysdall and Kitching (1963) (NHMUK R15944), locality L29 (NHCC LB16). NHCC LB17 was collected at locality L64.



◀ **Fig. 7.4** Zambian specimens of *Emydops* sp. and *Dicynodontoides* cf. *D. nowacki*, and comparative material. **a** Partially-prepared skull of *Emydops* sp. from Zambia (NHCC LB15) in dorsal view. **b** Partially-prepared skull of *Emydops* sp. from Zambia (BP/1/3347) in dorsal view. **c** Skull of *Emydops arctatus* from South Africa (SAM-PK-K1671) in dorsal view. **d** Partially-prepared skull of *Emydops* sp. from Zambia (BP/1/3347) in posterior view. **e** Skull of *Emydops arctatus* from South Africa (SAM-PK-11060) in posterior view. **f** Partially-prepared skull of *Emydops* sp. from Zambia (BP/1/3347) in left lateral view. **g** Skull of *Emydops arctatus* from South Africa (SAM-PK-10148) in right lateral view. **h** Partially-prepared skull and mandible of *Dicynodontoides* cf. *D. nowacki* from Zambia (NHMUK R15944) in left lateral view. **i** Skull

of *Dicynodontoides nowacki* from Tanzania (CAMZM T747) in right lateral view. **j** Partially-prepared skull of *Dicynodontoides* cf. *D. nowacki* from Zambia (NHMUK R15944) in dorsal view. **k** Partial skull of *Dicynodontoides nowacki* from Tanzania (NMT RB2) in dorsal view. **l** Snout of *Dicynodontoides* cf. *D. nowacki* from Zambia (NHCC LB16) in ventral view. **m** Coronal section through the skull of *Dicynodontoides* cf. *D. nowacki* from Zambia (NHCC LB17). Note the long, straight anterior pterygoid rami. **n** Skull of *Dicynodontoides nowacki* from Tanzania (GPIT K12) in ventral view. Note the long, straight anterior pterygoid rami and the similarity of the anterior palate to that of NHCC LB16. Upper left scale bar applies to panels **a–g**; lower scale bar applies to panels **h–n**. Scale bars are 20 mm

Identifying Characteristics: Angielczyk et al. (2009) provided a revised diagnosis for the two valid species of *Dicynodontoides*. NHMUK R15944 (Fig. 7.4h, j) is a poorly preserved specimen that is preserved in a hematitic nodule, and it has undergone only rudimentary preparation. We refer the specimen to *Dicynodontoides* primarily based on the absence of a postfrontal, the apparent occlusion of the mandibular fenestra by a lamina of the dentary, and the preserved anterior portion of the dentary seeming to be consistent with the original presence of an elongate, shovel-shaped symphysis. Our identification of NHCC LB16 (Fig. 7.4i) as *Dicynodontoides* is based on the absence of median anterior ridges on the palate, the presence of lateral anterior palatal ridges, the presence of a posterior median ridge flanked by elongate depressions, the presence of an embayment of the palatal rim anterior to the caniniform process, the presence of a postcaniniform keel, the absence of “postcanines,” the presence of very small, smooth palatine pads, and the absence of postfrontals on the skull roof. NHCC LB17 (Fig. 7.4m) is a skull and lower jaw that are preserved in a nodule. The nodule was recently burned when collected, and appears to have split open during the burning process, exposing a coronal section through the palate. NHCC LB17 is tusked, and possesses the very long, straight anterior pterygoid rami that are typical of *Dicynodontoides* (e.g., Fig. 7.4n). However, this identification must remain tentative until the specimen is more fully prepared. It is difficult to assign any of the specimens to one of the two species of *Dicynodontoides* with certainty. However, given that two of the three specimens are tuskless and all are relatively large (particularly NHCC LB16) they may be part of *D. nowacki* since that species seems to have attained large sizes and was more frequently tuskless than *D. recurvidens* (Angielczyk et al. 2009).

Synonyms in Luangwa Basin Literature: None.

Previous Reports: Angielczyk et al. (2009) were the first to report the presence of *Dicynodontoides* in the Luangwa Basin, based on NHMUK R15944. Gale (1989) referred an assemblage of juvenile dicynodonts to *Dicynodon clarencei*, a synonym of *Dicynodontoides recurvidens* (Angielczyk et al. 2009). These specimens do not appear to

represent *Dicynodontoides*, but their exact identification is uncertain (see above).

Cistecephalidae Broom, 1903

New Taxon

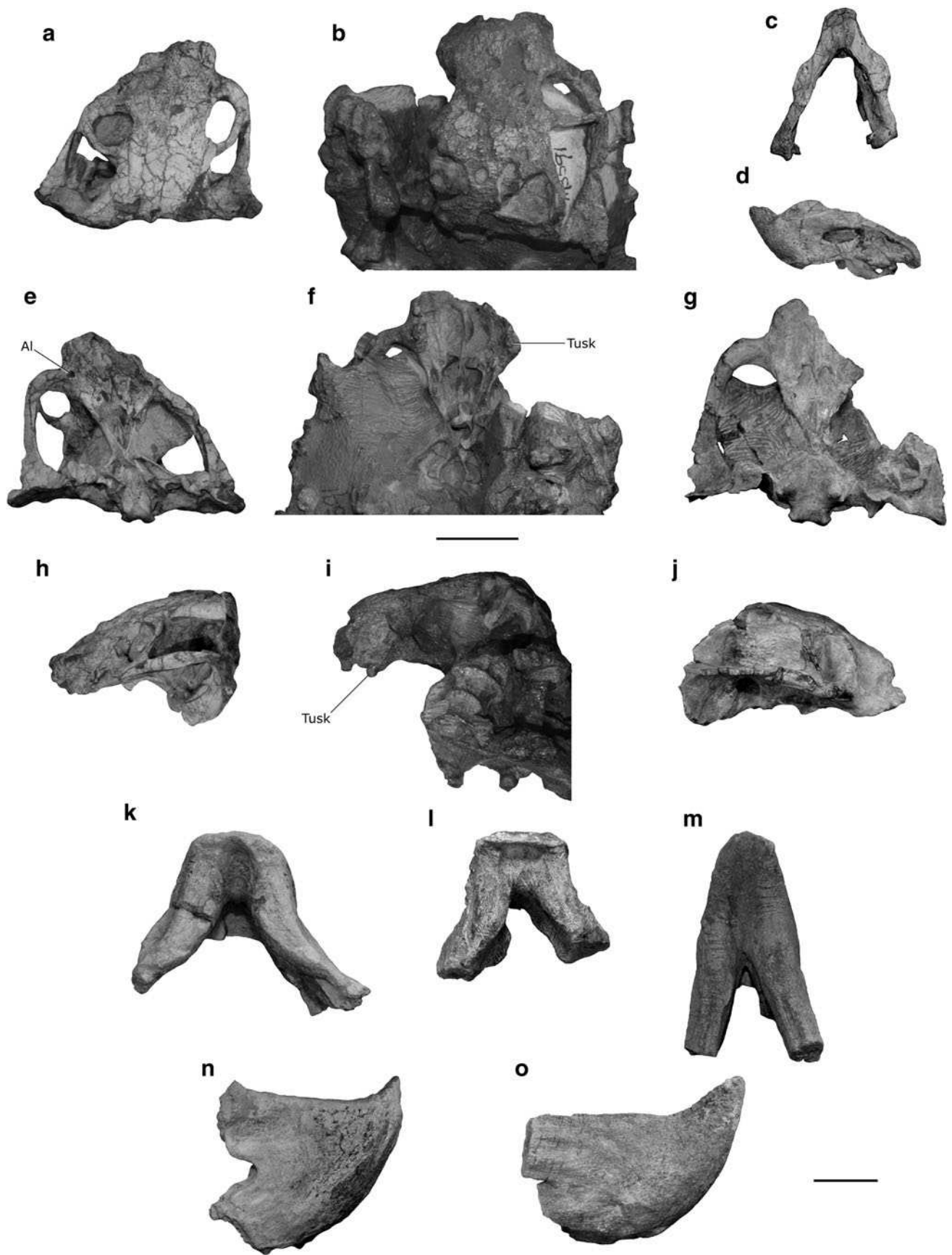
Figure 7.5a–j

Material: BP/1/3337, BP/1/3591, BP/1/3603, NHCC LB18, NHCC LB19. According to a handwritten note in the BP collections by J.W. Kitching, dated October 6, 1992, BP/1/3437 may represent a sixth specimen. However, we have been unable to locate this specimen and assume that it is lost.

Localities: Locality 4 of Drysdall and Kitching (1963) (BP/1/3337, BP/1/3591, BP/1/3603), locality L53 (NHCC LB18), locality L55 (NHCC LB19). BP/1/3437 was collected at Locality 5 of Drysdall and Kitching (1963).

Identifying Characteristics: Following Freeman (1993), we consider these specimens to represent a new cistecephalid taxon. Their cistecephalid affinities are indicated by their anteroposteriorly short skulls with broad intertemporal regions, the presence of a stapedial foramen, the absence of a preparietal, the absence of an interpterygoid vacuity, and large olecranon process of the ulna (see Kammerer and Angielczyk 2009 for a compilation of cistecephalid apomorphies). Freeman (1993) hypothesized that the specimens represented a new species of *Cistecephalus*, but we are hesitant to endorse this conclusion until the specimens are formally described and included in a phylogenetic analysis. Nevertheless, they do appear to differ in several ways from the three currently recognized cistecephalids, *Cistecephalus microrhinus*, *Cistecephaloides boonstrai*, and *Kawingasaurus fossilis*.

The most obvious diagnostic character of the Zambian cistecephalid is the presence of tusks, whereas all other cistecephalid species are tuskless (e.g., Cox 1972; Keyser 1973b; Cluver 1974a). Three of the specimens (BP/1/3337, BP/1/3591, and BP/1/3603) (Fig. 7.5f) possess tusks, one specimen NHCC LB18 (Fig. 7.5e) possesses empty tusk alveoli, and one specimen is tuskless (NHCC LB19) (Fig. 7.5g). We suspect that the presence of empty alveoli in NHCC LB18 likely represents a taphonomic artifact instead



◀ **Fig. 7.5** Zambia specimens of Cistecephalidae n. g. & sp. and cf. *Katumbia parringtoni*, and comparative material. **a** Skull of Cistecephalidae n. g. & sp. from Zambia (NHCC LB18) in dorsal view. **b** Partially-prepared skull of Cistecephalidae n. g. & sp. from Zambia (BP/1/3591) in dorsal view. **c** Mandible of Cistecephalidae n. g. & sp. from Zambia (NHCC LB18) in dorsal view. **d** Mandible of Cistecephalidae n. g. & sp. from Zambia (NHCC LB18) in left lateral view. **e** Skull of Cistecephalidae n. g. & sp. from Zambia (NHCC LB18) in ventral view. Note the presence of an empty tusk alveolus on the right maxilla. **f** Partially-prepared skull of Cistecephalidae n. g. & sp. from Zambia (BP/1/3591) in ventral view. Note the tusk in the left maxilla. **g** Partial skull of Cistecephalidae n. g. & sp. from Zambia (NHCC LB19) in ventral view. Note that this specimen is tuskless. **h** Skull of Cistecephalidae n. g. & sp. from Zambia (NHCC LB18) in left lateral view. **i** Partially-prepared skull of

Cistecephalidae n. g. & sp. from Zambia (BP/1/3591) in left lateral view. **j** Skull of Cistecephalidae n. g. & sp. from Zambia (NHCC LB19) in right lateral view. **k** Partial mandible of cf. *Katumbia parringtoni* from Zambia (NHCC LB20) in dorsal view. **l** Partial mandible of *Katumbia parringtoni* from Tanzania (CAMZM T791) in dorsal view. **m** Partial mandible of *Oudenodon bainii* (NMT RB37) in dorsal view. Note that the symphyseal region is longer in NMT RB37 than in NHCC LB20 and CAMZM T791, and that the dentary rami diverge at a shallower angle in NMT RB37. **n** Partial mandible of cf. *Katumbia parringtoni* from Zambia (NHCC LB20) in right lateral view. **o** Partial mandible of *Oudenodon bainii* (NMT RB37) in right lateral view. Note the shorter, more sharply-upturned symphysis in NHCC LB20. Upper scale bar applies to panels **a–j**; lower right scale bar applies to panels **k–o**. Scale bars are 20 mm

of tooth replacement or another biological process, since both specimens of *Compsodon* we collected feature empty tusk or “postcanine” alveoli, and NHCC LB14 in particular shows a preservation style that is extremely similar to NHCC LB18. The absence of tusks in NHCC LB19 may represent sexual dimorphism or another form of polymorphism. Such variability is not surprising given that several other dicynodonts recently have been shown to be sexually dimorphic or polymorphic for tusks (e.g., Angielczyk 2002; Sullivan et al. 2003; Botha and Angielczyk 2007; Fröbisch and Reisz 2008; Angielczyk et al. 2009), but a larger sample of specimens will be needed to determine whether sexual dimorphism is a likely cause.

The new Zambian cistecephalid can be further distinguished from *Cistecephalus microrhinus* by the absence of a depression or notch on the ventral surface of the maxilla lateral to the caniniform process (see Cluver 1974b), the presence of a small, triangular, ventrally-directed flange on the anterior pterygoid ramus, a mid-ventral vomerine plate that is wide and trough-like anteriorly, and a more robust, block-like crista oesophagea on the median pterygoid plate. It can be distinguished from *Cistecephaloides boonstrai* by the presence of a single embayment anterior to the caniniform process, the presence of a small, triangular, ventrally-directed flange on the anterior pterygoid ramus, a mid-ventral vomerine plate that is wide and trough-like anteriorly, a robust, block-like crista oesophagea on the median pterygoid plate, a larger lateral dentary shelf, and the absence of a tall cutting blade on the dorsal surface of the dentary near the level of the lateral dentary shelf. Finally, it can be distinguished from *Kawingasaurus fossilis* by larger size, the presence of a small, triangular, ventrally-directed flange on the anterior pterygoid ramus, a mid-ventral vomerine plate that is wide and trough-like anteriorly, and a robust, block-like crista oesophagea on the median pterygoid plate. The only mandible of *K. fossilis* (GPIT K55f) is poorly preserved, but the Zambian cistecephalid may additionally differ from this species in the presence of a posterior dentary sulcus and a larger lateral dentary shelf.

Synonyms in Luangwa Basin Literature: *Cistecephalus*, *Cistecephalus microrhinus*, *Cistecephalus planiceps* (Drysdall and Kitching 1962, 1963; Kitching 1963; Anderson and Cruickshank 1978; Cooper 1982; King 1988, 1992; Smith and Keyser 1995; Lucas 2002, 2005, 2006; Angielczyk 2002; Rubidge 2005; Fröbisch 2009).

Previous Reports: Drysdall and Kitching (1962, 1963) and Kitching (1963) were the first to report *Cistecephalus* from the Luangwa Basin. Specifically, they reported at least 13 specimens from localities in their middle and upper fossiliferous beds, but most of these occurrences appear to represent field identifications because they provided no specimen numbers or photographs. The only Zambian specimens in the BP collection that could be mistaken for *Cistecephalus* are BP/1/3337, BP/1/3591, and BP/1/3603, so we consider Drysdall and Kitching’s (1962, 1963) and Kitching’s (1963) reports to instead represent this new taxon. Numerous authors have cited Drysdall and Kitching’s papers as a basis for including *Cistecephalus* in the Zambian dicynodont fauna (Anderson and Cruickshank 1978; Cooper 1982; King 1988, 1992; Smith and Keyser 1995; Lucas 2002, 2005, 2006; Angielczyk 2002; Rubidge 2005; Fröbisch 2009), but only one author (Freeman 1993) recognized that the specimens represented a new taxon.

Bidentalia Owen, 1876

cf. *Katumbia parringtoni* (von Huene, 1942)

Figure 7.5k, n

Material: NHCC LB20.

Localities: Locality L59 (NHCC LB20).

Identifying Characteristics: NHCC LB20 consists of the symphyseal region of a dicynodont jaw that was collected as float. It is noteworthy in possessing extremely short dentary tables, dentary rami that strongly diverge posteriorly, and an upturned anterior margin of the symphysis that forms a relatively thin edge (Fig. 7.5k, n). In these characters, the specimen is very similar to the jaw of *Katumbia parringtoni* (Fig. 7.5l; also see Angielczyk 2007), but differs from jaws of most dicynodonts, which have

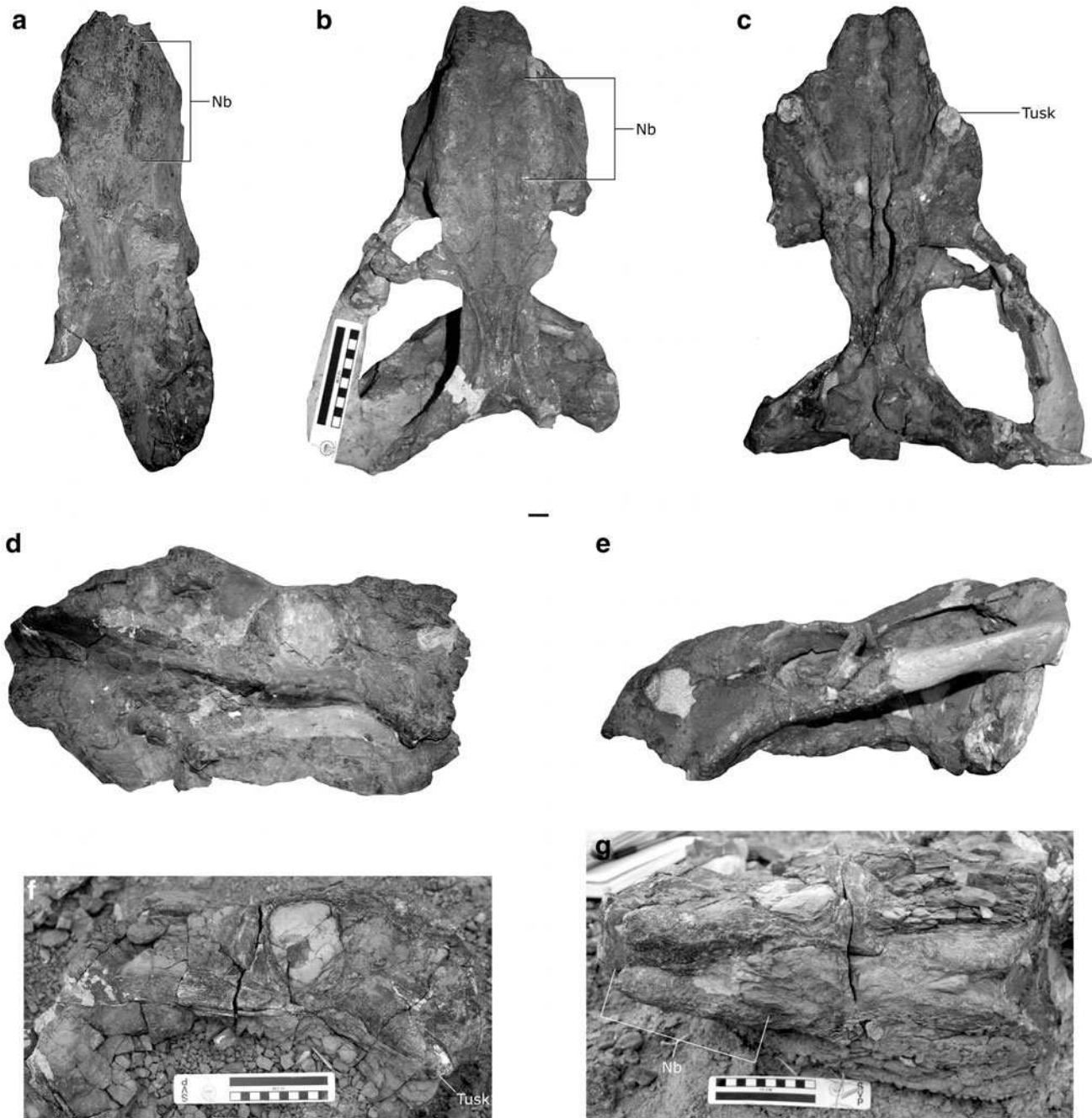


Fig. 7.6 Zambian specimens of *Odontocyclops whaitsi*. **a** Partial skull of *Odontocyclops whaitsi* (holotype of *Rhachiocephalus dubius*) (SAM-PK-11313) in dorsal view. **b** Partial skull of *Odontocyclops whaitsi* (BP/1/3419) in dorsal view. Note the elongate nasal bosses in this specimen and in SAM-PK-11313. **c** Partial skull of *Odontocyclops whaitsi* in ventral view. Note the presence of tusks. **d** Partial skull and mandible of *Odontocyclops whaitsi* (holotype of *Rhachiocephalus dubius*) (SAM-PK-11313) in right lateral view. **e** Partial skull of

Odontocyclops whaitsi (BP/1/3419) in left lateral view. **f** Field photograph of partial skull of *Odontocyclops whaitsi* (NHCC LB24) in right lateral view. Note the presence of a tusk. **g** Field photograph of partial skull of *Odontocyclops whaitsi* (NHCC LB24) in dorsal view. Note the presence of elongate nasal bosses similar to those of BP/1/3419 and SAM-PK-11313. Upper scale bar applies to panels **a–e** and is 20 mm. Scale bar in field photographs is 100 mm

proportionally longer dentary tables (e.g., *Oudenodon bainii*; Fig. 7.5m, o). Therefore, we tentatively refer the specimen to *K. parringtoni*, although confirmation of the

presence of this taxon in the fauna of the Upper Madumabisa Mudstone must await more complete and diagnostic material.

Synonyms in Luangwa Basin Literature: None.

Previous Reports: There are no previous reports of *K. parringtoni* in the Luangwa Basin.

Cryptodontia Owen, 1860a

Odontocyclops whaitsi (Broom, 1913)

Figure 7.6a–g

Material: BP/1/3244, BP/1/3419, BP/1/3585, BP/1/3586, BP/1/3587, BP/1/3589, NHCC LB24, SAM-PK-11313. SAM-PK-K7936 also likely represents *O. whaitsi*, although poor preservation of the specimen makes this identification tentative.

Localities: Locality 4 of Drysdall and Kitching (1963) (BP/1/3244, BP/1/3419, BP/1/3585, BP/1/3586, BP/1/3587, BP/1/3589, SAM-PK-11313), locality L39 (NHCC LB24). SAM-PK-K7936 was collected at Locality 3 of Drysdall and Kitching (1963).

Identifying Characteristics: Boonstra (1938), Keyser (1979), Keyser and Cruickshank (1979), and Angielczyk (2002) provided diagnoses of *O. whaitsi* based primarily on Zambian material, although Broom's (1913) initial description of the species was based on a South African specimen. The most distinctive autapomorphies of *O. whaitsi* are the elongate nasal bosses that extend from the posterodorsal corner of the external nares to contact the prefrontal bosses, and a concave dorsal surface of the snout between the nasal bosses (Fig. 7.6a, b, g). All of the specimens listed above except SAM-PK-K7936 show this character. Additional characters diagnostic of *Odontocyclops* include large size, variable presence of tusks, presence of a postcaniniform crest, absence of a labial fossa, and a relatively narrow temporal bar in which the parietals are well exposed between the postorbitals. SAM-PK-K7936 displays these characters, and the presence of tusks in that specimen allow it to be differentiated from similarly-sized *Oudenodon* specimens.

Synonyms in Luangwa Basin Literature: *Rhachiocephalus dubius*, *Odontocyclops dubius* (Boonstra 1938; Drysdall and Kitching 1963; Kitching 1963; Keyser 1979; Keyser and Cruickshank 1979). Boonstra (1938) identified SAM-PK-K7936 as *Dicynodon* cf. *D. breviceps*, and if this specimen is indeed *O. whaitsi*, then this would be an additional synonym. Cluver and King (1983) suggested that *Odontocyclops* was likely a synonym of *Dicynodon*, and King (1988) listed the genus *Odontocyclops* as synonym of *Dicynodon*. However, she included the species *Rhachiocephalus dubius* Boonstra, 1938 as a synonym of *Rhachiocephalus magnus*, despite the fact that Keyser (1979) and Keyser and Cruickshank (1979) used the former as the type species of *Odontocyclops*. As noted below, at least some of Kitching's (1962, 1963) and Drysdall and Kitching's (1963) field reports of *Aulacephalodon* likely represent *Odontocyclops*.

Previous Reports: Boonstra's (1938) description of "*Rhachiocephalus*" *dubius* is the first report of *O. whaitsi* from the Luangwa Basin. Drysdall and Kitching (1963), Kitching (1963), Cooper (1982), Anderson and Cruickshank (1978), Keyser (1979), Keyser and Cruickshank (1979), Angielczyk (2002), and Fröbisch (2009) all discuss Luangwa Basin specimens of *O. whaitsi* using various names.

Oudenodontidae Cope, 1871

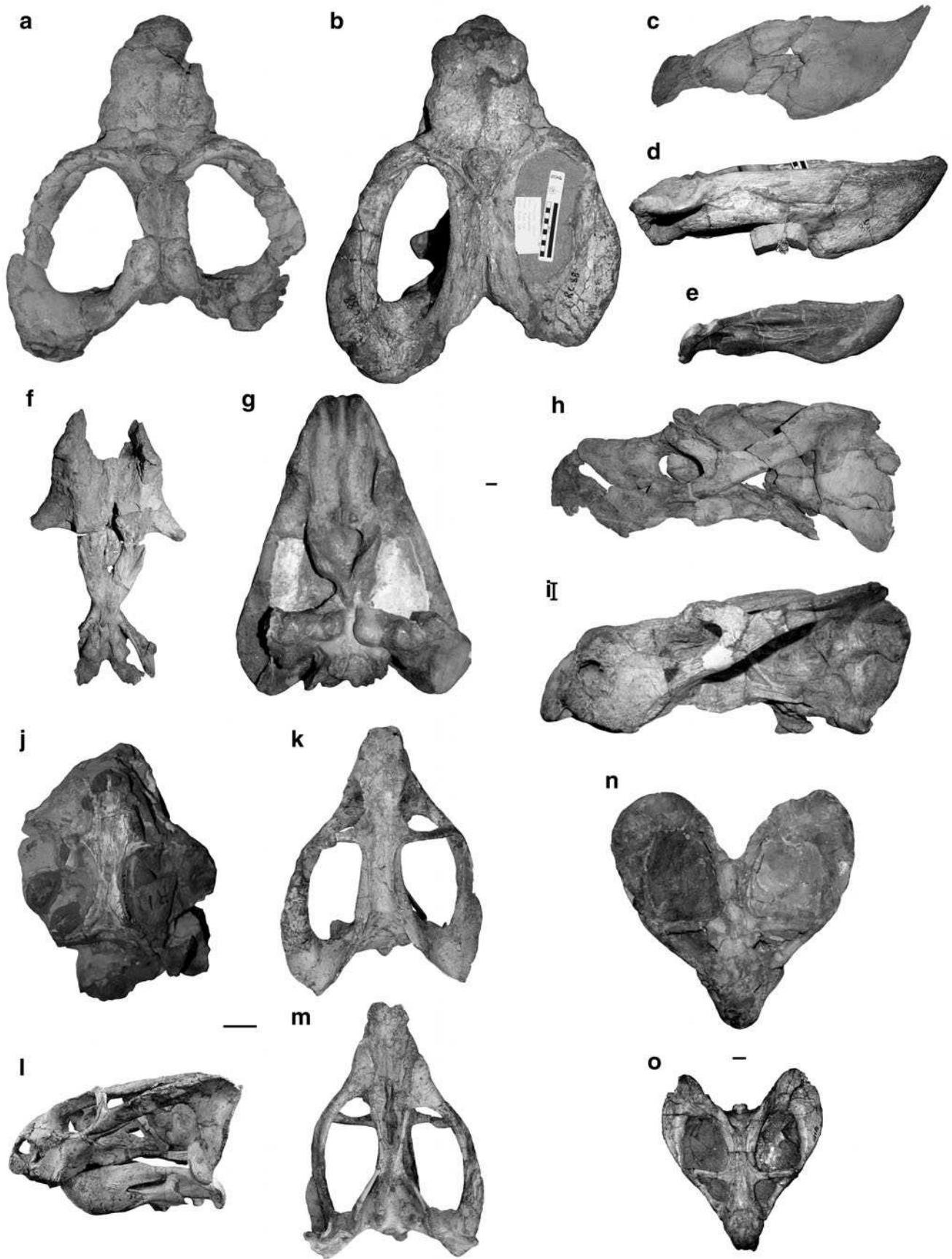
Oudenodon bainii Owen, 1860b

Figure 7.7j–n

Material: BP/1/3420, NHCC LB21, NHCC LB22, SAM-PK-11310, SAM-PK-11312, SAM-PK-11316, SAM-PK-11319, SAM-PK-K7940, SAM-PK-K7941, SAM-PK-K7944, TSK 67, TSK 69, TSK 70, TSK 95, TSK 101, TSK 107. NHCC LB23, SAM-PK-K7934, SAM-PK-K7943, SAM-PK-K7947, TSK 103, TSK 112 also are likely specimens of *O. bainii*, but incompleteness and/or lack of preparation make these identifications tentative.

Localities: Locality 4 of Drysdall and Kitching (1963) (BP/1/3420, SAM-PK-11310, SAM-PK-11312, SAM-PK-11316, SAM-PK-11319, SAM-PK-K7940, SAM-PK-K7941, SAM-PK-K7944), locality L30 (NHCC LB21), locality L37 (NHCC LB22), Kerr's (1974) Locality 11 (TSK 67, TSK 69, TSK 70, TSK 95, TSK 101, TSK 107). NHCC LB23 was collected at locality L59. TSK 103 was collected at Kerr's (1974) Locality 11, and TSK 112 was collected at Kerr's (1974) Locality 13. The locality information for SAM-PK-K7943 and SAM-PK-K7947 is: "Probably from horizon in Upper Green Marls. About 1 ¼ miles South of Mpundu. Horizon 4" (Boonstra 1938, p. 37), which would correspond to Drysdall and Kitching's (1963) Locality 4. Specific locality information is not available for SAM-PK-K7943; the SAM collections database only states that it is from the Luangwa Valley (S. Kaal, personal communication, 2010).

Identifying Characteristics: Keyser (1975), Cluver and Hotton (1981), and Botha and Angielczyk (2007) are the most detailed recent papers to address the ways in which *Oudenodon bainii* can be differentiated from other dicynodonts, and we follow the latter's hypothesis that Zambian *Oudenodon* specimens most likely represent *O. bainii* and not a distinct species. The Zambian specimens we refer to *O. bainii* vary widely in the quality of their preservation and the degree to which they have been prepared. The following characters are ones we focused on for identifying *O. bainii* specimens, although not all are preserved or visible in all specimens: medium size; thin ridge present on anterior surface of premaxilla; paired nasal bosses that are rounded and overhang the external nares; pineal boss absent; temporal bar in which the parietals are exposed between the postorbitals and are often slightly depressed relative to the postorbitals; tusks and "postcanines" absent;



◀ **Fig. 7.7** Zambian specimens of *Kitchinganomodon crassus* and *Oudenodon bainii*, and comparative material. **a** Skull of *Kitchinganomodon crassus* from Zambia (TSK 23) in dorsal view. **b** Holotype skull of *Kitchinganomodon crassus* from South Africa (RC 88) in dorsal view. **c** Mandible of *Kitchinganomodon crassus* from Zambia (TSK 23) in right lateral view. **d** Holotype mandible of *Kitchinganomodon crassus* from South Africa (RC 88) in right lateral view. **e** Mandible of *Rhachiocephalus magnus* from Tanzania [GPIT K30 g(uk)] in right lateral view. Note the steeper angulation of the posteroventral corner of the dentary in the *Kitchinganomodon* specimens. **f** Skull of *Kitchinganomodon crassus* from Zambia (TSK 23) in ventral view. Note that this photograph was taken before the specimen was completely reassembled. **g** Skull of *Kitchinganomodon crassus* from South Africa (BP/1/819) in ventral view. Note the robust anterior pterygoid rami in this specimen and in TSK 23. **h** Skull of *Kitchinganomodon crassus* from Zambia (TSK 23) in left lateral view. **i** Skull of *Kitchinganomodon crassus* from South Africa (RC 88)

in left lateral view. **j** Unprepared partial skull of *Oudenodon bainii* (holotype of *Dicynodon luangwanensis*) from Zambia (SAM-PK-11310) in dorsal view. **k** Skull of *Oudenodon bainii* from Zambia (TSK 67) in dorsal view. **l** Skull and mandible of *Oudenodon bainii* from Zambia (TSK 67) in left lateral view. **m** Skull of *Oudenodon bainii* from Zambia (TSK 67) in ventral view. **n** Skull of *Oudenodon bainii* (holotype of *Dicynodon helenae*) from Zambia (SAM-PK-11312) in dorsal view, showing the heart shape sometimes used as a character to differentiate Zambian *Oudenodon* specimens from South African specimens. **o** Skull of *Oudenodon bainii* from South Africa (CGP MIF 133) in dorsal view. Note that this specimen shows a similar heart shape in dorsal view as SAM-PK-11312. Upper scale bar applies to panels **a–i**, lower left scale bar applies to panels **j–m**, and lower right scale bar applies to panels **n–o**. Scale bars are 20 mm. Photographs in panels **a** and **h** courtesy of C. Kammerer; photographs in panels **k–m** courtesy of S. Jasinoski

postcaniniform crest present; labial fossa surrounded by the palatine, maxilla, and jugal absent; palatal surface of the palatine possesses raised rugose posterior section and a smoother anterior section that is flush with the secondary palate; interpterygoid vacuity relatively long, reaching the level of the palatal surface of the palatines; mid-ventral plate of vomer narrow and blade-like in ventral view; intertuberal ridge between basioccipital tubera absent.

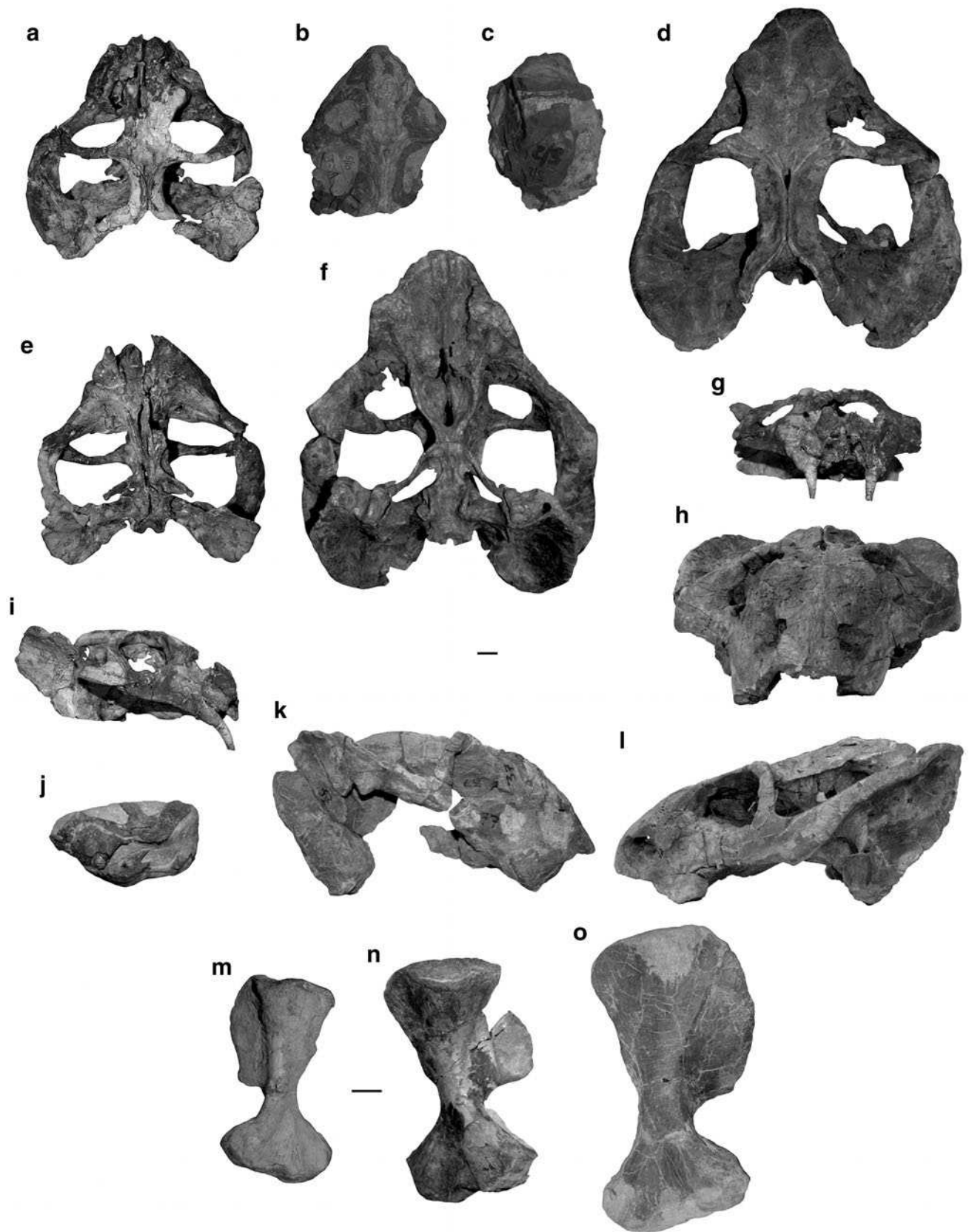
Keyser (1975) provided a detailed justification for why the holotypes of four species described by Boonstra (1938) (SAM-PK-11301, type of *Dicynodon luangwanensis* (Fig. 7.7j, n); SAM-PK-11312, type of *Dicynodon helenae*; SAM-PK-11316, type of *Dicynodon euryceps*; SAM-PK-11319, type of *Dicynodon parabreviceps*) are best regarded as part of *Oudenodon*. He favored retaining them as a species (*O. luangwanensis*) distinct from South African *O. bainii* on account of the wide zygomatic arches that give the skull a heart shape in dorsal view. We do not consider this to be a valid diagnostic character because a similar morphology can be found among South African specimens (Fig. 7.7o), and the morphometric results of Botha and Angielczyk (2007) are consistent with the presence of only one species.

The remaining specimens show varying numbers of the characters listed above depending on the quality of their preservation and the degree to which they have been prepared (e.g., compare Fig. 7.7j–m). For example, TSK 67 is extremely well preserved and completely prepared, and it shows all of the diagnostic characters listed above (Fig. 7.7k, l, m). TSK 101 is a nearly complete skull, but it is mostly unprepared. Nevertheless, it possesses a thin snout ridge, rounded nasal bosses, and a temporal bar in which the parietals are exposed but depressed below the level of the postorbitals; tusks are absent, but a postcaniniform crest is present. NHCC LB21 also is relatively complete, but even though it is entirely unprepared, the snout ridge, nasal bosses, temporal bar, and caniniform processes are

sufficiently visible to confirm that it is *O. bainii*. TSK 69 consists only of a snout, but it is well-prepared, and paired, rounded nasal bosses, a median snout ridge, palatines with rugose posterior surfaces and smoother, flush anterior surfaces, postcaniniform crest, and absence of tusks can all be easily observed. Finally, TSK 103 and NHCC LB23 are examples of specimens that can only be tentatively identified as *O. bainii*. TSK 103 is a well preserved and prepared occiput that includes part of the temporal bar and part of the zygomatic portion of the squamosal. The size of the specimen and the morphology of the preserved portion of the temporal bar are consistent with it representing *O. bainii*, but it presents too few diagnostic features to confirm its identity. Likewise, NHCC LB23 is a fragmentary, unprepared snout. The specimen is tuskless, and the general shapes of the snout and caniniform process are consistent with *O. bainii*, but additional preparation would be necessary to confirm this identification.

Synonyms in Luangwa Basin Literature: *Dicynodon lutriceps*, *Dicynodon* cf. *breviceps*, *Dicynodon corstorphine*, *Dicynodon* cf. *corstorphine*, *Dicynodon* cf. *milletti*, *Dicynodon latirostris*, *Dicynodon luangwanensis*, *Dicynodon helenae*, *Dicynodon euryceps*, *Dicynodon parabreviceps*, *Oudenodon luangwanensis* (Boonstra 1938; Drysdall and Kitching 1963; Kitching 1963; Keyser 1975; Fröbisch 2008, 2009). The majority of these species are based on types from the Karoo Basin of South Africa, and justifications of these synonymies can be found in Keyser (1975). Two misspellings of the species name *luangwanensis* Boonstra, 1938 are commonly used in the literature with the genus name *Oudenodon*: *O. luangwaensis* (Drysdall and Kitching 1963; Kitching 1963; Keyser 1972, 1975; Cluver and Hotton 1981; Jacobs et al. 2005) and *O. luangwensis* (King 1988; Botha and Angielczyk 2007).

Previous Reports: Boonstra (1938) made the first report of material from the Luangwa Basin that was eventually referred to *O. bainii*. Drysdall and Kitching (1962, 1963),



◀ **Fig. 7.8** Zambian specimens of *Dicynodon huenei* and comparative material. **a** Skull of *Dicynodon huenei* from Zambia (TSK 14) in dorsal view. **b** Unprepared skull likely of *Dicynodon huenei* from Zambia (NHMUK field number 5-10) in dorsal view. **c** Unprepared partial skull likely of *Dicynodon huenei* from Zambia (NHMUK field number 5-2) in left dorsolateral view. NHMUK field number 5-2 and NHMUK field number 5-10 are the primary evidence for the presence of *Dicynodon huenei* in the northern sub-basin of the Luangwa Basin. **d** Skull of *Dicynodon huenei* from Tanzania (CAMZM T1089) in dorsal view. **e** Skull of *Dicynodon huenei* from Zambia (TSK 14) in ventral view. **f** Skull of *Dicynodon huenei* from Tanzania (CAMZM T1089) in ventral view. **g** Skull of *Dicynodon huenei* from Zambia (TSK 14) in anterior view. **h** Skull of *Dicynodon huenei* from Tanzania (CAMZM T1089) in anterior view. Note the expanded

suborbital bar and plate-like distal end of the postorbital bar in both specimens. **i** Skull of *Dicynodon huenei* from Zambia (TSK 14) in right lateral view. **j** Unprepared skull of *Dicynodon huenei* from Zambia (TSK 27) in anterolateral view. **k** Skull of *Dicynodon huenei* from Zambia (TSK 37) in right lateral view. **l** Skull of *Dicynodon huenei* from Tanzania (CAMZM T1089) in left lateral view. Note the thickened anterior portion of the zygomatic arch, especially in TSK 14, TSK 27, and CAMZM T1089. **m** Left humerus of *Dicynodon huenei* from Zambia (TSK 14) in dorsal view. **n** Right humerus of *Dicynodon huenei* from Zambia (TSK 37) in dorsal view. **o** Right humerus of *Dicynodon huenei* from Tanzania (NMT RB44) in dorsal view. Upper scale bar applies to panels **a–l**; lower scale bar applies to panels **m–o**. Scale bars are 20 mm

Kitching (1963), Keyser (1972, 1975), Anderson and Cruickshank (1978), Cluver and Hotton (1981), Cooper (1982), King (1988, 1992), King and Jenkins (1997), Angielczyk (2002), Rubidge (2005), and Fröbisch (2009) all mentioned the presence of *Oudenodon* in the Luangwa Basin, although Drysdall and Kitching (1963) and Kitching (1963) primarily did so using synonyms.

Rhachiocephalidae Maisch, 2000

Kitchinganomodon crassus Maisch, 2002a

Figure 7.7a, c, f, h

Material: TSK 23.

Localities: Kerr's (1974) Locality 2 (TSK 23).

Identifying Characteristics: Maisch (2002a; also see Maisch 1999) erected the genus *Kitchinganomodon* and identified characters that can be used to distinguish *K. crassus* from *Rhachiocephalus magnus*. Among Maisch's (2002a) characters, TSK 23 possesses broadened anterior pterygoid rami, a wide, robust snout, and large nasal bosses that are located directly above the external nares. A rod of bone that seems to be formed by the vomer also extends along the midline of the interpterygoid vacuity, much like the condition in *K. crassus* that Maisch (2002a) described as closure of the interpterygoid vacuity by the vomer. Maisch's (2002a) remaining diagnostic characters are difficult to assess because of preservation, but TSK 23 is suggestive of the presence of at least some of these (e.g., the extensive ossification of the lateral wall of the braincase). In addition, the overall shape of the skull of TSK 23 (Fig. 7.7a), especially in dorsal view, shows a strong resemblance to the type of *K. crassus* (Fig. 7.7b). Finally, the shape of the mandible in lateral view in TSK 23 (Fig. 7.7c) is much more similar to *K. crassus* (Fig. 7.7d) than that of *R. magnus* (Fig. 7.7e). The symphyseal region of the dentary is much deeper than the postdentary bones in TSK 23 and RC 88 (the holotype of *K. crassus*), with the ventral and posterior edges of the symphyseal region meeting in a sharp corner. In contrast, although symphyseal region of *R. magnus* also is deeper than the postdentary bones, the disparity is not as marked, and the posterior and ventral edges form a much more obtuse angle.

Synonyms in Luangwa Basin Literature: Strictly speaking, there are no synonyms of *Kitchinganomodon crassus* in the Luangwa Basin literature. However, Angielczyk and Kurkin (2003), Angielczyk (2007), and Angielczyk and Rubidge (2010) included TSK 23 among the *Rhachiocephalus* specimens they consulted for character state codings in their phylogenetic analyses.

Previous Reports: There are no previous reports of *Kitchinganomodon crassus* from Zambia.

Dicynodontoidea (Owen, 1860a)

Dicynodon huenei Haughton, 1932

Figure 7.8a–c, e, g, i–k, m, n

Material: TSK 14, TSK 27, TSK 37. TSK 40 may represent *D. huenei*, but is mostly unprepared. TSK 83 includes several juvenile specimens that were described by Gale (1988) and referred to *Diictodon*, but this identification has been questioned (Angielczyk and Sullivan 2008; also see above). *Dicynodon huenei* may be a better identification but is somewhat tentative because independent data on the earliest ontogenetic stages of this taxon are unavailable. Three specimens in the NHMUK that were collected by the 1963 expedition (field numbers 5-2, 5-4, 5-10) may represent *D. huenei*, but these specimens are unprepared.

Localities: Kerr's (1974) Locality 1 (TSK 14), Kerr's (1974) Locality 3 (TSK 27, TSK 37). TSK 40 was collected at Kerr's (1974) Locality 7. TSK 83 was collected at "Locality 14." This may correspond to Kerr's (1974) Locality 6 (because the locality is described as producing several small dicynodont skulls in that reference), but this is uncertain. The NHMUK specimens with field numbers were collected at Locality 5 of Drysdall and Kitching (1963).

Identifying Characteristics: Kammerer et al. (2011) discussed the basis for recognizing *Dicynodon huenei* as a distinct and valid species. TSK 14 was described in detail by King (1981), and she referred the specimen to *Dicynodon trigonocephalus*. Kammerer et al. (2011) concluded that the holotype of *D. trigonocephalus* (RC 38) is a somewhat distorted juvenile of *Dicynodon lacerticeps*, and that *D. lacerticeps* and *D. huenei* are closely related. Two of the primary distinguishing features of *D. huenei* are an autapomorphic

thickening of the zygomatic arch, such that the structure appears somewhat flattened in lateral view, and twisting and widening of the postorbital bar, such that its distal end forms a mediolaterally-oriented, flattened plate on the zygomatic arch. Together, these characteristics give the suborbital portion of the face a wide, flattened appearance in anterior view (e.g., Fig. 7.8g). TSK 14 displays all of these characters, and also shows a strong resemblance to other specimens of *D. huenei* in other respects (e.g., CAMZM T1089; Fig. 7.8d, f, h, i). TSK 27 (Fig. 7.8j) is mostly unprepared, but the left zygomatic arch is well exposed, showing the autapomorphic thickening of the zygomatic arch typical of *D. huenei*. TSK 37 (Fig. 7.8k) consists of a relatively well preserved but somewhat unprepared skull, jaw, and portions of the postcranial skeleton. The skull resembles that of other *D. huenei* specimens, including in the presence of a thickened zygoma, and the postcranial elements are also comparable to other *D. huenei* material (e.g., Fig. 7.8m, n, o). TSK 40 is a nearly unprepared skull preserved in a broken nodule, but a thickened zygoma is apparent. Specimen 5-2 (Fig. 7.8c) and 5-4 are incomplete and unprepared, but both have portions of their temporal bars exposed. These show extensive overlap of the postorbitals by the parietals, a morphology most consistent with *D. huenei* among Zambian dicynodonts. Specimen 5-10 (Fig. 7.8b) is somewhat more complete, and appears to have originally possessed a plate-like zygomatic arch and postorbital bar, although these areas are currently not well preserved. Although their poor preservation makes their identification somewhat tentative, these three specimens are important data points for establishing *D. huenei* in the northern part of the Luangwa Basin.

Synonyms in Luangwa Basin Literature: *Dicynodon lacerticeps*, *Dicynodon trigonocephalus*, “*Dicynodon*” *trigonocephalus* (Boonstra 1938; Drysdall and Kitching 1963; Kitching 1963; King 1981, 1988; King and Jenkins 1997; Fröbisch 2008, 2009).

Previous Reports: Boonstra (1938) reported a fragmentary specimen consisting of an occiput and an intertemporal bar in which the postorbitals strongly overlapped the parietals. He referred this specimen to *Dicynodon lacerticeps*, and referred to it by the field number R.40. None of the catalogued Zambian material at the SAM has this field number associated with it (S. Kaal, personal communication, 2011), so we were unable to examine the specimen. Although Boonstra’s description is not detailed enough to definitively state whether the specimen is *D. lacerticeps* or *D. huenei*, we regard the most parsimonious interpretation of this report as the latter species. Drysdall and Kitching (1962, 1963) and Kitching (1963) also reported *Dicynodon* from the Luangwa Basin, but most of these reports represent *Diictodon* or *Oudenodon* instead (see above). Drysdall and Kitching’s (1963) and Kitching’s (1963) specific mentions of *Dicynodon lacerticeps* are only

repetitions of Boonstra’s (1938) original report. Anderson and Cruickshank (1978), Cooper (1982), King (1988, 1992), and Rubidge (2005) all noted the presence of *Dicynodon* in Zambia, but did not refer to a particular species. King’s (1981) paper focused on the skeletal morphology and function of TSK 14, but she did note the Zambian origin of the specimen and referred it to *D. trigonocephalus*. King and Jenkins (1997) also mentioned the presence of *D. trigonocephalus* in the Luangwa Basin as part of the biostratigraphic context for their putative specimen of *Lystrosaurus*. In the taxonomic framework used here, both of these reports should be considered to represent *D. huenei*. Lucas (1997, 1998a, 2002, 2005, 2006, 2009) used the occurrence of *Dicynodon* in the Luangwa Basin as part of his tetrapod biochronology for the Permian, but in most cases did not explicitly discuss any particular species of the genus. He does mention *D. trigonocephalus* in Lucas (1997, 1998a) following King (1981), and his later citations of King and Jenkins (1997) would imply that his usage focuses on this species as well (here recognized as *D. huenei*; see above and Kammerer et al. 2011). However, the locality he gives [e.g., “‘Horizon 5’ of Boonstra in the Luangwa Valley, 4.8–6.4 km north of Nt’awere, Zambia” (Lucas 2006, p. 83; also see Lucas 1997, 1998a, 2001)] corresponds to the type locality of *Dicynodon roberti*, a junior synonym of *Syops vanhoepeni* (see Kammerer et al. 2011, and below). Fröbisch (2009) regarded four species of *Dicynodon* sensu lato as potentially valid and occurring in the Luangwa Basin: *D. lacerticeps*, “*D.*” *trigonocephalus*, “*D.*” *roberti*, and “*D.*” *vanhoepeni*. The first two of these correspond to material we assign to *D. huenei*.

Syops vanhoepeni (Boonstra, 1938)

Figure 7.9a–i

Material: NHCC LB25, SAM-PK-11311, SAM-PK-11325a, SAM-PK-11325b.

Localities: Locality 4 of Drysdall and Kitching (1963) (SAM-PK-11311), Locality 5 of Drysdall and Kitching (1963) (SAM-PK-11325a, SAM-PK-11325b), locality L61 (NHCC LB25).

Identifying Characteristics: Kammerer et al. (2011) discuss the basis for recognizing *Syops vanhoepeni* as a valid species and the rationale for considering *D. roberti* to be its junior synonym. The four specimens of *S. vanhoepeni* are unprepared, but enough morphology is exposed in each to allow them to be grouped together confidently. All four possess a similar long, low snout profile, large external nares, caniniform processes with a postcaniniform crest, and large, robust tusks. SAM-PK-11325a and NHCC LB25 also share a unique pattern of ornamentation on the dorsal surface of the snout: a thick, rounded median ridge that is flanked laterally by shallow depressions, which in turn are bounded laterally by elongate, ridge-like nasal bosses

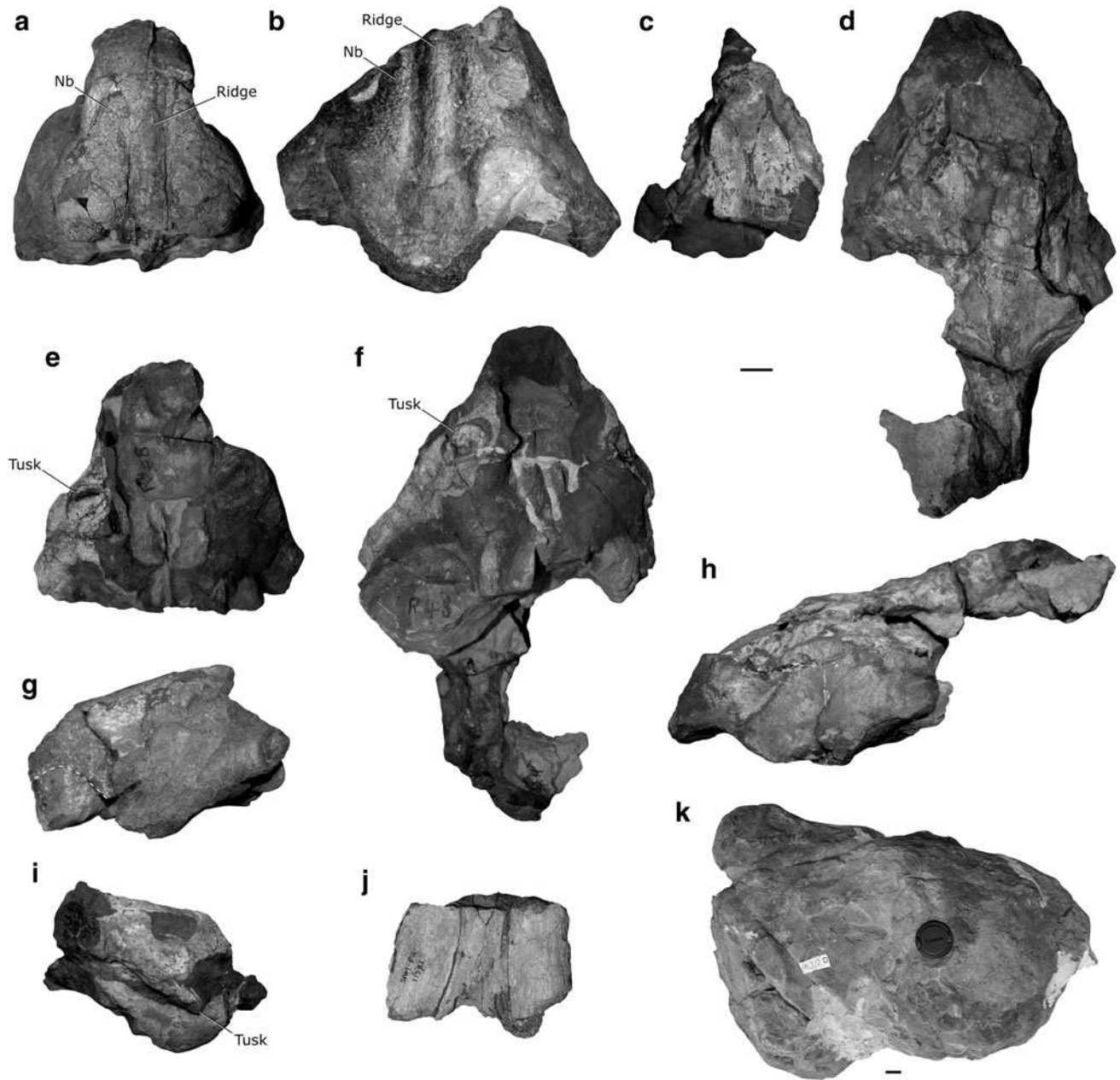


Fig. 7.9 Zambian specimens of *Syops vanhoepeni* and *Haughtoniana magna*, and supposed Zambian specimen of *Aulacephalodon bainii*. **a** Snout of *Syops vanhoepeni* [SAM-PK-11325a (paratype of *Dicynodon roberti*)] in dorsal view. **b** Snout of *Syops vanhoepeni* (NHCC LB25) in dorsal view. Note the similar configuration of paired nasal bosses separated by a strong median ridge in NHCC LB25 and SAM-PK-11325a. **c** Snout of *Syops vanhoepeni* (holotype of *Dicynodon vanhoepeni*) (SAM-PK-11311) in dorsal view. **d** Partial skull of *Syops vanhoepeni* (holotype of *Dicynodon roberti*) (SAM-PK-11325b) in dorsal view. **e** Snout of *Syops vanhoepeni* (paratype of *Dicynodon roberti*) (SAM-PK-11325a) in ventral view. **f** Partial skull of *Syops vanhoepeni* (holotype of *Dicynodon roberti*) (SAM-PK-11325b) in ventral view. **g** Snout of *Syops vanhoepeni* (paratype of *Dicynodon roberti*) (SAM-PK-11325a) in left lateral view. Dashed line highlights

the alveolar margin (*below the line is matrix*). **h** Partial skull of *Syops vanhoepeni* (holotype of *Dicynodon roberti*) (SAM-PK-11325b) in left lateral view. **i** Snout and partial mandible of *Syops vanhoepeni* (holotype of *Dicynodon vanhoepeni*) (SAM-PK-11311) in right lateral view. **j** Posterior portion of temporal bar of the holotype of *Haughtoniana magna* (SAM-PK-11321) in dorsal view. **k** Probable left lateral view of an unprepared large dicynodont skull (BP/1/3242) identified in the BP collections catalogue as *Aulacephalodon bainii*. The exact orientation of this specimen is uncertain because no diagnostic structures are exposed on its surface. Upper scale bar applies to panels **a–j**; lower scale bar applies to panel **k**. Scales bars are 20 mm. Photograph in panel **j** courtesy of C. Kammerer; photograph in panel **k** courtesy of B. Rubidge

(Fig. 7.9a, b). The snout region is more poorly preserved in SAM-PK-11311 and SAM-PK-11325b, making it impossible to confirm whether these specimens had the same pattern of ornamentation, but part of a median ridge is preserved on the premaxilla of SAM-PK-11325b. NHCC LB25 and SAM-PK-11325b (e.g., Fig. 7.9d) also share a relatively narrow intertemporal bar in which the postorbitals extensively overlap the parietals, but this portion of the skull is not preserved in SAM-PK-11325a or SAM-PK-11311. *Syops vanhoepeni* shows a number of superficial similarities to *Odontocyclops* and *Kitchinganomodon*, but can be differentiated from both even with the fragmentary material currently available. *Syops vanhoepeni* can be distinguished from *Odontocyclops* based on the latter taxon's much more concave dorsal snout surface, absence of a strong median ridge on the dorsal surface of the snout, and wider exposure of the parietals between the postorbitals on the temporal bar. *Syops vanhoepeni* differs from *Kitchinganomodon crassus* in possessing tusks, more elongate nasal bosses, a wide rounded median ridge on the dorsal surface of the snout, and the absence of a pineal boss.

Synonyms in Luangwa Basin Literature: *Dicynodon vanhoepeni*, *Dicynodon roberti* (Boonstra 1938; King 1988); “*Dicynodon*” *vanhoepeni*, “*Dicynodon*” *roberti* (Fröbisch 2008, 2009).

Previous Reports: Boonstra (1938) described *Dicynodon vanhoepeni* and *D. roberti*. Drysdall and Kitching (1963) included both *D. vanhoepeni* and *D. roberti* in their list of taxa reported from the Luangwa Basin, but Kitching (1963) only included *D. vanhoepeni*. King (1988) listed both species in the systematic section of her monograph, but only included the genus *Dicynodon* without reference to particular species in her faunal list for Zambia. Anderson and Cruickshank (1978), King (1992), and Rubidge (2005) also only included the genus *Dicynodon* without reference to particular species. As noted above, at least some of the material referred to the genus *Dicynodon* by Lucas (1997, 1998a, 2001, 2002, 2005, 2006, 2009) and used in his tetrapod biochronology corresponds to specimens of *S. vanhoepeni*. Fröbisch (2009; also see Fröbisch 2008) included both *D. vanhoepeni* and *D. roberti* in his compilation, but noted that their validity had not been reassessed since their description.

Permian Dicynodonts Whose Presence in Zambia Cannot be Confirmed

Pachytegos stockleyi Haughton, 1932

Previous Reports: King (1988) included *Pachytegos* in her faunal list for Zambia. However, we are aware of no other reports of *Pachytegos* from Zambia and suspect this is an error since *Pachytegos* is not included in her faunal list for Tanzania, despite the fact that the only published material attributed to the taxon originated in Tanzania (Haughton 1932; Cox 1964; Gay and Cruickshank 1999).

Cistecephalus microrhinus Owen, 1876

Synonyms in Luangwa Basin Literature: *Cistecephalus planiceps* (Drysdall and Kitching 1963; Kitching 1963). Keyser (1973b) discusses the synonymy of *C. planiceps* and *C. microrhinus*.

Previous Reports: Drysdall and Kitching (1962, 1963) and Kitching (1963) were the first authors to report specimens of *Cistecephalus* in the Luangwa Basin. Several additional authors subsequently cited these records, primarily in biogeographic and biostratigraphic contexts (Anderson and Cruickshank 1978; Cooper 1982; King 1988, 1992; Smith and Keyser 1995; Lucas 2002, 2005, 2006; Angielczyk 2002; Rubidge 2005; Fröbisch 2009). However, as noted above, Drysdall and Kitching did not provide photographs of or specimen numbers for any of their *Cistecephalus* records. Because all Zambian cistecephalid material available in collections appears to be referable to a new taxon (see above), we consider there to be no reliable evidence of *Cistecephalus* in the Luangwa Basin at this time.

Tropidostoma microtrema (Seeley, 1889)

Previous Reports: Drysdall and Kitching (1963) and Kitching (1963) stated that they collected specimens of *Dicynodon acutirostris* in Zambia, a species that Keyser (1973a) and Botha and Angielczyk (2007) considered to be a junior synonym of *Tropidostoma microtrema*. Based on this taxonomic change, Fröbisch (2009) included *Tropidostoma* in the dicynodont fauna of the Madumabisa Mudstone in Zambia. Keyser (1981) also stated that *Tropidostoma* was present in the Luangwa Basin. The type of *D. acutirostris* was collected in South Africa, and we have not identified any Zambian specimens in our search of museum collections or our fieldwork that can be referred to *T. microtrema*. Drysdall and Kitching (1963) and Kitching (1963) did not provide numbers for any of the specimens they identified as *D. acutirostris*, so the accuracy of their identification cannot be checked. Therefore, because there are no voucher specimens documenting the presence of *T. microtrema* (= *T. dubium*; see Kammerer et al. 2011), it should not be included in the Permian dicynodont fauna of the Luangwa Basin.

Rhachiocephalus magnus (Owen, 1876)

Previous Reports: Boonstra (1938) was the first to refer a Zambian dicynodont specimen to *Rhachiocephalus* (the holotype of *Rhachiocephalus dubius*). Keyser (1975) included this species in his taxonomic review but hinted that the specimens in question may represent a distinct taxon, an observation that was confirmed with the erection of *Odontocyclops* (Keyser 1979; Keyser and Cruickshank 1979; Angielczyk 2002). Drysdall and Kitching (1963) and Kitching (1963) reported *Neomegacyclops* and *Platycyclops*, now recognized as junior synonyms of *Rhachiocephalus* (Keyser 1975; Cluver and King 1983; also see

Maisch 2002a). Anderson and Cruickshank (1978), King (1988, 1992), and Fröbisch (2009) included *Rhachiocephalus* in their faunal tabulations for the Luangwa Basin following Drysdall and Kitching (1963). However, Drysdall and Kitching's (1963) and Kitching's (1963) reports of *Rhachiocephalus* appear to be based on field observations, and we know of no voucher specimens that can confirm the presence of this taxon in Zambia. The best potential candidate (TSK 23) instead represents *Kitchinganomodon*. Therefore we cannot include *Rhachiocephalus* in the fauna of the Madumabisa Mudstone at this time.

Haughtoniana magna Boonstra, 1938

Figure 7.9j

Material: SAM-PK-11321.

Localities: Locality 4 of Drysdall and Kitching (1963) (SAM-PK-11321).

Identifying Characteristics: The holotype of *Haughtoniana magna* consists of fragmentary cranial and postcranial material of a large dicynodont. Boonstra (1938) erected the species primarily on the basis of the construction of the intertemporal bar. In particular, he noted that the postorbitals were wide, nearly horizontal, and in the same plane as the parietals; the parietals were relatively narrow; and the interparietal extended onto the dorsal surface of the skull roof (Fig. 7.9j). Keyser (1975) and Cluver and King (1983) considered it to be a likely nomen dubium, and King (1988) also cast doubt on its validity, although she suggested it might be referable to *Aulacephalodon*. We agree that the type of *H. magna* is too fragmentary to allow a definitive identification, either as a valid species or as a synonym of another species. Moreover, the temporal bar fragment appears to have lost some of its original bone surface, either through weathering or preparation in which the hematitic matrix was not removed cleanly from the bone. We suggest that this may account for the fact that the parietals and postorbitals are in the same plane and potentially explains the oddly-shaped exposure of the interparietal on the skull roof. The general size and appearance of the type is similar to the temporal bar of *Odontocyclops* (e.g., BP/1/3419; Fig. 7.6b), although uncertainty about whether the exposure of the interparietal on the skull roof is real or an artifact prevents the definitive identification of *H. magna* as a synonym of *O. whaitsi* (the interparietal is not exposed on the skull roof in *O. whaitsi*; Angielczyk 2002).

Synonyms in Luangwa Basin Literature: None.

Previous Reports: Boonstra (1938) described *Haughtoniana magna*, and Drysdall and Kitching (1963) and Kitching (1963) noted its occurrence in the Luangwa Basin. Keyser (1975), Cluver and King (1983), and King (1988) considered it in their systematic treatments, and King (1988) also included it in her faunal list for Zambia. Fröbisch (2009) also mentioned *H. magna*, but noted that its

taxonomic status was uncertain and did not include it in his final faunal list for Zambia.

Aulacephalodon bainii (Owen, 1845)

Figure 7.9k

Previous Reports: Drysdall and Kitching (1962, 1963) and Kitching (1963) were the first to report *Aulacephalodon*, including the species *A. laticeps* (a synonym of *A. bainii*; see Cluver and King 1983) from the Luangwa Basin. The records appear to represent field identifications of specimens from at least their Localities 1 and 4 because no specimen numbers for collected material were cited. Kitching (1963) also used the name *Aulacocephalodon*, which is an often-repeated misspelling of *Aulacephalodon* (Tollman et al. 1980). Several subsequent authors included *Aulacephalodon* in the Zambian dicynodont fauna based on these reports (Anderson and Cruickshank 1978; Cooper 1982; King 1988, 1992; Angielczyk 2002; Fröbisch 2009). However, in our examination of material in collections, we found no specimens that can be positively identified as *Aulacephalodon*. BP/1/3242, a specimen originating at Drysdall and Kitching's Locality 1 that is identified in the BP catalogue as *Aulacephalodon*, is completely unprepared (Fig. 7.9k) and displays no characters allowing it to be identified. King's (1988) suggestion that *Haughtoniana magna* might represent *Aulacephalodon* also is likely incorrect (see above). We did not observe any specimens that could be positively identified as *Aulacephalodon* during our fieldwork, and we suspect that previous reports likely represent *Odontocyclops* specimens, *Syops vanhoepeni* specimens, or large *Oudenodon* specimens that were misidentified in the field. Therefore, *Aulacephalodon* should not be included in faunal lists for the Madumabisa Mudstone.

Dicynodon lissops Broom, 1913

Previous Reports: Drysdall and Kitching (1963) stated that *Dicynodon lissops* was among a collection of four small anomodonts collected at their Locality 21, but provided no figures of or specimen numbers for this material. The holotype of *Dicynodon lissops* (AMNH 5508) is from the *Dicynodon* Assemblage Zone of South Africa, and was considered a junior synonym of *Daptocephalus leoniceps* by Kammerer et al. (2011). Given that this would be the only known occurrence of *Daptocephalus* from the Luangwa Basin of Zambia, we are hesitant to consider the report valid due to the lack of voucher specimens. Therefore we recommend that *Dicynodon lissops* and its senior synonym *Daptocephalus leoniceps* be excluded from the dicynodont fauna of the Luangwa Basin until positively identifiable material comes to light.

Dicynodon rhodesiensis

Previous Reports: Boonstra (1938, p. 384) included the name *D. rhodesiensis* in a list of *Dicynodon* species from Zambia. However, he does not mention or describe the species elsewhere in the paper, and we are unaware of any

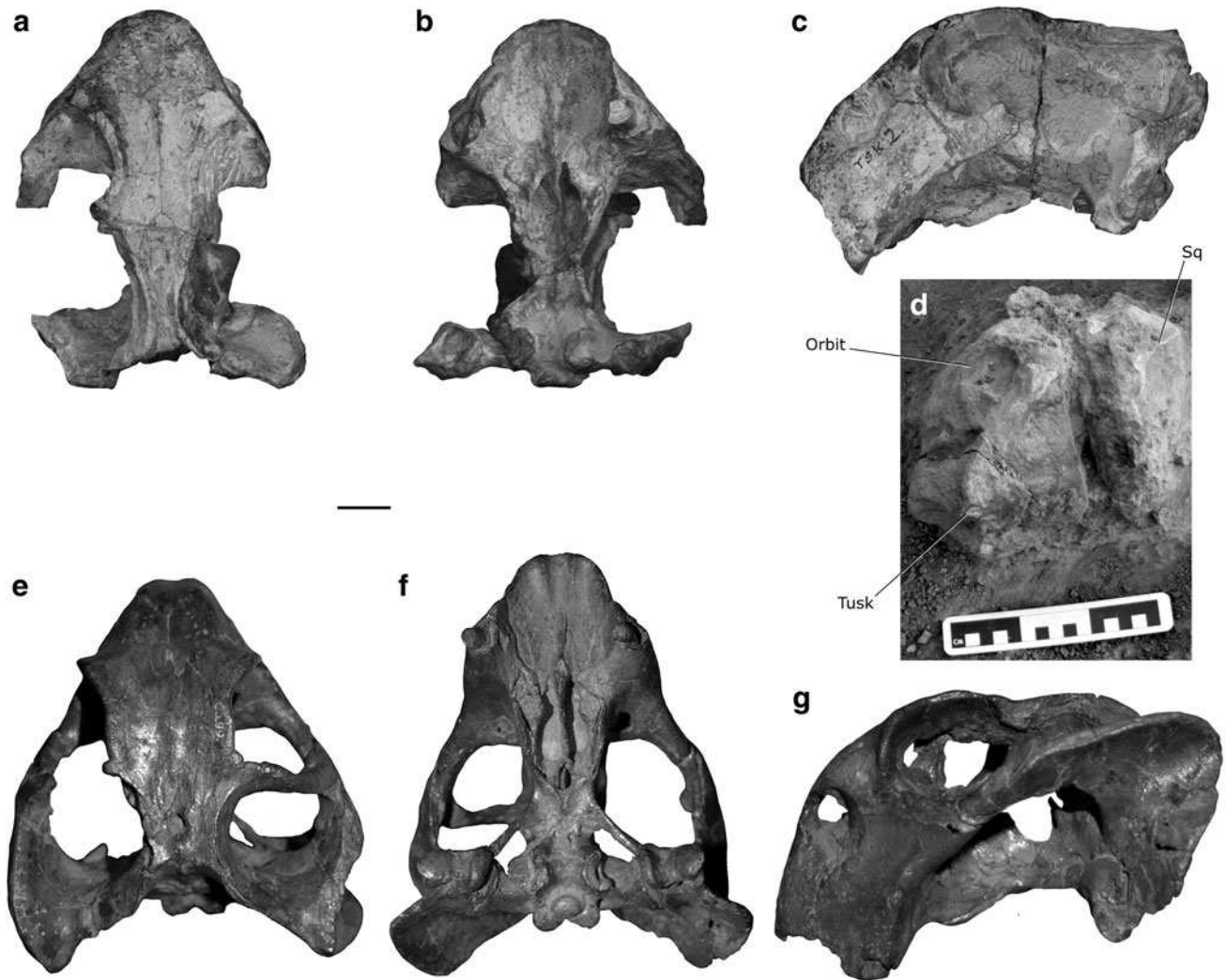


Fig. 7.10 Zambian specimens of Lystrosauridae n. g. & sp. and comparative specimen of *Lystrosaurus curvatus*. **a** Skull of Lystrosauridae n. g. & sp. from Zambia (TSK 2) in dorsal view. **b** Skull of Lystrosauridae n. g. & sp. from Zambia (TSK 2) in ventral view. **c** Skull of Lystrosauridae n. g. & sp. from Zambia (TSK 2) in left lateral view. **d** Field photograph of a probable specimen of the same

species represented by TSK 2. **e** Skull of *Lystrosaurus curvatus* from South Africa (NMQR 3595, formerly NMQR C299) in dorsal view. **f** Skull of *Lystrosaurus curvatus* from South Africa (NMQR 3595) in ventral view. **g** Skull of *Lystrosaurus curvatus* from South Africa (NMQR 3595) in left lateral view. Central scale bar applies to panels **b–c** and **e–g**, and is 20 mm. Scale bar in field photograph is 150 mm

mention of the species in the literature before or after this aside from Drysdall and Kitching's (1963) and Kitching's (1963) inclusion of the species in their lists of dicynodonts reported previously from the basin. Therefore, we conclude that the inclusion of the name must have been a mistake or oversight by Boonstra, and no species of this name was ever described from Zambia or elsewhere.

Lystrosaurus cf. *L. curvatus* (Owen, 1876)

Figure 7.10a–d

Material: TSK 2.

Localities: “East side of hunter’s track from Luangwa River, along north side of Munyamadzi River, Luangwa Valley, Zambia; Madumabisa Mudstones, Upper Permian”

(King and Jenkins 1997, p. 152). This corresponds to Kerr’s (1974) Locality 1 (also see Davies, 1981).

Identifying Characteristics: In their discussion of TSK 2, King and Jenkins (1997) listed a shortened basicranial axis, exposure of the parietals between the postorbitals on the skull roof, the deepened, ventrally-angled snout, the smooth premaxilla-maxilla suture, the extension of the premaxilla to the level of the prefrontals, and the pear shaped external naris bounded posteroventrally by a rugose ridge as characters that were typical of *Lystrosaurus*. They also suggested that the smoothly curving snout profile, the absence of a nasofrontal ridge and ornamentation on the frontals, the absence of strong prefrontal bosses, and a laterally flared squamosal implied the specimen most closely

resembled *L. curvatus* since these characters were included in diagnoses of *L. curvatus* available at the time (e.g., Cluver 1971; Cosgriff et al. 1982). They also have been included in diagnoses of *L. curvatus* in subsequent works dealing with the species composition of *Lystrosaurus* (e.g., Ray 2005; Grine et al. 2006; Botha and Smith 2007).

Although we agree that the TSK 2 shows some features similar to *Lystrosaurus*, and *L. curvatus* in particular, there are other characters that do not fit well with this identification and seem to fall outside of the ranges of intraspecific and intrageneric variation identified by authors such as Ray (2005) or Grine et al. (2006). For example, TSK 2 possesses an ectopterygoid, whereas the ectopterygoid is absent in *Lystrosaurus* (Cluver 1971) and recent authors have not identified this as a variable character within the taxon. Similarly, although the parietals are exposed between the postorbitals on the skull roof, the exposure is narrower than typical in *Lystrosaurus*, and the temporal bar is relatively longer anteroposteriorly in TSK 2 (e.g., compare Fig. 7.10a–e). The latter character is especially interesting because both Ray (2005) and Grine et al. (2006) noted that the temporal region displays negative allometry in *Lystrosaurus*. NMQR 3595 (*L. curvatus*; Fig. 7.10e) is consistent with this pattern, with the temporal bar being approximately 9 % of the basal length of the skull. In contrast, the temporal bar is approximately 21 % of the basal skull length in TSK 2 (Fig. 7.10a), despite the two specimens having nearly identical basal skull lengths. The frontal region, although slightly damaged in TSK 2, appears to have been narrower than typical in *L. curvatus*. This also is inconsistent with TSK 2 being part of *Lystrosaurus* because Ray (2005) and Grine et al. (2006) found that this measurement was isometric to positively allometric. The snout is angled ventrally in TSK 2, but the angle of deflection is less than in *L. curvatus* and it does not extend as far downwards (e.g., compare Fig. 7.10c–g). TSK 2 also lacks most of the conspicuous skull ornamentation in *Lystrosaurus*, such as a sagittal ridge on the premaxilla or a prefrontal nasal crest. Although these characters tend to be weakly developed in *L. curvatus* (Grine et al. 2006) and show evidence of sexual dimorphism (Ray 2005), their complete absence in a relatively large specimen such as TSK 2 (basal length approximately 144 mm) is surprising. These characters usually manifest in specimens with basal lengths in the range of 80–100 mm and are present in at least some *L. curvatus* specimens with sizes comparable to TSK 2 (Grine et al. 2006). Taken together, the differences between TSK 2 and definite specimens of *L. curvatus* (and other *Lystrosaurus*) species do not appear consistent with patterns of ontogenetic variation or sexual dimorphism identified by previous authors. Because of this, as well as the fact that a ventrally-extended snout is present in other dicynodonts such as *Kwazulusaurus shakai*, *Euptychognathus*

bathyrhynchus, and *Basilodon woodwardi* (Maisch 2002b; Kammerer et al. 2011), we do not think that TSK 2 can be identified unequivocally as *Lystrosaurus curvatus* or even *Lystrosaurus*. It may instead represent a new taxon (likely a lystrosaurid; see Kammerer et al. 2011), and it should be possible to collect additional material to characterize this taxon more fully. For example, Fig. 7.10d shows a specimen that we observed in 2009 but did not collect that has a relatively long, downturned snout and a narrow temporal region.

Synonyms in Luangwa Basin Literature: None.

Previous Reports: King and Jenkins (1997) were the first to report *Lystrosaurus* from the Luangwa Basin, and the occurrence was noted in other compilations examining therapsid biogeography (Angielczyk and Kurkin 2003; Rubidge 2005; Fröbisch 2009). It also was cited in a number of papers considering biostratigraphic correlations between the Luangwa and other basins (e.g., Lucas 1998b, 2006; Gay and Cruickshank 1999; Ray 1999; Catuneanu et al. 2005), as well as in studies of the end-Permian extinction and the origin and survivorship of *Lystrosaurus* during that event (e.g., Rubidge and Sidor 2001; Maisch 2002b; Botha and Smith 2006, 2007; Fröbisch 2007, 2008; Lucas 2009).

Triassic Dicynodont Fauna

We use the higher-level taxonomy of Maisch (2001) for Triassic dicynodonts, with minor changes reflecting the results of Kammerer et al. (2011). Our taxonomic results for Triassic dicynodonts are summarized in Table 7.2.

Systematic Paleontology

Dicynodontoidea (Owen, 1860a)

Kannemeyeriiformes Maisch, 2001

Kannemeyeriidae von Huene, 1948

Kannemeyeria lophorhinus Renault et al., 2003

Figure 7.11a–d

Material: BP/1/3638.

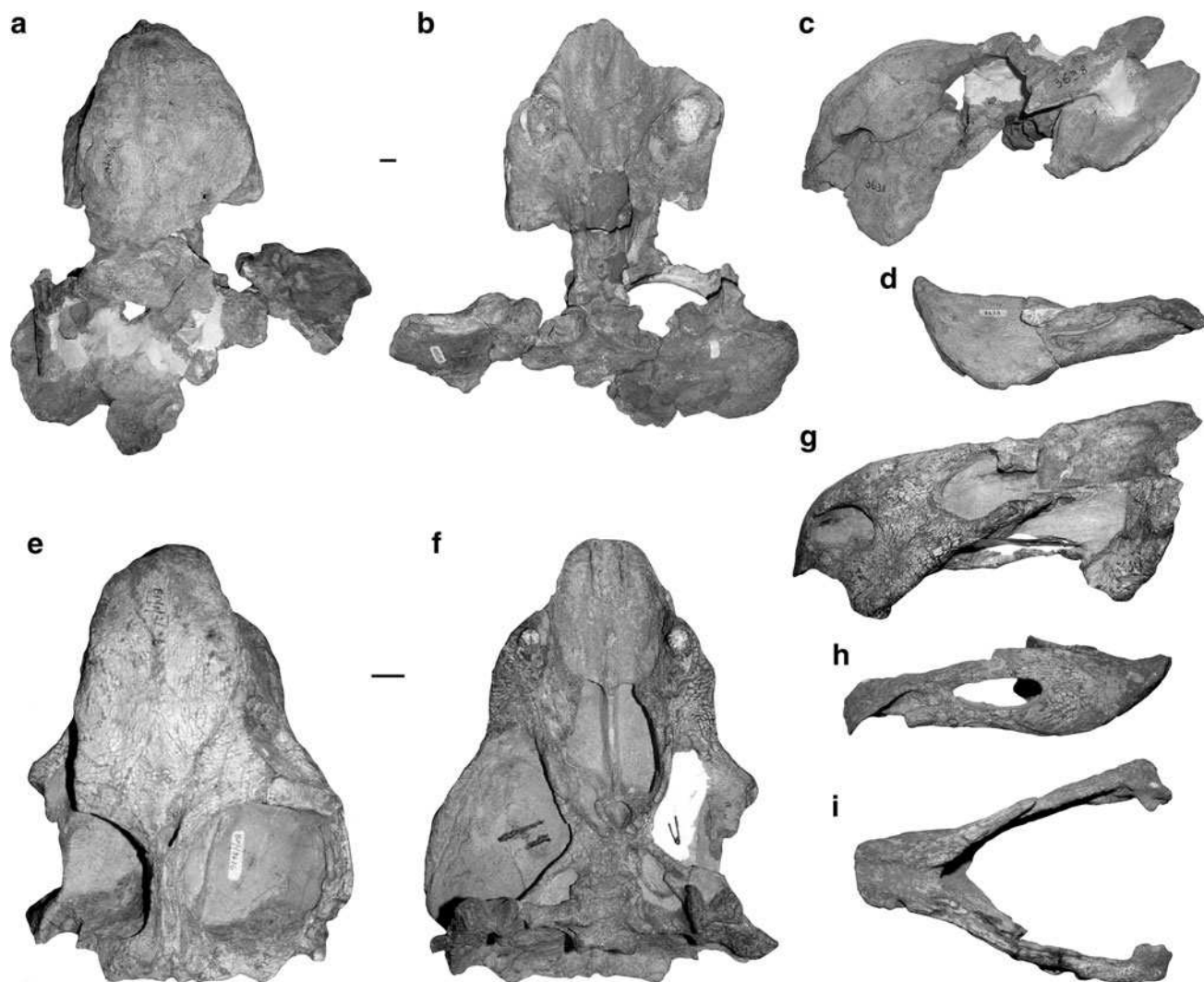
Localities: Locality 16 of Drysdall and Kitching (1963) (BP/1/3636). This locality is in Drysdall and Kitching's (1963; also see Kitching 1963) lower fossiliferous horizon of the Ntawere Formation.

Identifying Characteristics: Renault et al. (2003) provided the first diagnosis of *K. lophorhinus*, which was based on the detailed morphological study of Renault (2000). They implied that it possessed all of the diagnostic characters of *Kannemeyeria* identified by Renault (2000), such as a prominent median ridge on the snout, prominent caniniform

Table 7.2 Dicynodont taxa present in the Middle Triassic Ntawere Formation, Luangwa Basin, Zambia, and synonyms used in the literature on the Luangwa Basin

Taxon	Synonyms in Luangwa Basin literature
<i>Kannemeyeria lophorhinus</i>	<i>Rechnisaurus cristarhynchus</i> , <i>Rechnisaurus</i> , <i>Kannemeyeria cristarhynchus</i> , <i>Kannemeyeria</i>
<i>“Kannemeyeria” latirostris</i>	<i>Kannemeyeria</i> , <i>Kannemeyeria latirostris</i> , <i>“Kannemeyeria” latirostris</i> , <i>Dolichuranus latirostris</i> , <i>Dolichuranus</i> , <i>Shansiodon</i>
<i>Zambiasaurus submersus</i>	<i>Zambiasaurus</i> , <i>Zambiasaurus submersus</i>
<i>Sanguisaurus edantatus</i>	<i>Sanguisaurus</i> , <i>Sanguisaurus</i>
<i>Kannemeyeriiformes incertae sedis</i>	None

See text for details

**Fig. 7.11** Zambian specimens of *Kannemeyeria lophorhinus* and *“Kannemeyeria” latirostris*. **a** Holotype skull of *Kannemeyeria lophorhinus* (BP/1/3638) in dorsal view. **b** Holotype skull of *Kannemeyeria lophorhinus* (BP/1/3638) in ventral view. **c** Holotype skull of *Kannemeyeria lophorhinus* (BP/1/3638) in left lateral view. **d** Holotype mandible of *Kannemeyeria lophorhinus* (BP/1/3638) in left lateral view. **e** Skull of *“Kannemeyeria” latirostris* (holotype of *Kannemeyeria latirostris*) (BP/1/3636) in dorsal view. **f** Skull of *“Kannemeyeria” latirostris* (holotype of *Kannemeyeria latirostris*)(BP/1/3636) in ventral view. **g** Skull of *“Kannemeyeria” latirostris* (holotype of *Kannemeyeria latirostris*) (BP/1/3636) in left lateral view. **h** Mandible of *“Kannemeyeria” latirostris* (holotype of *Kannemeyeria latirostris*) (BP/1/3636) in right lateral view. **i** Mandible of *“Kannemeyeria” latirostris* (holotype of *Kannemeyeria latirostris*) (BP/1/3636) in dorsal view. Upper scale bar applies to panels **b–d**; lower scale bar applies to panels **e–i**. Scale bars are 20 mm. Photographs in panels **a–d** courtesy of C. Kammerer

processes, tusks, a crest-like temporal bar that forms a sharp angle with the interorbital region, an anteriorly-sloping occipital plate, limited facial exposure of the lacrimal, the presence of a labial fossa, and the absence of an ectopterygoid. In addition, they differentiated *K. lophorhinus* from *K. simocephalus* on the basis of a more robust skull, a stronger median ridge on the snout that is flanked by depressions, a deeper, wider snout, larger caniniform processes, a broader intertemporal region, shorter temporal openings and secondary palate, and the absence of a fossa on the ventral surface of the median pterygoid plate, among other characters. Although BP/1/3638 is not completely preserved, most of Renaut et al.'s (2003) diagnostic characters are visible on the specimen, and the robust snout, strong median snout ridge, and large caniniform processes are especially apparent (Fig. 7.11a–c).

Synonyms in Luangwa Basin Literature: *Rechnisaurus cristarhynchus*, *Rechnisaurus*, *Kannemeyeria cristarhynchus*, *Kannemeyeria*. Renaut et al. (2003; also see Renaut 2000) provided an excellent review of the complex taxonomic history of BP/1/3638. In her initial description, Crozier (1970) referred the specimen to *Rechnisaurus cristarhynchus* Roy Chowdhury, 1970, with Keyser (1973c), Battail (1978, 1993), and Ochev and Shishkin (1989) following this identification. Keyser (1974) expressed uncertainty about whether *R. cristarhynchus* (including BP/1/3638) was distinct from *Kannemeyeria* and Keyser and Cruickshank (1979) elaborated this argument, concluding that it should be treated as a species of *Kannemeyeria* (*K. cristarhynchus*). A number of authors followed this taxonomy (Anderson and Cruickshank 1978; Cooper 1980, 1982; Cox and Li 1983; Cruickshank 1986; Bandyopadhyay 1988). However, Bandyopadhyay (1985, 1989) argued that the Indian holotype of *Rechnisaurus cristarhynchus* Roy Chowdhury, 1970 could not be assigned to *Kannemeyeria* and was distinct from the Namibian and Zambian specimens that Keyser and Cruickshank (1979) considered. She retained *R. cristarhynchus* Roy Chowdhury, 1970 for the Indian specimen, and used the name “*Kannemeyeria cristarhynchus* (Crozier, 1970; Keyser and Cruickshank, 1979)” for the Namibian and Zambian specimens. King (1988) followed this taxonomy, although she referred to the Zambian and Namibian specimens as “*Kannemeyeria cristarhynchus* Keyser and Cruickshank, 1979” and erroneously stated that Keyser and Cruickshank used the emended spelling “*cristarhyncha*.” King (1990), Cox (1991), Renaut (2000), and Renaut and Hancox (2001) used the name *K. cristarhynchus* for the Zambian and Namibian specimens and accepted that they were distinct from *Rechnisaurus*, although Lucas (1993b, 1996, 1998b, 1999, 2001, 2010; also see Lucas and Wild 1995) argued repeatedly for their synonymy. Renaut et al. (2003) argued that the name *Kannemeyeria cristarhynchus* violated Article 49

of the International Code of Zoological Nomenclature and coined the new species name *Kannemeyeria lophorhinus* as its replacement. Abdala et al. (2005) and Fröbisch (2008, 2009) used the name *Kannemeyeria lophorhinus*.

Previous Reports: Crozier (1970) was the first to formally describe and figure BP/1/3638, but the specimen is one of two “*Kannemeyeria*-like” dicynodonts that Drysdall and Kitching (1963) and Kitching (1963) mentioned collecting at Locality 16 (also see Brink 1963; Cox 1969; note that Chernin 1974 mistakenly reported these specimens as originating in the upper fossiliferous horizon at Drysdall and Kitching's (1963) Locality 15). Keyser (1974), Keyser and Cruickshank (1979), Cox and Li (1983), Bandyopadhyay (1985, 1988, 1989), King (1988), Renaut (2000), Renaut and Hancox (2001), and Renaut et al. (2003) discussed various aspects of the taxonomy and phylogenetic relationships of BP/1/3638 using various names. Many authors noted the presence of *Kannemeyeria* “*cristarhynchus*,” *K. lophorhinus*, or more generally *Kannemeyeria* in Zambia in a biogeographic or biostratigraphic framework (Keyser 1973c, 1981; Anderson and Cruickshank 1978; Cooper 1980, 1982; Cruickshank 1986; King 1988, 1990; Cox 1991; Lucas 1993b, 1996, 1998b, 1999, 2001, 2010; Lucas and Wild 1995; Abdala et al. 2005; Fröbisch 2009; although note that Keyser 1981 erroneously reported the occurrence in the Upper Madumabisa Mudstone). Battail (1978, 1993) and Ochev and Shishkin (1989) also considered the biostratigraphic implications of BP/1/3638, but used the name *Rechnisaurus*. Battail (1993) also mistakenly reported that it occurred in the upper horizon of the Ntawere Formation. The studies of DeFauw (1989), and Fröbisch (2008) are more evolutionary in focus, but they do mention *Kannemeyeria* from Zambia. Finally, it is important to note that even though BP/1/3638 was initially referred to *Rechnisaurus* by Crozier (1970) and BP/1/3636 (see below) was referred to *Kannemeyeria* in the same paper, the rapid reassignment of these specimens to *Kannemeyeria* and *Dolichuranus* (respectively) means that nearly all subsequent literature reports of *Kannemeyeria* from Zambia refer to BP/1/3638, not BP/1/3636.

“*Kannemeyeria*” *latirostris* Crozier, 1970

Figure 7.11e–i

Material: BP/1/3636.

Localities: Locality 16 of Drysdall and Kitching (1963) (BP/1/3636). This locality is in Drysdall and Kitching's (1963; also see Kitching 1963) lower fossiliferous horizon of the Ntawere Formation.

Identifying Characteristics: In her diagnosis of “*K.*” *latirostris*, Crozier (1970) emphasized the broad snout, absence of any ridges on the snout, vertical orientation of the tusks, antero-posteriorly short interpterygoid vacuity, and short dentary symphysis as distinguishing features of

the species. There have been three main suggestions for the generic affinities of BP/1/3636: (1) it is a specimen of *Kannemeyeria*, perhaps representing a distinct species (e.g., Crozier 1970); (2) it is a specimen of *Dolichuranus*, perhaps representing a distinct species (e.g., Keyser 1973c; Keyser and Cruickshank 1979; King 1988); (3) it is a specimen of *Shansiodon*, although its species-level taxonomy in this scenario has not been discussed (e.g., Cooper 1980; Lucas 1993a, b, 1996, 2001).

A full consideration of the taxonomic and phylogenetic status of “*K.*” *latirostris* is beyond the scope of this study, but some discussion of the taxonomic problem is warranted. It is unlikely to be a part of *Shansiodon* sensu stricto for several reasons. For example, BP/1/3636 (basal skull length 241 mm) is notably larger than most adult *Shansiodon* specimens (e.g., IVPP V2416 has a basal length of 150 mm; IVPP V2417 has a basal length of 165 mm). It also has proportionally much smaller tusks that are positioned farther anteriorly relative to the anterior orbital margin, a longer, wider preorbital region, and anteroposteriorly shorter temporal openings. Finally, it is worth noting that the reason BP/1/3636 was referred to *Shansiodon* was the hypothesis that *Dolichuranus* was its junior synonym. However, recent phylogenetic analyses that included both *Dolichuranus* and *Shansiodon* did not recover a close relationship between the two taxa (Damiani et al. 2007; Govender and Yates 2009; Kammerer et al. 2011).

BP/1/3636 also does not fit perfectly within *Dolichuranus* or *Kannemeyeria*. Crozier (1970) did not provide a detailed justification for her referral of BP/1/3636 to *Kannemeyeria*, only noting that it was of “*Kannemeyeria* type.” In general appearance, the specimen does resemble *Kannemeyeria* in features such as its relatively large snout and narrow, crest-like temporal bar (e.g., Fig. 7.11d, g). However, comparison with the Renault’s (2000) diagnosis of *Kannemeyeria* highlights several differences. For example, there is no midline ridge on the snout, the occipital plate is relatively vertical, and the temporal bar is not strongly angled dorsally, although it is somewhat offset from the interorbital region of the skull. Furthermore, although Renault (2000) did not explicitly state what he thought was the correct identity for BP/1/3636, he did not include it in his list of referred specimens for either of the species of *Kannemeyeria* that he recognized (*K. simocephalus* and *K. lophorhinus*).

Keyser (1973c) referred the specimen to *Dolichuranus* based on overall similarities in shape with the type material from Namibia, although he noted that the secondary palate of BP/1/3636 was somewhat shorter. BP/1/3636 does possess similar proportions of the snout and temporal openings to *Dolichuranus* specimens such as CGP/1/711 (the holotype of *D. primaevus*), as well as a similarly long, straight midventral vomerine plate and small interpterygoid vacuity

(Fig. 7.11e). However, it also departs from Damiani et al.’s (2007) diagnosis of *Dolichuranus* in characters such as its more curved alveolar margin in lateral view, its lack of strongly differentiated nasal bosses and a trough-like furrow on the anterior surface of the snout, and the absence of an ectopterygoid.

An additional complication is the possible juvenile status of BP/1/3636. Crozier (1970) suggested the specimen might be a sub-adult based on its relatively small size compared to other *Kannemeyeria* specimens, and the specimen shows other potential juvenile features as well. For example, the orbits are large relative to the overall size of the skull. Orbit length shows negative allometry in *Kannemeyeria* (Renaut 2000) and other dicynodonts (Tollman et al. 1980; Ray 2005; Angielczyk 2007; although see Grine et al. 2006), and the proportions of BP/1/3636 are comparable to similarly-sized juvenile specimens of *K. simocephalus* (e.g., BP/1/2092; Renault 2000). The tusks are also relatively small, and although different dicynodont taxa show different patterns of allometry for this character (compare Renault 2000; Ray 2005; Grine et al. 2006), tusk diameter is positively allometric in *Kannemeyeria*. At the same time, these comparisons assume that the taxon represented by BP/1/3636 underwent a *Kannemeyeria*-like ontogeny, which would be logical if BP/1/3636 is eventually shown to be part of *K. lophorhinus* but potentially incorrect if it represents a distinct taxon.

Given these uncertainties, and the fact that BP/1/3636 cannot be easily accommodated within other roughly coeval taxa such as *Tetragonias*, *Vinceria*, *Dinodontosaurus*, or *Angonisauros*, it is clear that the identity of BP/1/3636 requires further investigation. We follow Fröbisch (2009) in referring to the specimen as “*Kannemeyeria*” *latirostris* until its affinities can be resolved. However, we add that use of this specimen for making biogeographic or biostratigraphic inferences is questionable because of its uncertain identity.

Synonyms in Luangwa Basin Literature: *Kannemeyeria*, *Kannemeyeria latirostris*, “*Kannemeyeria*” *latirostris*, *Dolichuranus latirostris*, *Dolichuranus*, *Shansiodon*. Much like BP/1/3638, BP/1/3636 has had a complex taxonomic history. Crozier (1970) named “*K.*” *latirostris*. Keyser (1973c; also see Keyser 1973d) considered the specimen to be referable to his newly-created genus *Dolichuranus*, but retained *latirostris* Crozier, 1970 as a valid species. Many subsequent authors followed this synonymy (Keyser 1974; Battail 1978, 1993; Anderson and Cruickshank 1978; Keyser and Cruickshank 1979; Cooper 1982; King 1988, 1990; Surkov 2000; Renault 2000; Rubidge 2005). Given that Ochev and Shishkin (1989) also report *Rechnisauros* from Zambia, it appears that their record of *Kannemeyeria* from the Ntawere Formation refers to BP/1/3636. Cox (1991) stated that only *Kannemeyeria*

was present in the lower fossiliferous horizon of the Ntawere Formation, although he did not discuss the species *latirostris* Crozier, 1970 specifically. Other workers, often arguing from a biostratigraphic perspective, considered *Dolichuranus*, including *D. latirostris* from Zambia, to be a junior synonym of *Shansiodon* (Cooper 1980; Lucas 1993a, b, 1996, 2001; Lucas and Wild 1995). In their redescription of *Dolichuranus*, Damiani et al. (2007) stated that they did not consider the species *latirostris* Crozier, 1970 to be referable to this genus, but they did not elaborate on why they concluded this or their preferred placement for the species. Based on Damiani et al. (2007), Fröbisch (2008, 2009) referred to the species as “*Kannemeyeria*” *latirostris*, reflecting its uncertain taxonomic status.

Previous Reports: Although Crozier (1970) described BP/1/3636, the specimen is one of two “*Kannemeyeria*-like” dicynodonts that Drysdall and Kitching (1963) and Kitching (1963) mentioned collecting at Locality 16 [also see Brink 1963; Cox 1969; note that Chernin 1974 mistakenly reported these specimens as originating in the upper fossiliferous horizon at Drysdall and Kitching’s (1963) Locality 15]. Kitching (1977) included a photograph of BP/1/3636 and referenced it in a discussion of Karoo taphonomy. Anderson and Cruickshank (1978), King (1988), Surkov (2000), Rubidge (2005), and Fröbisch (2009) included “*K.*” *latirostris* in their biogeographic compilations under various names. Battail (1978, 1993) and Cooper (1982) used the occurrence of “*K.*” *latirostris* (called *Dolichuranus* in those papers) as a datum for correlating the lower Ntawere Formation with units in other basins, as did Ochev and Shishkin (1989), but using the name *Kannemeyeria*. Lucas (1993a, b, 1996, 2001; also see Lucas and Wild 1995), following Cooper (1980), regarded “*K.*” *latirostris* as a synonym of *Shansiodon*, and discussed the biostratigraphic implications of this synonymy. In other works (e.g., Lucas 1998b, 2010), however, he reported only *Kannemeyeria* from the lower Ntawere Formation. Keyser (1973c, d, 1974), Keyser and Cruickshank (1979), Cooper (1980), King (1990), Renaut (2000), and Damiani et al. (2007) discussed “*K.*” *latirostris* (often under the name *Dolichuranus*) in taxonomic or phylogenetic contexts. Finally, it is important to note that even though BP/1/3636 was initially referred to *Kannemeyeria* by Crozier (1970) and BP/1/3638 (see above) was referred to *Rechnisaurus* in the same paper, the rapid reassignment of these specimens to *Dolichuranus* and *Kannemeyeria* (respectively) means that nearly all subsequent literature reports of *Kannemeyeria* from Zambia refer to BP/1/3638, not BP/1/3636.

Stahleckeriidae (Lehman, 1961)

Zambiasaurus submersus Cox, 1969

Figure 7.12a–j

Material: Cox (1969) provided a list of 499 identifiable elements or fragments of elements, but provides specimen numbers for 174 specimens in two series: LM/NH 2 to LM/NH 35 and NHMUK R9001 to NHMUK R9140. The collection includes at least 18 juvenile individuals (based on the number of distal right humeri) and at least one large adult.

Localities: All specimens originated at Locality 15 of Drysdall and Kitching (1963). The type locality of *Z. submersus* is in Drysdall and Kitching’s (1963; also see Kitching 1963) upper fossiliferous horizon of the Ntawere Formation (Cox 1969).

Identifying Characteristics: Cox (1969) provided a diagnosis for *Zambiasaurus submersus*. Diagnostic characters he listed include edentulous skull and jaws; short median suture between nasals; preparietal absent; interparietal that does not extend far forwards on skull roof; sharp transition between the skull roof and occipital plate; paired anterior ridges present on the palatal surface of the premaxilla; at least four sacral vertebrae; tall, narrow scapular blade with a ridge on its lateral surface; coracoid foramen entirely within the procoracoid.

Synonyms in Luangwa Basin Literature: *Zambiasaurus*, *Zambiasaurus submersus* (Surkov 2000; Fröbisch 2009). These appear to be misspellings.

Previous Reports: Although Cox (1969) provided the first description of *Zambiasaurus submersus*, Attridge et al. (1964) made a passing reference to the specimens that eventually were assigned to this species. King (1988, 1990), Fröbisch (2009), and Sues and Fraser (2010) included *Zambiasaurus* in their faunal lists for the Ntawere Formation. Battail (1978, 1993), Cox (1991), and DeFauw (1993) included *Zambiasaurus* in their discussions of Triassic biostratigraphy, and Surkov (2000) mentioned it in his biogeographic study. Various authors considered *Zambiasaurus* in taxonomic or phylogenetic contexts (e.g., Roy Chowdhury 1970; Keyser and Cruickshank 1979, 1980; Cooper 1980; Cox and Li 1983; Bandyopadhyay 1988, 1989; Cox 1998; Maisch 2001; Irmis 2005; Kemp 2005, Surkov et al. 2005).

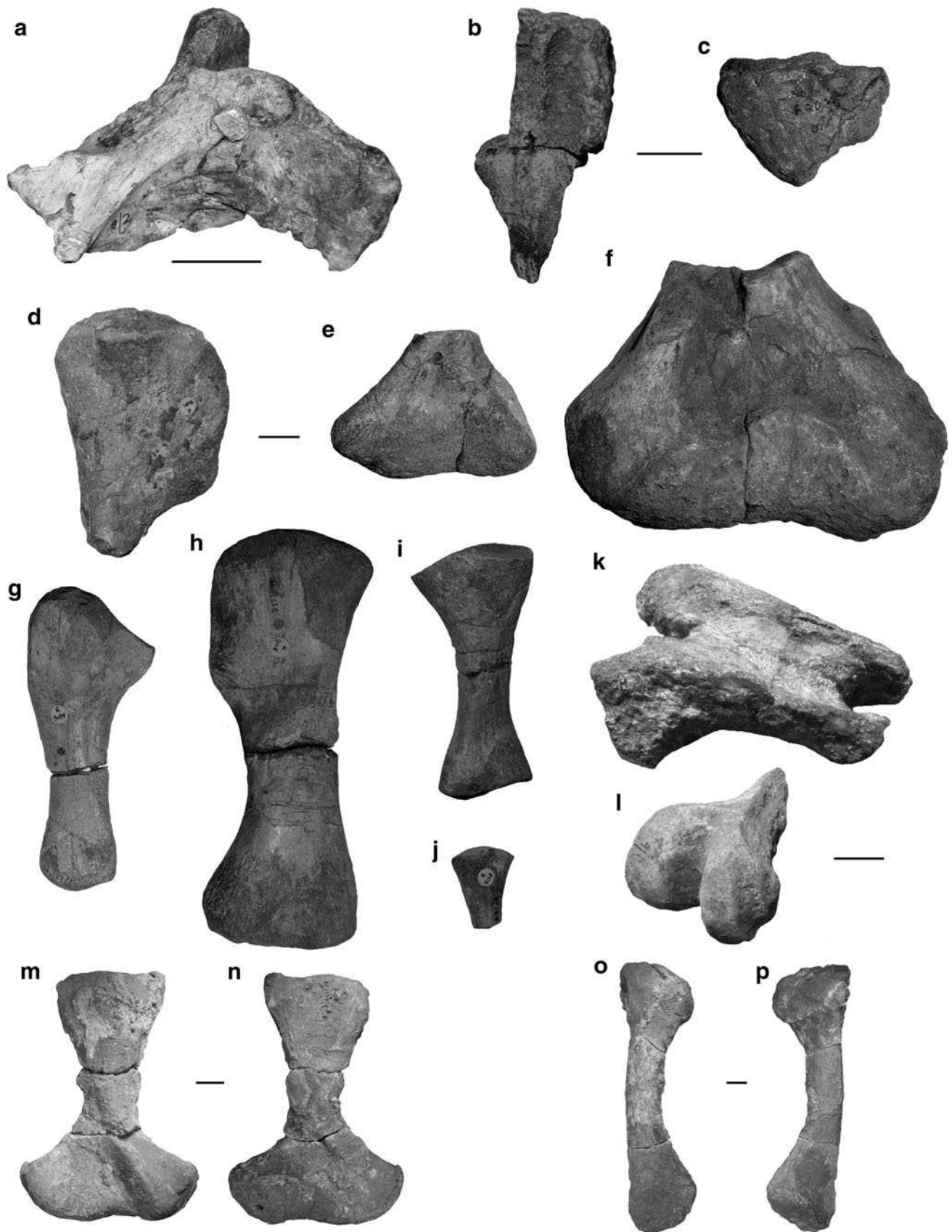
Sangusaurus edentatus Cox, 1969

Figure 7.12k–l

Material: LM/NH 9/1.

Localities: Locality 15 of Drysdall and Kitching (1963) (LM/NH 9/1). The type locality of *S. edentatus* is in Drysdall and Kitching’s (1963; also see Kitching 1963) upper fossiliferous horizon of the Ntawere Formation (Cox, 1969).

Identifying Characteristics: Cox (1969) and Cruickshank (1986) provided diagnoses of *Sangusaurus edentatus* and information on how it could be distinguished from the Tanzanian species *S. parringtonii*. The primary diagnostic



◀ **Fig. 7.12** Zambian specimens of *Zambiasaurus submersus*, *Sangusaurus edentatus*, and *Kannemeyeriiformes incertae sedis*. **a** Holotype temporal bar of *Zambiasaurus submersus* (LM 9/2) in left anterolateral view. **b** Partial premaxilla of *Zambiasaurus submersus* (NHMUK R9002) in ventral view. **c** Partial mandible of *Zambiasaurus submersus* (NHMUK R9039) in left lateral view. **d** Proximal portion of a juvenile right humerus of *Zambiasaurus submersus* (NHMUK R9091) in dorsal view. **e** Distal portion of a juvenile left humerus of *Zambiasaurus submersus* (NHMUK R9089) in ventral view. **f** Distal portion of an adult left humerus of *Zambiasaurus submersus* (NHMUK R9140) in ventral view. **g** Juvenile right ulna of *Zambiasaurus submersus* (NHMUK R9098) in anterior view. **h** Juvenile right femur of *Zambiasaurus submersus* (NHMUK R9118) in anterior view. **i** Juvenile right tibia of *Zambiasaurus submersus* (NHMUK R9123) in posterior view. **j** Proximal end of juvenile right fibula of

Zambiasaurus submersus (NHMUK R9128) in lateral view. **k** Holotype temporal bar of *Sangusaurus edentatus* (LM 9/1) in right dorsolateral view. **l** Holotype right quadrate of *Sangusaurus edentatus* (LM 9/1) in anterodorsal view. **m** Right humerus of *Kannemeyeriiformes incertae sedis* (NHCC LB26) in dorsal view. **n** Right humerus of *Kannemeyeriiformes incertae sedis* (NHCC LB26) in ventral view. **o** Right fibula of *Kannemeyeriiformes incertae sedis* (NHCC LB26) in anterior view. **p** Right fibula of *Kannemeyeriiformes incertae sedis* (NHCC LB26) in posterior view. Upper left scale bar applies to panel **a**, upper right scale bar applies to panels **b**, **c**, middle left scale bar applies to panels **d**–**j**, middle right scale bar applies to panels **k**, **l**, lower left scale bar applies to panels **m**, **n**, and lower right scale bar applies to panels **o**, **p**. Scale bars are 20 mm. Photographs in panels **a**, **k**, and **l** courtesy of C. Mateke; photographs in panels **b**–**j** courtesy of C. Kammerer

characters for *Sangusaurus* are absence of tusks, temporal bar with a midline groove, presence of a boss posterior to the pineal foramen, exposure of the interparietal on the dorsal surface of the temporal bar. Cruickshank (1986) differentiated *S. edentatus* from *S. parringtonii* on the basis of the shape and size of the caniniform process.

Synonyms in Luangwa Basin Literature: *Sangusaurus*, *Sangausaurus* (Keyser and Cruickshank 1979). Both of these names appear to be misspellings of *Sangusaurus*.

Previous Reports: Cox (1969) was the first to describe *Sangusaurus* from the Luangwa Basin. Anderson and Cruickshank (1978), King (1988, 1990), and Fröbisch (2009) included *Sangusaurus* in their biogeographic compilations. Battail (1978, 1993), Jain and Roy Chowdhury (1987), Cox (1991), and DeFauw (1993) discussed *S. edentatus* in a primarily biostratigraphic context, and various authors have considered it in a taxonomic or phylogenetic context (e.g., Roy Chowdhury 1970; Keyser and Cruickshank 1979, 1980; Cooper 1980; Cox and Li 1983; Cruickshank 1986; Bandyopadhyay 1988, 1989; Cox 1998; Maisch 2001). Sues and Fraser (2010) included *Sangusaurus* in their faunal list for the Ntawere Formation.

Kannemeyeriiformes incertae sedis

Figure 7.12m–p

Material: NHCC LB26.

Localities: Locality L12 (NHCC LB26). This locality is within the outcrops designated as Locality 16 by Drysdall and Kitching (1963), which is part of their lower fossiliferous horizon of the Ntawere Formation.

Identifying Characteristics: The material in this collection consists of a medium-sized dicynodont humerus (length approximately 183 mm) (Fig. 7.12m, n), a large dicynodont fibula (length approximately 279 mm) (Fig. 7.12o, p), and a rib fragment that likely belonged to an animal of similar size as that which produced the fibula. Of the dicynodonts known from the Triassic of Zambia, only *Zambiasaurus* includes definite postcranial material (Cox 1969), although Govender and Yates (2009) described

specimens from Namibia that they assigned to *Dolichuranus*, cf. *Dolichuranus*, and cf. *Kannemeyeria lophorhinus* that make for relevant comparisons. The humerus of NHCC LB26 is comparable in size to the juvenile humerus (consisting of specimens NHMUK R9088 and NHMUK R9089; Fig. 7.12d, e) figured by Cox (1969), but it differs in having much more fully ossified joint surfaces (particularly on the distal end) and more strongly flaring ect- and entepicondyles (also compare to NHMUK R9091; Fig. 7.12d). The adult distal humerus of *Zambiasaurus* has comparably well-ossified joint surfaces, although it is much larger and has less flared ect- and entepicondyles. The humerus shows greater similarity to the humeri of cf. *Dolichuranus* and cf. *K. lophorhinus* described by Govender and Yates (2009). Their specimens of cf. *K. lophorhinus* (both from CGP R316) possess similarly flared ect- and entepicondyles, but the entepicondyles of their specimens of cf. *Dolichuranus* (CGP/1/191A and CGP/1/412) do not seem as strongly flared as in NHCC LB26. Both the specimens of cf. *K. lophorhinus* and cf. *Dolichuranus* figured by Govender and Yates (2009) also are noteworthy in having a tab-like projection on the posterior surface of the proximal end, near the insertion of M. subcoracoscaphularis. This area is somewhat damaged in NHCC LB26, but the preserved morphology is suggestive of a similar tab having been present originally.

In addition to *Sangusaurus*, *Zambiasaurus*, *K. lophorhinus*, and *Dolichuranus*, several other dicynodont taxa are documented from coeval beds in southern and eastern Africa: *Kannemeyeria simocephalus*, *Tetragonias njalilus*, *Rechnisaurus cristarhynchus*, *Angonisaurus cruickshanki*, and *Shansiodon* sp. (e.g., von Huene 1942; Cruickshank 1967; Cox and Li 1983; King 1988; Hancox and Rubidge 1997, 2001; Hancox 2000; Rubidge 2005, Fröbisch 2009; Hancox et al. 2013). There are also reports of an additional taxon from Tanzania that was informally named “*Ruhuhuungulasaurus croucheri*” in an unpublished thesis (Larkin 1994; this specimen, NHMUK R12710, was listed as *Shansiodon* in Surkov and Benton 2004). Although humeri are not available for *Rechnisaurus* or

“*Ruhuhuungulasaurus*,” comparisons are possible with the other taxa. NHCC LB26 differs from the humeri of *K. simocephalus* (e.g., Govender et al. 2008) in having more flared distal ect- and entepicondyles. NHCC LB26 may differ from *K. simocephalus* in having a tab on the posterior surface of the proximal end if such a structure was originally present. Cox and Li (1983) did not discuss the humerus of *Angonisauros* that is part of the holotype (NHMUK R9723), but it is relatively complete with minor damage to the proximal end, deltopectoral crest, and distal end. As preserved this specimen appears to have a less flared distal end than NHCC LB26 and no tab-like projection on the proximal end, and these observations are confirmed by a more fragmentary specimen (NMT RB155) that likely represents *Angonisauros*, which our team collected in Tanzania in 2007. The humeri are somewhat better preserved in the holotype of *Tetragonias* (GPIT 292) than the referred specimen (CAMZM T753) described by Cruickshank (1967). GPIT 292 possesses a comparably flared distal end and a well-developed tab-like projection on the posterior surface of the proximal end. The humeral head is also prominent and well-ossified in GPIT 292, and a similar situation seems to be the case in NHCC LB26, although this area is also somewhat damaged. Unfortunately, the deltopectoral crest of NHCC LB26 is not preserved, so we cannot determine whether it possessed the hook-like anterodistal corner present in *Tetragonias* (Cruickshank 1967). A humerus for the South African *Shansiodon* specimen is not available for comparison. However, comparison to Chinese material of *Shansiodon* (e.g., IVPP V.2415; see Yeh 1959) shows that NHCC LB26 may show some similarities (e.g., well-defined humeral head, tab-like projection on the posterior surface of proximal end). At the same time, NHCC LB26 is larger and also appears to have a more flared distal end.

The fibula of *Zambiasaurus* is known only from juvenile material (NHMUK R9128, R9129) (e.g., Fig. 7.12j). Those elements show a similar degree of curvature to NHCC LB26, but the joint surfaces are nearly entirely unossified, precluding detailed comparisons. The fibula of cf. *K. lophorhinus* (CGP R316) figured by Govender and Yates (2009) has a much straighter shaft than that of NHCC LB26. Although not prepared, NHCC LB26 appears to lack the groove on the posterior surface seen in CGP R316. The proximal and distal ends of CGP R316 also seem less expanded than those of NHCC LB26, although Govender and Yates' (2009) photographs make it seem like these areas may be somewhat weathered. NHCC LB26 shows similarity to the fibula of *Dolichuranus* (BP/1/4578) described by Govender and Yates (2009), particularly in the curvature of the shaft. However, the curvature of the shaft is greater in NHCC LB26 (and this does not appear to be a taphonomic artifact given that the specimen is well

preserved and does not show signs of crushing or plastic deformation) and there is no evidence of a groove on the posterior surface of the shaft comparable to that in BP/1/4578.

Fibulae also are available for comparison for *Tetragonias*, *K. simocephalus*, and “*Ruhuhuungulasaurus*.” The fibula of the holotype of *Tetragonias* (GPIT 292) is strongly curved, but the profile of this curvature is different than in NHCC LB26. In the latter specimen the shaft smoothly curves, whereas in GPIT K292 the offset between the proximal and distal ends of the fibula is more of a distinct kink. The fibula of the referred specimen (CAMZM T754) described by Cruickshank (1967) is more smoothly curved, giving it a profile more comparable to that of NHCC LB26. The proximal and distal ends of NHCC LB26 are more expanded and more strongly ossified than those of either *Tetragonias* specimen, though, and NHCC LB26 is considerably larger. The fibula of *K. simocephalus* (e.g., Govender et al. 2008) also is smoothly curved, but again is typically somewhat smaller than NHCC LB26. The latter specimen also differs from *K. simocephalus* in having a well developed ridge-like edge that forms the posterior margin of the distal articular surface, although some of this difference may stem from the fact that NHCC LB26 represents an animal that is larger than most known *Kannemeyeria* specimens. The longitudinal groove on the posterior surface of the shaft of the fibula in *K. simocephalus* described by Govender et al. (2008) appears to be absent in NHCC LB26. Finally, the fibula of “*Ruhuhuungulasaurus*” (NHMUK R12710) shows a similar degree of curvature as NHCC LB26, and its proximal and distal ends are relatively expanded. The articular surfaces are well-defined, but the distal surface is somewhat damaged, making it uncertain whether the posterior edge of distal surface had the form of a distinct ridge. NHCC LB26 also represents a considerably larger animal.

Only two major clades of dicynodonts are known to occur in the Middle Triassic, the emydopoids (represented only by *Kombuisia frerensis* in the Karoo Basin), and the much more diverse *Kannemeyeriiformes*. The elements included in NHCC LB26 are much larger than any known emydopoid specimens (Permian or Triassic), so we are confident in their referral to *Kannemeyeriiformes*. However, the limited amount of material available, and the fact that the specimens show a mixture of similarities to and differences from coeval dicynodonts known from southern and eastern Africa, prevent us from unequivocally assigning them to a specific dicynodont taxon. Their similarities to likely *Kannemeyeria lophorhinus* specimens from Namibia and their occurrence in outcrops assigned to Locality 16 by Drysdall and Kitching (1963) make *K. lophorhinus* a potential identification that deserves more scrutiny as additional postcranial material referable to that species becomes available. Likewise, as more comparative material

of *Z. submersus* and *S. edentatus* become available, and the taxonomic uncertainty regarding BP/1/3636 (“*K.*” *latirostris*) is resolved, it will be important to determine whether NHCC LB26 falls within the ranges of variation for any of these taxa. Finally, the fact that the humerus of NHCC LB26 shows similarities to shansiodontids such as *Tetragonias* and *Shansiodon* is intriguing because this specimen could represent the first occurrence of this clade in Zambia. However, additional specimens, particularly cranial material, will be necessary to confirm this possibility.

Triassic Dicynodonts Whose Presence in Zambia Cannot be Confirmed

Shansiodon Yeh, 1959

Previous Reports: Cooper (1980) and Lucas (1993a, b, 1996, 2001) suggested that *Shansiodon* was present in the Ntawere Formation. This occurrence was based on a two-step reasoning process that accepted Keyser’s (1973c) referral of BP/1/3636 to *Dolichuranus* and then posited that *Dolichuranus* was a junior synonym of *Shansiodon*. Neither Cooper (1980) nor Lucas (1993a, b, 1996, 2001) specified whether the putative Zambian occurrence of *Shansiodon* represented the type species *Shansiodon wangi* Yeh, 1959 or a different species. As noted above, both steps in this reasoning are questionable. BP/1/3636 diverges from the diagnosis of *Dolichuranus* and is not clearly referable to the genus (Damiani et al. 2007). Even if BP/1/3636 is eventually shown to be part of *Dolichuranus*, the synonymy between it and *Shansiodon* is unlikely because recent phylogenetic analyses suggest that *Shansiodon* and *Dolichuranus* are not closely related (Damiani et al. 2007; Govender and Yates 2009; Kammerer et al. 2011). We are unaware of any Zambian specimens that can be referred unequivocally to *Shansiodon*. Therefore, we do not consider it part of the Zambian Triassic dicynodont fauna.

Angonisauros cruickshanki Cox and Li, 1983

Previous Reports: Sues and Fraser (2010) included *Angonisauros* in their list of dicynodont taxa known from the Ntawere Formation in the Luangwa Basin, and cited Cox (1969, 1991) as sources. However, *Angonisauros* was not reported from Zambia in either of these papers, and we are unaware of any unpublished specimens that would support this record. Therefore, we do not consider *Angonisauros* to be part of the Zambian Triassic dicynodont fauna.

Rechnisauros cristarhynchus Roy Chowdhury, 1970

Previous Reports: Crozier (1970) initially referred BP/1/3638 to *Rechnisauros cristarhynchus*. Keyser (1973c; also see Battail 1978, 1993 and Ochev and Shishkin 1989) followed this taxonomy, but by 1974 was expressing doubts that later culminated in the transfer of the specimen to *Kannemeyeria* (Keyser and Cruickshank 1979). Several

subsequent authors further highlighted the distinctions between BP/1/3638 (and the specimen of *K. lophorhinus* from Namibia) and *Rechnisauros* (Bandyopadhyay 1985, 1989; King 1988; Renaut 2000; Renaut et al. 2003), and if these observations are accepted, then *Rechnisauros* is not present in the Ntawere Formation of Zambia. Lucas argued repeatedly that *Rechnisauros* and *K. lophorhinus* (usually *K. cristarhynchus* in his papers) are synonyms (1993b, 1996, 1998, 1999, 2001, 2010; also see Lucas and Wild, 1995). If this synonymy is correct, it still would not imply the presence of *Rechnisauros* in Zambia, since that taxon would be a junior synonym of *Kannemeyeria* (i.e., it would imply the presence of *Kannemeyeria* in India instead). Given these observations, and the fact that there are currently no other specimens from the Ntawere Formation that could represent *Rechnisauros* (if it is a valid taxon), we conclude that *Rechnisauros* is not part of the Zambian Triassic dicynodont fauna.

Dolichuranus Keyser, 1973c

Previous Reports: Keyser (1973c) was the first author to suggest that *Dolichuranus* occurred in the Ntawere Formation when he referred BP/1/3636, the holotype of *Kannemeyeria latirostris* Crozier, 1970, to the genus. Many subsequent authors followed this synonymy (Keyser 1974; Anderson and Cruickshank 1978; Battail 1978, 1993; Keyser and Cruickshank 1979; Cooper 1982; King 1988, 1990; Surkov 2000; Renaut 2000; Rubidge 2005). Most only referred to the genus *Dolichuranus* in Zambia, but Keyser and Cruickshank (1979) and King (1988) listed *Dolichuranus latirostris* as a valid species. As noted above however, BP/1/3636 differs from Damiani et al.’s (2007) diagnosis of *Dolichuranus*, making its assignment to the genus questionable. Likewise, although NHCC LB26 shows some similarities to *Dolichuranus* postcrania collected in Namibia, we do not consider it complete enough to provide a definitive identification. Until the identity of BP/1/3636 is resolved and/or new specimens are discovered that can be unequivocally identified as *Dolichuranus*, we do not consider it to be a part of the Zambian Triassic dicynodont fauna.

Discussion

How Many Faunal Assemblages are Preserved in the Fossiliferous Beds of the Upper Madumabisa Mudstone?

The idea that the Upper Madumabisa Mudstone preserves multiple Permian assemblages can be traced back to the earliest works on the paleontology of the Luangwa Basin. Dixey (1937) reported fossils in five horizons that are now

considered part of the Madumabisa Mudstone (Drysdall and Kitching 1963) in the northern part of the basin. Based on comparisons of the fossils Dixey collected with specimens in South Africa, Boonstra (1938) concluded that some of these horizons might be coeval, but that assemblages corresponding to the *Endothiodon* and *Cistecephalus* zones of the South African Karoo (equivalent to the *Tropidostoma*, *Cistecephalus*, and *Dicynodon* assemblage zones of Rubidge et al. 1995) were present. Drysdall and Kitching (1962, 1963) and Kitching (1963) considered the problem in more detail, recognized that sets of Dixey's horizons were parts of single layers offset by faulting, and added several additional fossil localities to Dixey's list. Based on perceived faunal differences, they recognized lower, middle, and upper fossiliferous horizons in their Upper Madumabisa Mudstone. They considered the lower horizon to be equivalent to rocks of the *Endothiodon* zone of South Africa (now the *Tropidostoma* Assemblage Zone), and the middle and upper horizons to be equivalent to rocks of the *Cistecephalus* zone (equivalent to the current *Cistecephalus* and/or *Dicynodon* assemblage zones). The discovery of Permian fossils in the central Luangwa Basin (Kemp 1975) generally has been regarded as adding a fourth fossiliferous horizon that is equivalent to rocks of the *Dicynodon* Assemblage Zone of South Africa, a conclusion reinforced by the suggested co-occurrence of *Dicynodon* and *Lystrosaurus* in one of these localities (King and Jenkins 1997). Most recent biostratigraphic works included two assemblages in the Upper Madumabisa Mudstone equivalent to those of the *Cistecephalus* and *Dicynodon* assemblage zones of South Africa (e.g., Lucas 1998a, 2002, 2005, 2006; Rubidge 2005), although Fröbisch (2009) included four assemblages (consisting of Drysdall and Kitching's three horizons from the north of the basin and Kemp's horizon from the central basin) in his biogeographic study.

Our taxonomic revision of the dicynodonts of the Upper Madumabisa Mudstone provides an opportunity to reassess whether there is strong evidence of multiple assemblages in the formation or if the various localities throughout the basin are better regarded as sampling a single assemblage. To test the hypotheses of single versus multiple assemblages, we compiled faunal lists for each of Drysdall and Kitching's (1963) three fossiliferous horizons and Kemp's (1975) horizon based on voucher specimens identified from historical localities and our new localities in their immediate proximity. Because none of our new fossil localities fall within Drysdall and Kitching's (1963) lower and middle horizons, and we identified few or no voucher specimens from these horizons in museum collections, we supplemented the faunal lists with our reidentifications of Drysdall and Kitching's (1963) field identifications.

A clear pattern emerges from these results (Table 7.3). Kemp's (1975) central Luangwa Basin localities have the

greatest taxonomic richness, with 14 species represented. Drysdall and Kitching's (1963) upper horizon is a close second (10 species), followed by the lower horizon (six species) and the middle horizon (at least two species). More importantly, the assemblages of all three of Drysdall and Kitching's (1963) horizons consist of subsamples of the assemblage present in Kemp's (1975) localities; no taxa are confined only to one or more of the lower horizons. Importantly, the subsamples all include taxa that have been hypothesized to have biostratigraphic utility, such as *Endothiodon*, *Odontocyclops*, *Dicynodon huenei*, and the new cistecephalid, not just stratigraphically long-ranging taxa such as *Pristerodon* or *Diictodon*. Based on these observations, we consider it most conservative to posit only a single assemblage in the Upper Madumabisa Mudstone, similar to the situation recognized for the Usili Formation of Tanzania (Sidor et al. 2010). We hypothesize that the assemblage from the central Luangwa Basin localities is more completely sampled primarily because of taphonomic issues. In particular, specimens from these localities tend to be more complete and easier to prepare than those from the northern localities, which are often encased in highly resistant hematite nodules. This nodular preservation style makes field identifications of specimens and collecting decisions difficult, in addition to slowing preparation. Nevertheless, Drysdall and Kitching's (1963) upper horizon, particularly their Locality 4, shows that it is possible to gain a relatively complete picture of the assemblage even in areas characterized by preservation in hematite nodules.

Permian Biostratigraphy and Biogeography

As noted above, most previous workers who considered the biostratigraphy of the Upper Madumabisa Mudstone correlated it with rocks belonging to one or more of the biozones of the South African Karoo Basin (e.g., Boonstra 1938; Drysdall and Kitching 1963; Kemp 1975; King and Jenkins 1997; Lucas 1998a, 2002, 2005, 2006; Angielczyk 2002; Rubidge 2005; Fröbisch 2009). Stratigraphic ranges for taxa that occur in South Africa and Zambia, as well as *Dicynodon lacerticeps* (which is closely related to *D. huenei*; Kammerer et al. 2011) and *Cistecephalus* (the likely closest South African relative of the Zambian tusked cistecephalid) are shown in Fig. 7.13. Given the long ranges of several of the taxa, it is easy to see why previous authors suggested the presence of multiple faunal assemblages corresponding to two to three South African assemblage zones.

The assumption of a single faunal assemblage in the Upper Madumabisa Mudstone greatly simplifies the problem. The taxa found in both the Karoo Basin and the

Table 7.3 Occurrences of dicynodont taxa in previously-recognized horizons of the Upper Madumabisa Mudstone

Taxon	Drysdall and Kitching Lower Horizon	Drysdall and Kitching Middle Horizon	Drysdall and Kitching Upper Horizon	Kemp Horizon
<i>Endothiodon</i> sp.	X			X
<i>Pristerodon mackayi</i>	X ^a		X	X
<i>Diictodon feliceps</i>	X ^b		X	X
<i>Compsodon helmoedi</i>				X
<i>Emydops</i> sp.	X ^c	X ^f	X	X
<i>Dicynodontoides</i> cf. <i>D. nowacki</i>			X	X
Cistecephalidae n. g. & sp.		X ^{g, h}	X	X
cf. <i>Katumbia parringtoni</i>				X
<i>Odontocyclops whaitsi</i>	X ^d		X	X
<i>Oudenodon bainii</i>	X ^e		X	X
<i>Kitchinganomodon crassus</i>			X ⁱ	X
<i>Dicynodon huenei</i>			X ^j	X
<i>Syops vanhoepeni</i>			X	X
Lystrosauridae n. g. & sp.				X

Drysdall and Kitching's (1963) horizons crop out in the northern part of the Luangwa Basin (Area 1 in Fig. 7.1); Kemp's horizon crops out in the central part of the basin (Area 3 and Area 4 in Fig. 7.1). The Lower Horizon includes Drysdall and Kitching's (1963) localities 3, 18, 19, 20, and 22. The Middle Horizon includes Drysdall and Kitching's (1963) localities 2, 11, and 17. The Upper Horizon includes Drysdall and Kitching's (1963) localities 1, 4, 5, 7, 8, 9, 10, 12, 13, and 21, as well as our localities L6 and L7. Kemp's (1975) Horizon includes Kerr's (1974) localities 1, 2, 3, 4, 5, 6, 7, 8, 9, 11, and 14 (although this might correspond to locality 4; see text), as well as our localities L26, L29, L30, L31, L32, L37, L38, L45, L48, L49, L50, L52, L53, L55, L59, and L61

^a Record based on Drysdall and Kitching's (1963) field observations of *Parringtoniella*

^b Record based on Drysdall and Kitching's (1963) field observations of *Dicynodon sollasi* and *Dicynodon grimbeeki*

^c Record based on Drysdall and Kitching's (1963) field observations of *Emydops*

^d Tentative record based on SAM-PK-K7936

^e Record based on Drysdall and Kitching's (1963) field observations of *Dicynodon breviceps* and *Dicynodon corstorphine*

^f Record based on Drysdall and Kitching's (1963) field observations of *Emydops*

^g Tentative record based on Drysdall and Kitching's (1963) field observations of *Cistecephalus*

^h Drysdall and Kitching (1963) note that medium and large anomodonts occur at their Middle Horizon localities, but do not provide identifications or specimen numbers for this material

ⁱ Tentative record based on Drysdall and Kitching's (1963) field observations of *Platycyclops* and *Neomegacyclops*

^j Tentative record based NHMUK 5-2, NHMUK 5-4, and NHMUK 5-10

Luangwa Basin all only overlap stratigraphically in the *Cistecephalus* Assemblage Zone of Rubidge et al. (1995; roughly equivalent to Faunachron I of Lucas 2002 and the Steilkransian of Lucas 2005, 2006) (Fig. 7.13). Even if some diachroneity in stratigraphic ranges is allowed between the two basins, it still seems likely that the Upper Madumabisa Mudstone primarily represents *Cistecephalus* Assemblage Zone time, with only limited overlap with the *Tropidostoma* and/or *Dicynodon* assemblage zones. This conclusion is significant because if true, it implies that the Upper Madumabisa Mudstone cannot provide direct insight into faunal turnover at the Permo-Triassic boundary.

Our faunal revision also demonstrates that Zambia is an important biostratigraphic link between the South African Karoo Basin and the Ruhuhu Basin of Tanzania. A number of authors noted that the Ruhuhu Basin includes a mixture of widespread and endemic taxa, as well as taxa that do not overlap stratigraphically in the Karoo Basin, complicating correlations between the two areas (e.g., Gay and

Cruickshank 1999; Maisch 2002c; Abdala and Allinson 2005; Angielczyk 2007; Weide et al. 2009; Sidor et al. 2010). However, the presence of *Dicynodon huenei* in both Tanzania and Zambia allows a direct correlation between the Usili Formation and the Upper Madumabisa Mudstone. A second direct correlation between the two formations may be possible with *Katumbia parringtoni* if more definitive specimens than the jaw we collected in 2009 come to light. In turn, the well-supported correlation between the Upper Madumabisa Mudstone and the rocks of the *Cistecephalus* Assemblage Zone in the Karoo Basin implies that the Usili Formation also may best be regarded as primarily representing *Cistecephalus* Assemblage Zone time.

Finally, our results also have implications for biogeographic patterns in the Late Permian of southern and eastern Africa. As noted above, there has been much discussion of endemism in the Usili Formation assemblage (e.g., Gay and Cruickshank 1999; Maisch 2002c; Abdala and Allinson 2005; Angielczyk 2007; Weide et al. 2009; Sidor et al.

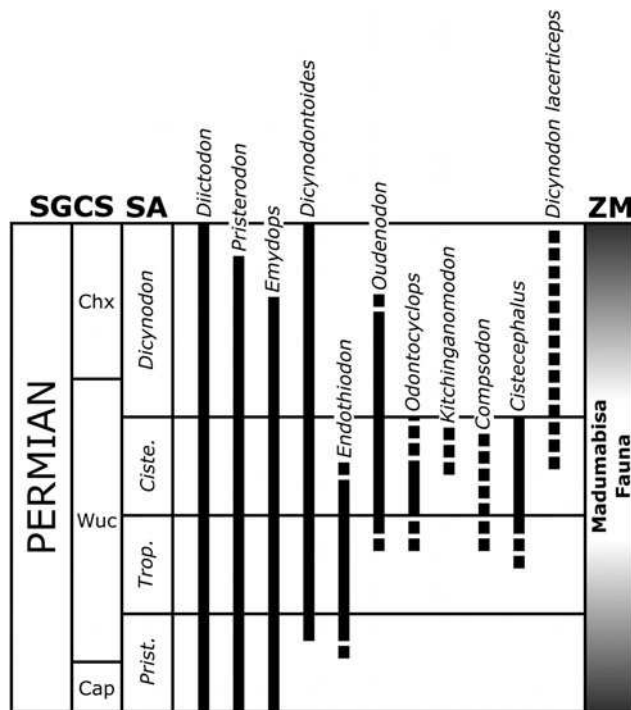


Fig. 7.13 Biostratigraphic comparison of the South African Beaufort Group (Karoo Basin) and the Zambian Upper Madumabisa Mudstone (Luangwa Basin). Stratigraphic ranges of nine dicynodont genera in both basins are plotted; *Cistecephalus* and *Dicynodon lacerticeps* occur only in the Karoo Basin but are closely related to the tusked Zambian cistecephalid and *Dicynodon huenei*, respectively. Ranges for the Karoo Basin are based primarily on Rubidge et al. (1995), with modifications from Angielczyk (2002), Angielczyk et al. (2005, 2009), Botha and Smith (2006), Botha and Angielczyk (2007), and Botha-Brink et al. (2013). The range for *Compsodon* is uncertain because it is known from only a single specimen in the Karoo Basin. This specimen was discovered at a locality that also yielded *Rhachiocephalus* and *Oudenodon* (Kitching, 1977), and the stratigraphic range shown for *Compsodon* represents the overlap of the ranges of these two taxa. The stratigraphic range of *Dicynodon lacerticeps* is uncertain because the taxonomic revision of Kammerer et al. (2011) has greatly modified the content of that species compared to other recent usages. The upper limit of its range is based on Botha-Brink et al.'s (2013) report of *D. lacerticeps* specimen BP/1/4026 close to the Permo-Triassic boundary. SA South African vertebrate assemblage zones, SGCS standard global chronostratigraphic scale, ZM biostratigraphic correlation of the Upper Madumabisa Mudstone (Luangwa Basin, Zambia) vertebrate fauna based on dicynodonts

2010), but most of this work focuses on comparisons with the South African Karoo Basin. Despite its intermediate geographic location, the Upper Madumabisa Mudstone assemblage received little attention on its own or in relation to the Tanzanian assemblage. Table 7.4 shows dicynodont species present in the *Cistecephalus* Assemblage Zone of South Africa, the Upper Madumabisa Mudstone, and the Usili Formation. Our focus on the species level introduces some uncertainty because species-level identifications for some of the taxa occurring in Zambia are difficult (e.g., *Endothiodon*, *Emydops*, *Dicynodontoides*). Nevertheless,

we think it is important to use as detailed information as possible because previous research on this question showed that the results can be influenced by choice of taxonomic level (Abdala and Allinson 2005).

Three important points emerge from this comparison. First, in terms of their dicynodont assemblages, the Karoo, Luangwa, and Ruhuhu basins form something of a faunal gradient: eight to nine of the 14 (57–64 %) species present in Zambia also are found in the Karoo Basin, whereas only five of the 14 (36 %) species present in Tanzania also occur in South Africa. However, this pattern is not perfect because each basin shares different taxa with the others. Thus, the Luangwa Basin and the Karoo basin show roughly the same degree of similarity to the Ruhuhu Basin (only four to six, or 29–43 %, of the species in the Luangwa Basin also are found in the Ruhuhu Basin; five of 20 or 25 % of the species in the Karoo Basin are present in the Luangwa Basin). This fact is surprising given the closer proximity of the Ruhuhu and Luangwa basins now and during the Permian. Second, both the Luangwa Basin and the Ruhuhu Basin include endemic dicynodont species, but Tanzania is characterized by slightly more endemism (three of 14, or 21 %, endemic in Zambia; five to seven of 14, or 36–50 %, endemic in Tanzania). Interestingly, the Karoo Basin itself shows a previously unappreciated degree of endemism during *Cistecephalus* Assemblage Zone times (eight to 11 species, or 40–55 %), so the Luangwa Basin may be unusual in having fewer endemic species than its neighbors. Third, there does not seem to be an obvious relationship between ecology and dispersal abilities among the dicynodonts in the three basins. For example, it might be expected that larger species were more likely to be widespread given their greater resource needs. However, more than half of the species that are definitely restricted to a single basin (*Aulacephalodon baini*, *Dicynodon lacerticeps*, *Syops vanhoepeni*, *Dinanomodon gilli*, *Oudenodon grandis*, *Pachytegos stockleyi*, *Rhachiocephalus behemoth*) also are of large body size (maximum skull lengths in excess of 300 mm; estimated for *Pachytegos* based on comparisons with *Endothiodon*), whereas several small-bodied species are found in two or more basins (e.g., *Compsodon helmoedi*, *Diictodon feliceps*, *Pristerodon mackayi*, either *Emydops arctatus* or *Emydops oweni*). Ecological specialization also seems to have an inconsistent effect. *Cistecephaloides boonstrai*, *Kawingasaurus fossilis*, and the Zambian tusked cistecephalid each are restricted to a single basin, as might be expected for animals characterized by a specialized fossorial lifestyle (Cox 1972; Cluver 1974a), but *Cistecephalus microrhinus* shares a comparable lifestyle (Cluver 1978) and also is found in India (Kutty 1972; Ray 1997, 1999, 2000, 2001; Ray and Bandyopadhyay 2003). Taken together, these observations emphasize Angielczyk's (2007) and Angielczyk and Sullivan's (2008) suggestions that the

Table 7.4 Comparison of the dicynodont faunas of the *Cistecephalus* Assemblage Zone of the Karoo Basin, South Africa, the Upper Madumabisa Mudstone, Luangwa Basin, Zambia, and the Usili Formation, Ruhuhu Basin, Tanzania

Taxon	<i>Cistecephalus</i> Assemblage Zone (South Africa)	Upper Madumabisa Mudstone (Zambia)	Usili Formation (Tanzania)
<i>Endothiodon</i> n. sp.			X ^a
<i>Endothiodon uniseries</i>	X	X ^b	X
<i>Pachyegos stockleyi</i>			X
<i>Pristerodon mackayi</i>	X	X	X
<i>Diictodon feliceps</i>	X	X	
<i>Compsodon helmoedi</i>	X	X	
<i>Emydops arctatus</i>	X	X ^c	
<i>Emydops oweni</i>	X	X ^c	
<i>Dicynodontoides recurvidens</i>	X	X ^d	
<i>Dicynodontoides nowacki</i>		X ^d	X
<i>Myosauroides minaari</i>	X		
<i>Cistecephalus microrhinus</i>	X		
<i>Cistecephaloides boonstrai</i>	X		
<i>Kawingasaurus fossilis</i>			X
Cistecephalidae n. g. & sp.		X	
<i>Katumbia parringtoni</i>		X ^e	X
Cryptodontia n. g. & sp.			X
<i>Keyseria benjamini</i>	X ^f		
<i>Oudenodon bainii</i>	X	X	X
<i>Oudenodon grandis</i>	X ^g		
<i>Odontocyclops whaitsi</i>	X	X	
<i>Rhachiocephalus magnus</i>	X		X
<i>Rhachiocephalus behemoth</i>			X
<i>Kitchinganomodon crassus</i>	X	X	
<i>Aulacephalodon bainii</i>	X		
<i>Geikia locusticeps</i>			X
<i>Dicynodon lacerticeps</i>	X		
<i>Dicynodon huenei</i>		X	X
<i>Dinanomodon gilli</i>	X		
<i>Syops vanhoepeni</i>		X	
<i>Euptychognathus bathyrhynchus</i>	X ^h		X
Lystrosauridae n. g. & sp.		X	
<i>Basilodon woodwardi</i>	X		

Faunal list for the *Cistecephalus* Assemblage Zone based on Rubidge et al. (1995), with additional data from Angielczyk (2002), Botha and Angielczyk (2007), Angielczyk et al. (2009), Fröbisch (2009), and Kammerer et al. (2011). Faunal list for the Upper Madumabisa Mudstone based on this paper. Faunal list for the Ruhuhu Basin based on Sidor et al. (2010)

^a Attridge et al. (1964) and Cox (1964, 1991) reported this material was preserved in the Ruhuhu Formation of Tanzania, but Sidor et al. (2010) suggested that it may have come from the basal portion of the Usili Formation

^b For the purposes of this comparison, the Zambian specimens of *Endothiodon* are assumed to be *E. uniseries*, although they are too fragmentary to identify to the species level with certainty

^c It is uncertain which species of *Emydops* is present in Zambia

^d It is uncertain which species of *Dicynodontoides* is present in Zambia

^e For the purposes of this comparison, the jaw assigned to cf. *Katumbia parringtoni* is considered to definitely represent that species

^f Because it has only been recently been confirmed as a valid species (Kammerer et al. 2011), the stratigraphic range of *Keyseria benjamini* in the Karoo Basin is not well-constrained

^g It is uncertain whether *Oudenodon grandis* is a valid species (e.g., Botha and Angielczyk 2007)

^h Kammerer et al. (2011) were the first to report *Euptychognathus bathyrhynchus* from the Karoo Basin of South Africa, and the range of this species in that basin is poorly constrained because it is known from only three specimens

factors controlling Permian dicynodont distributions were complex, and a combination of quantitative approaches such as those of Fröbisch (2009) and techniques that incorporate phylogeny (see Angielczyk and Kurkin 2003 for a simple example) will be important in resolving their biogeographic history.

Triassic Biostratigraphy and Biogeography

Although our review of the Zambian Triassic dicynodonts does not result in changes in the number or identities of the currently-recognized species, it does underscore the fact that a good deal of uncertainty surrounds these taxa, making their use in biogeographic and biostratigraphic studies difficult. The dicynodonts of the lower Ntawere Formation show the greatest similarity to the Triassic dicynodonts of Namibia. Indeed, the presence of *Kannemeyeria lophorhinus* in the lower Ntawere Formation provides a direct correlation between these rocks and those of the upper Omingonde Formation of Namibia (e.g., Keyser 1973c; Keyser and Cruickshank 1979; Cooper 1982; Cox 1991; Lucas 1998a, b; Rubidge 2005). However, considering that this species is known from only two specimens (i.e., one specimen each from Zambia and Namibia; Renaut 2000; Renaut et al. 2003), its stratigraphic ranges in Namibia and Zambia are not well-constrained and correlations based on it will necessarily be imprecise until additional material can be recovered. If “*Kannemeyeria*” *latirostris* eventually proves to pertain to *Dolichuranus*, it would provide a second direct link between the lower Ntawere and the upper Omingonde formations (e.g., Keyser 1973c; Keyser and Cruickshank 1979; Cooper 1982; Battail 1993; Abdala et al. 2005; Rubidge 2005), and potentially to the *Cynognathus* C subzone of South Africa if a temporal bar tentatively referred to *Dolichuranus* by Abdala et al. (2005) truly represents this taxon. Alternatively, if it is not *Dolichuranus*, “*K.*” *latirostris* could represent an endemic species or provide biogeographic and/or biostratigraphic links with other basins both in Africa and elsewhere. This issue will not be resolved until the morphology, taxonomy and phylogenetic relationships of the specimen are reexamined in detail. The problem of “*K.*” *latirostris* also highlights the fact that alphataxonomic work on Triassic dicynodonts has lagged behind corresponding Permian work, and that this discrepancy has implications extending beyond simple measures of dicynodont diversity.

The dicynodonts of the upper Ntawere Formation are known from much more fragmentary material than those of the lower Ntawere, even though they are represented by a much greater number of individual specimens. *Sangusaurus* has received more biostratigraphic attention than

Zambiasaurus because it also occurs in the Lifua Member of the Manda beds of Tanzania, providing a direct link between the Luangwa and Ruhuhu basins (Cruickshank 1986; Jain and Roy Chowdhury 1987; Cox 1991; Battail 1993; DeFauw 1993). However, the Zambian specimen is very fragmentary, and nearly all of the descriptive and phylogenetic work carried out on *Sangusaurus* focuses on Tanzanian material (Cruickshank 1986; Bandyopadhyay 1989; Maisch 2001; Surkov and Benton 2004; Kammerer et al. 2011). The question of whether *S. edentatus* and *S. parringtonii* are distinct species will be particularly important to address with future material from Zambia. *Zambiasaurus* is of little biostratigraphic utility because it is endemic to the Luangwa Basin. It may be of biogeographic significance if it is closely related to *Stahleckeria* (Cox 1969; Cox and Li 1983; Bandyopadhyay 1988; King 1988; Maisch 2001) since this would suggest an African origin for the lineage, but the only phylogenetic analysis to include *Zambiasaurus* did not recover such a relationship (Surkov et al. 2005). Again, both a detailed reassessment of the currently available *Zambiasaurus* specimens and the discovery of more complete specimens, particularly cranial material, are needed to improve our understanding of this taxon.

Conclusions

- (1) The Upper Permian Upper Madumabisa Mudstone in the Luangwa Basin of Zambia preserves a single assemblage of dicynodonts consisting of 14 taxa: *Pristerodon mackayi*, *Endothiodon* sp., *Diictodon feliceps*, *Compsodon helmoedi*, *Emydops* sp., *Dicynodontoides* cf. *D. nowacki*, a new tusked cistecephalid represented by five specimens (BP/1/3337, BP/1/3591, BP/1/3603, NHCC LB18, NHCC LB19), cf. *Katumbia parringtoni*, *Kitchinganomodon crassus*, *Oudenodon bainii*, *Odontocyclops whaitsi*, *Dicynodon huenei*, *Syops vanhoepeni*, and a new lystrosaurid taxon represented by one specimen (TSK 2). Importantly, we find no evidence of *Lystrosaurus* sensu stricto in the Upper Madumabisa Mudstone. Previous reports of a number of additional taxa are duplications of one of the above taxa, mistakes, or based on non-diagnostic material.
- (2) The Middle Triassic Ntawere Formation preserves two dicynodont assemblages. The lower Ntawere assemblage consists of *Kannemeyeria lophorhinus* and “*Kannemeyeria*” *latirostris*. The upper Ntawere assemblage includes *Zambiasaurus submersus* and *Sangusaurus edentatus*. Previous reports of additional dicynodont taxa primarily reflect the complex taxonomic histories of *K. lophorhinus* and “*K.*” *latirostris*.

- (3) The Upper Madumabisa Mudstone dicynodont assemblage is best correlated with the *Cistecephalus* Assemblage Zone of the Karoo Basin of South Africa. In turn, the presence of *Dicynodon huenei* in the Luangwa and Ruhuhu basins, as well as the probable occurrence of *Katumbia parringtoni* in both basins, suggests that the dicynodont assemblage of the Tanzanian Usili Formation also can be correlated with the *Cistecephalus* Assemblage Zone.
- (4) The Upper Madumabisa Mudstone dicynodont assemblage shows greater similarity to the dicynodont fauna of the South African *Cistecephalus* Assemblage Zone than to the assemblage preserved in the Tanzanian Usili Formation, despite the closer proximity of the Ruhuhu and Luangwa Basins. Both the Usili Formation and the *Cistecephalus* Assemblage Zone include more endemic species than the Madumabisa Mudstone, but the distribution of species in these and other basins suggests that the factors controlling the geographic ranges of Permian dicynodonts were complex.
- (5) The lower Ntawere Formation dicynodont assemblage resembles the upper Omingonde Formation of Namibia in the presence of *Kannemeyeria lophorhinus*. However, the stratigraphic range of this species is poorly constrained because it is represented by a single specimen in each place. If “*Kannemeyeria*” *latirostris* is part of *Dolichuranus*, it would provide an additional tie between these formations, but resolution of this issue must await a reconsideration of the taxonomy and phylogenetic relationships of “*Kannemeyeria*” *latirostris*.
- (6) *Sangusaurus* provides a link between the upper Ntawere Formation and the Lifua Member of the Manda beds, and an important question to address in the future is whether *S. edentatus* and *S. parringtonii* are distinct species. *Zambiasaurus submersus* is endemic to the Luangwa Basin and therefore is of little biostratigraphic utility. It may have biogeographic significance if it is a close relative of *Stahleckeria*, but additional work is needed to test this hypothesis.

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